Article

Leaf senescence exhibits stronger climatic responses during warm than during cold autumns

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A warmer world could extend growing seasons for plants. Changes in spring phenology have been studied, yet autumn phenology remains poorly understood. Using >500,000 phenological records of four temperate tree species between 1951 and 2013 in Europe, we show that leaf senescence in warm autumns exhibits significantly stronger climate responses, with a higher phenological plasticity, than in cold autumns, indicating a nonlinear response to climate. The onset of leaf senescence in warm autumns was delayed due to the stronger climate response, primarily caused by nighttime warming. However, daytime warming, especially during warm autumns, imposes a drought stress which advances leaf senescence. This may counteract the extension of growing season under global warming. These findings provide guidance for more reliable predictions of plant phenology and biosphere-atmosphere feedbacks in the context of global warming.

Plant phenology, the timing of periodic developmental events, influences carbon, water, nutrient cycling, fitness and distribution of tree species, trophic interactions, and community structures[1-3]. Under global warming, advanced spring phenology has been widely reported in recent decades[1,4]. Contrary to spring phenology, autumn phenology responses to climate warming are inconsistent, with advanced and delayed trends as well as no response having been reported[5]; the mechanisms of the complex climatic responses of autumn phenology remain poorly understood[1,6]. Consequently, current tree phenology models often fail to simulate and predict autumn phenological changes[7,8]. This leaves the ability of the models to forecast responses of growing season length and biosphere–atmosphere feedbacks under future climatic scenarios in doubt[9].

In addition to temperature, autumn phenology has been found to be influenced by other environmental cues, i.e., photoperiod, precipitation, and solar radiation[5,10,11]. In particular, photoperiod provides a more consistent and reliable signal of seasonality than the other climatic factors. Accordingly, when trees rely on photoperiodic cues to signal the arrival of autumn, leaf senescence would be expected to show no or limited climatic responses[12]. For example, plants in cold regions with frequent frosts track photoperiod to determine the growth cessation in autumn[12] in order to reduce the risk of frost damage[13]. However, whether photoperiodic sensitivity and climatic responses of plant phenology are consistent under different autumn conditions remains unclear. Using >500,000 records of leaf senescence timing of four temperate tree species monitored *in situ* between 46 °N and 55 °N during 1951-2013 in Europe (Supplementary Fig. 1), we investigated and compared the effects of climatic factors on the onset of leaf senescence in years with warm and cold autumn seasons.

Climatic response in cold and warm autumns

The concept of climatic sensitivity has been widely used to quantify and predict the climatic responses of plant phenology under global warming[14]. To investigate the difference in the climatic responses of leaf senescence under cold and warm conditions, we calculated the climatic sensitivities of leaf senescence in cold and warm autumns at cold and warm sites (G1-G4). The classification of the cold and warm sites was based on their latitudes and elevations (see Methods), representing a temperature gradient from the coldest (G1) to the warmest (G4) sites (Supplementary Table 1). The cold and warm autumns were identified by comparing whether mean daily maximum temperature (T_{max}, °C) during the period 1st August – 31st October of each year and site group was below or above its long-term average for 1951-2013, respectively.

In order to calculate the climatic sensitivities, we first used partial correlation analysis to calculate the optimal preseason length for each combination of climatic factor, species, and site group. The optimal preseason was defined as the period before the onset of leaf senescence with the highest absolute partial correlation coefficient[14,15] between leaf senescence dates and the particular climatic factor for the period of 1951-2013. The length of the optimal preseason ranged from 8 to 120 days across different species, consistent with earlier results of both spring and autumn phenology[4,14,24](Supplementary Fig. 2). Ridge regression reduces the variance of regression coefficients and improves the estimations when multicollinearity occurs [16,17], as was the case in this work. We first calculated the average of each climatic factor during the optimal preseason and those of leaf senescence dates at each site group for each species. Then, ridge regression models were applied to calculate the climatic sensitivities of leaf senescence for daily maximum temperature (T_{max},°C), daily minimum temperature (T_{min},°C), daily sunshine duration (hour), and daily precipitation (mm) in cold and warm autumns. In all models, normalized anomalies of response and predictor variables were used to calculate the climatic sensitivities, which were then used in the comparisons of the effects of different climatic factors on leaf senescence in cold and warm autumn seasons[18]. Positive and negative sensitivities indicate delayed and advanced senescence, respectively.

We found that average climatic sensitivities of leaf senescence to T_{min}, sunshine duration and precipitation during 1951-2013 were significantly higher in warm than in cold autumns across the four studied species ($P<0.001$, Fig. 1a). Furthermore, the climatic sensitivities of leaf senescence to T_{max} were significantly more negative in warm than in cold autumns ($P<0.001$, Fig. 1a and Supplementary Fig. 3a), i.e., leaf senescence advanced more in warm than in cold autumns with the increase in T_{max}. In order to assess the extent to which the climatic factors influence the onset of leaf senescence in cold and warm autumns, without considering the direction of the effect (delay or advance), the concept of climatic signal, defined as the absolute value of climatic sensitivity, was introduced. We found that climatic signals were significantly stronger in warm than in cold autumns ($P<0.001$, Fig. 1b and Supplementary Fig. 3b). To further test the generality of this finding, we collected records of five additional species and examined their climatic responses of leaf senescence in cold and warm autumns. As with the four initial species, the average climatic signals of all of the five additional species were significantly higher in warm than in cold autumns ($P<0.01$, Supplementary Fig. 4). These results suggest that leaf senescence exhibited significantly stronger climatic response in warm than in cold autumns.

To test the robustness of our results, we calculated the climatic sensitivity for each climatic factor based on a fixed preseason in autumn (1st August to 31st October). Consistent with the result based on the optimal preseason, we observed significantly stronger climatic responses of autumn leaf senescence in warm than in cold autumns also when using the fixed preseason ($P<0.001$, Supplementary Fig. 5). Because previous studies reported autumn phenology is influenced by spring phenology[19,20], we further accounted for the effects of spring leaf unfolding using a joint modelling approach, where both spring leaf unfolding dates and climatic factors were incorporated into the ridge regression models. In all species, leaf unfolding dates had positive effects on leaf senescence dates (Supplementary Fig. 6a), indicating delayed leaf senescence with delayed leaf unfolding, and vice-versa. This is consistent with previous findings[19,20]. After accounting for the effects of spring phenology, leaf senescence of all species still showed significantly stronger climatic responses in warm than in cold autumns ($P<0.01$, Supplementary Fig. 6b).

Phenological plasticity in cold and warm autumns

We compared the plasticity of autumn leaf senescence in each species at each site group between cold and warm autumn seasons based on the coefficient of variation (CV) of leaf senescence. In accordance with the stronger climatic responses found in warm than in cold autumns, a significantly higher phenological plasticity, as indicated by a higher CV, was observed in warm than in cold autumn seasons ($P<0.001$, Fig. 2). In addition, the onset of leaf senescence occurred later in warm than in cold autumns (Fig. 3 and Supplementary Fig. 7).

Limited climatic responses, with a lower plasticity of phenological events, is expected when trees are under a strong photoperiodic control[12]. We found such conservative climatic responses and reduced plasticity of leaf senescence in cold, but not in warm, autumn seasons (Figs. 1 and 2). On one hand, before leaf senescence, trees need to assimilate sufficient carbohydrate and nutrients for overwintering and budburst during the following spring[10]. The accumulated GDD was significantly higher in warm than in cold autumns across all of the site groups ($P<0.001$, Fig. 4). Under the favorable conditions, trees may therefore prefer to delay leaf senescence and increase carbon uptake in warm autumns[10], especially in warmer sites. This is supported by the observed later onset of leaf senescence in warm autumns (Fig. 3 and Supplementary Fig. 7). On the other hand, trees also need to harden sufficiently early to avoid frost damage[21]. As a compensating factor, photoperiod may act as a safety mechanism for trees to avoid too late leaf senescence to reduce the risk of frost in cold autumns. This may explain why, compared to warm autumns, the onset of leaf senescence showed a lower phenological plasticity (Fig. 2) and occurred earlier (Fig. 3 and Supplementary Fig. 7) in cold autumns.

Effects of daytime and night-time warming

Among all of the climatic factors analyzed, the mean climatic signal was highest for T_{max}, and second highest for T_{min} ($P<0.05$, Fig. 5a). This is in accordance with the earlier findings of stronger influence of daytime than nighttime temperature on spring phenology[22]. However, it is noteworthy that here climatic sensitivities of T_{max} and T_{min} were negative and positive, respectively (Fig. 5b). This indicates that the onset of leaf senescence was advanced by daytime warming, but it was delayed by nighttime warming. Wu et al.[15] recently observed advanced leaf senescence caused by daytime warming in regions with continental climates. A possible explanation for the observed advanced leaf senescence by daytime warming is drought stress[15,23]. To test this hypothesis, we calculated the Standardized Precipitation-Evapotranspiration Index (SPEI), which considers effects of both precipitation and potential evapotranspiration on drought severity[24], and examined the effect of drought stress on the onset of leaf senescence. The averaged SPEI was positive in cold autumn seasons, but negative in warm autumn seasons (Supplementary Fig. 8). This indicated drier environmental conditions in warm autumn seasons. We further observed a significant effect of drought stress on the onset of leaf senescence, with a stronger effect in warm autumns ($P<0.001$, Supplementary Table 2). This suggests that a higher daytime temperature may increase evaporative demand and impose a drought stress on tree growth, especially in warm autumns, and eventually advance autumn leaf senescence[10,15].

Among the four studied species, leaf senescence advanced by daytime warming was greater in *Fagus sylvatica* L. and *Quercus robur* L. than in *Aesculus hippocastanum* L. and *Betula pendula* Roth (Fig. 1a). This is possibly due to a difference in the drought tolerance among species[25,26]. Accordingly, under drought stress, onset of leaf senescence is less likely to advance in a species with a high drought tolerance than in a species with a low drought tolerance. However, the physiological mechanisms behind the species-specific climatic response of leaf senescence remain to be tested experimentally. Using the simulated climate data by Community Earth System Model (CESM) Large Ensemble (CESM-LENS) (http://www.cesm.ucar.edu/projects/community-projects/LENS/)[27], we investigated the trends in the T_{max} and T_{min} in the autumn season (1st August-31st October) during 2021-2050 in Europe. We found both average T_{max} and T_{min} showed significant increases through the years of 2021-2050 ($P<0.001$, Supplementary Fig. 9). Therefore, drought-induced advance of leaf senescence might continue in the future decades. This may counteract the delayed leaf senescence and offset the extension of growing season duration in Europe.

Conclusion

Using a long-term and large-scale dataset of field observations in Europe, we demonstrated that: (1) climatic response of leaf senescence was significantly stronger in warm than in cold autumns, and (2) the onset of leaf senescence was delayed by nighttime warming, but was advanced by daytime warming. These findings provide important guidance for the understanding of complicated climatic responses of plants' autumn phenology in the context of global climate change. Our results can be used to facilitate more reliable predictions of the timing of autumn phenological events, and, as a result, biosphere-atmosphere feedbacks under future climatic scenarios. However, further studies should experimentally investigate the physiological mechanisms behind the species-specific climatic responses in controlled environments and examine whether the observed nonlinear climatic response of autumn phenology also exists in other parts of Northern Hemisphere, including Asia and North America.

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Methods

Leaf phenology and climate data

The leaf senescence dataset was obtained from the Pan European Phenology (PEP) network (www.pep725.eu), which provides an open access to *in situ* phenology records across central Europe[28]. The leaf senescence dates, expressed as the day of year (DOY), were defined according to the BBCH (Biologische Bundesanstalt, Bundessortenamt und CHemische Industrie) code. Most of the records used in the study are from between the 46th and 55th parallels (Supplementary Fig. 1). Because records of PEP725 network may include erroneous data points, median absolute deviation (MAD) method (Leys et al., 2013) was used to identify and exclude outliers[14,29,30]. MAD is a robust alternative to the standard deviation measure of the central tendency in a dataset. For a dataset with values of X_1, X_2, ..., X_i, the MAD is defined as follows:

$$\mathrm{MAD} = \mathrm{median}\,(|X_i - \mathrm{median}(X)|).$$

Using a conservative criterion, any data point deviating more than 2.5 times MAD was considered as an outlier and removed from the dataset before the analyses[31]. In this way, we selected 547,000 records of leaf senescence during 1951-2013 from approximately 10,000 sites between 46°N and 55°N across all nine temperate tree species examined. The primary analysis focused on four species: *Betula pubescens* Ehrh. (Downy birch), *Fagus sylvatica* L. (European beech), *Quercus robur* L. (European oak), *Aesculus hippocastanum* L. (Horse chestnut). An additional five species were examined in supplementary analysis: *Sorbus aucuparia* L. (Mountain ash), *Acer platanoides* L. (Norway maple), *Betula pendula* Roth (Silver birch), *Tilia cordata* Mill. (Small-leaved lime), early cultivar of *Prunus avium* (L.) L. (Wild cherry (early)), and late cultivar of *Prunus avium* (L.) L. (Wild cherry (late)). Note that the two cultivars of *Prunus avium* (L.) L. were examined separately.

Gridded daily maximum temperature (T_{max}, °C), minimum temperature (T_{min}, °C) and precipitation (mm) data between 1951 and 2013 with a spatial resolution of 0.25° were downloaded from the database E-OBS (http://ensembles-eu.metoffice.com). Because gridded solar radiation dataset with 0.25° spatial resolution was only available since 1980, the daily measured sunshine duration (hours) dataset between 1951 and 2013 obtained from E-OBS database was used to account for the effect of solar radiation on leaf senescence. In addition, daily measured temperature and precipitation datasets between 1951 and 2013 were downloaded from E-OBS database. In the E-OBS climate database, the quality of the observations is classified into valid, suspect, or missing. We used only the values classified as valid in the data analysis.

To investigate differences in the climate-phenology relationship in cold and warm regions, we divided the phenological observation sites into four groups based on their latitudes and elevations: elevation > 300 m a.s.l. and latitude > 51 °N (G1), elevation > 300 m a.s.l. and latitude < 51 °N (G2), elevation < 300 m a.s.l. and latitude > 51 °N (G3), and elevation < 300 m a.s.l. and latitude < 51 °N (G4). The four groups represent a temperature gradient from the coldest (G1) to the warmest (G4) sites (Supplementary Table 1). We also tried other grouping criteria (e.g., elevation <100 or 200 m) and obtained similar results.

Among the nine selected species, there were approximately 517, 000 records for *Aesculus hippocastanum* L., *Betula pendula* Roth*, Fagus sylvatica* L.*,* and *Quercus robur* L. These records accounted for 95% of all of the records and were also well-distributed across the four site groups. In contrast, the records of other five species were more limited and only distributed across one or two site groups. We therefore mainly present results based on the four widely distributed species with massive records in this study. The results of the additional other five species were used to test the generality of the results found from the more representative abovementioned four species.

Climatic sensitivity and climatic signal

In order to calculate climatic sensitivities of each species to each climatic factor, we first used partial correlation analysis to calculate the optimal length of preseason of each climatic factor for each species at each site group. For each climatic factor, the optimal preseason was defined as the period before the onset of leaf senescence with the highest absolute partial correlation coefficient [14,15] between leaf senescence dates and corresponding climatic factors during 1951-2013 (with 8-d steps). Using the period corresponding to the optimal length of preseason, we then calculated the climatic sensitivity as the slope of a ridge regression[16,17] between the onset of leaf senescence (DOY) and the averaged climatic factor during the preseason period for each species at a site group. The climatic sensitivity was calculated in this way for the daily maximum temperature (T_{max}, ^oC), daily minimum temperature (T_{min}, ^oC), daily sunshine duration (hour), and daily precipitation (mm). Positive and negative sensitivities indicate delayed and advanced senescence, respectively. Climatic signal was defined as the absolute value of climatic sensitivity. It indicates the extent to which the climatic factor influences the onset of leaf senescence, without considering the direction of the effect (delay, advance).

In addition to the full data set used, the results of climatic sensitivities are reported separately for species and for site groups, and for years with cold and warm autumns seasons. The seasons were classified into cold and warm ones based on whether mean daily T_{max} during the autumn season (1st August – 31st October) of the particular year at the particular site was below or above its long-term average for 1951 – 2013, respectively.

Multicollinearity is a problem when two or more predictors in multiple regression models are highly correlated[16]. The estimated regression coefficients based on ordinary least square regression can be unreliable when multicollinearity occurs[16]. By adding a penalty parameter in the model, ridge regression reduces the variance of regression coefficient and produces more reliable estimates[17]. In order to take into account the potential multicollinearity between climatic factors, ridge regressions were therefore used in the calculations of climatic sensitivity[16,17]. The spatial resolution of sunshine duration dataset was too coarse to obtain the sunshine duration hours for each site. To address this, we averaged climatic data, including T_{max}, T_{min}, precipitation and sunshine duration, and leaf senescence dates for each site group (G1-G4), and analyzed the effect of the averaged climatic factors on autumn leaf senescence. A total of 128 models were applied to calculate the climatic sensitivities, one for each combination of site group, species, and season type (4 climate factors × 4 climate groups × 4 species × 2 season types). The response variable was the mean leaf senescence date, the predictors were the averaged climatic factors during the optimal preseason of each species at each site group. Normalized anomalies of climatic factors and leaf senescence dates were used in all of the models when calculating the climatic sensitivities, which were then used for comparing the effects of different climatic factors on the onset of leaf senescence in cold and warm autumns in different species and different site groups[18]. To test the robustness of our results, we calculated the climatic sensitivity also based on a fixed preseason in autumn (1st August to 31st October) for each climatic variable. We also addressed the effects of spring phenology on autumn leaf senesce in cold and warm autumns via a joint modelling approach where both spring leaf unfolding dates and climatic factors were incorporated into the ridge regression models. Both the response variables and the predictors were normalized also in these models.

Due to the coarse spatial resolution of sunshine duration dataset, we could not analyze the effects of all of the four climatic factors on leaf senescence at the site level. To address this, we performed an additional analysis using the climatic data that could be obtained for each site (see Supplementary Fig. 10). Specifically, we first excluded the outliers deviating more than 2.5 times

MAD and selected sites with at least 40 years records of leaf senescence between 1951 and 2013. Second, we used the bilinear interpolation method to extract the daily T_{max}, daily T_{min}, and daily precipitation between 1951 and 2013 for each site using the "raster" package[32] in R version 3.6.1[33]. After determining the optimal preseason length of climatic factors, we calculated the mean temperature and precipitation during the optimal preseason for each year at each site. Finally, we obtained year-to-year normalized anomalies (relative to average year) of both climatic variables and leaf senescence dates, and calculated climatic signals in cold and warm autumns for each species at each site using ridge regressions.

Linear mixed models are widely used to analyze hierarchical data, because they allow inclusion of both fixed and random effects[34]. By pooling all of the species at different site groups, a linear mixed model was used to examine the difference in climatic sensitivity or climatic signal between cold and warm autumn seasons. In the linear mixed model, the response variable was climatic sensitivity or signal, the fixed effect was autumn season type (a categorical variable with two levels: cold and warm autumn), with random intercepts among species. Tukey's HSD (Honestly Significant Difference) test is a common post-hoc test used to compare the means between groups based on the studentized range distribution[35]. Here Tukey's HSD test followed by linear mixed model was used to examine the differences in climatic signals among the climatic factors addressed.

Growing degree days

Based on the following equation, we calculated the growing degree days (GDD) to assess the climatic forcing in cold and warm autumns at different site groups:

$$GDD = \left[\frac{(T_{\max} + T_{\min})}{2} \right] - T_{base} \qquad \text{Eq. (1),}$$

where GDD = 0 when $(T_{max}+T_{min})/2 < T_{base}$. Based on Eq. (1), we calculated the accumulated GDD5 (T_{base} = 5 °C) and GDD10 (T_{base} = 10 °C) during the optimal preseason[36] of leaf senescence. These calculations were carried out separately for years with cold and warm autumns. Linear mixed models were used to examine the difference in the accumulated GDD5 and GDD10 between years with cold and warm autumns. The response variable was GDD5 or GDD10, the fixed effect was autumn season type (a categorial variable with two levels: warm and cold) with random intercepts among species.

Phenological plasticity

We calculated the coefficient of variation (CV) of leaf senescence dates to indicate the plasticity of autumn leaf senescence for each species at each site group during years with cold and warm autumn seasons. A total of 32 CV values were obtained to quantify the autumn phenological plasticity, one for each of the combinations of 4 site groups × 4 species × 2 season types. A linear mixed model was used to test the mean difference of the CV between the years with warm and cold autumn seasons. The response variable was the CV of leaf senescence dates, the fixed effect was autumn season type (a categorial variable with two levels: warm and cold) with random intercepts among species.

Effects of drought on leaf senescence

The Standardized Precipitation-Evapotranspiration Index (SPEI), which considers effects of both precipitation and potential evapotranspiration on drought severity[24], was calculated to examine the effects of drought stress on the onset of leaf senescence. The mean SPEI during the autumn season (1st August – 31st October) across different site groups was selected to examine the effects of drought on leaf senescence. A linear mixed model was used to test the effects of drought on the timing of leaf senescence during years with cold and warm autumn seasons. The response variable was the leaf senescence DOY, the predictor variables were the SPEI and the type of the season (a categorical variable with two levels: warm and cold autumn season), with random intercepts among site groups. Both response variable and predictors were normalized in the models.

Using the simulated climate data by Community Earth System Model (CESM) Large Ensemble (CESM-LENS) (http://www.cesm.ucar.edu/projects/community-projects/LENS/)[27], we investigated the trends in the averaged T_{max} and T_{min} in autumn (1 August-31 October) under RCP8.5 scenario[37] during 2021-2050 in Europe to project the effect of drought on the onset of leaf senescence under future climate scenarios.

Data availability

Phenology data are available from the Pan European Phenology (PEP) network (www.pep725.eu). Climate data can be downloaded from E-OBS site: http://ensembles-eu.metoffice.com.

Code availability

The codes used for data processing and analysis in this study are available on Figshare: https://doi.org/10.6084/m9.figshare.12291245.v6.

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Author contributions

L.C., J.L. and Z.L. designed this research. L.C. and Z.L. performed the data analysis. L.C. drafted the paper with the inputs of H.H., S. R., N.G.S., Z.L., S.P., G.F., J.G. and J.L. All authors contributed to the interpretation of the results and approved the final manuscript.

Competing interests

The authors declare no competing interests.

Figure legends

Fig. 1 Climatic responses of leaf senescence of four temperate tree species in Europe during 1951-2013. (a) Climatic sensitivity, (b) climatic signal, with the results given separately for warm (red) and cold (blue) autumn seasons, based on whether mean T_{max} during the autumn season from 1st August to 31st October of the particular year was above or below its long-term average for 1951 – 2013, respectively. Climatic sensitivities were calculated for daily maximum temperature (T_{max}, ^oC), daily minimum temperature (T_{min}, ^oC), daily sunshine duration (Sun, hours), and daily precipitation (Prec, mm) during the optimal preseason (see Methods for details). Climatic signal, the absolute value of climatic sensitivity, indicates the extent to which climatic factors influence leaf senescence without considering the direction of the effect (delay, advance). The averaged climatic signal represents the mean of the four climatic factors. The climatic sensitivities and signals reported were calculated using normalized response and predictor variables. 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 black points outside the boxes represent outliers. The four temperate tree species addressed are *Aesculus hippocastanum* L., *Betula pendula* Roth*, Fagus sylvatica* L. and *Quercus robur* L. The asterisks in (b) indicate significant differences between cold and warm autumns ($P<0.05$).

Fig. 2 Coefficient of variation (CV) of the leaf senescence onset day of four temperate tree species in Europe during 1951 – 2013. (a) Averaged over the four species and all observation sites and (b) separately for each species at different phenological observation site groups. The site groups represent a climatic gradient from cold (G1) to warm (G4) observation sites (see Supplementary Table 1). The results are presented separately for cold (blue) and warm (red) autumn seasons (1st August – 31st October), based on whether mean daily T_{max} during the autumn season of the particular year was below or above its long-term average for 1951 – 2013, respectively. Total number of CV values is equal to 32 (4 species × 4 site groups × 2 season types). In (a), 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 black points outside the boxes represent outliers. The four temperate tree species addressed are *Aesculus hippocastanum* L., *Betula pendula* Roth*, Fagus sylvatica* L.*,* and *Quercus robur* L. The asterisks in (a) indicate significant differences between cold and warm autumns ($P<0.05$).

Fig. 3 Average leaf senescence dates of four temperate tree species at different phenological observation site groups in Europe during 1951 – 2013. The site groups represent a climatic gradient from cold (G1) to warm (G4) observation sites (see Table S1). The results are presented separately for cold (blue) and warm (red) autumn seasons (1 August – 31 October), based on whether mean daily T_{max} during the autumn season of the particular year was below or above its long-term average for 1951-2013, respectively. Error bars indicate standard error of the mean. The four temperate tree species addressed are *Aesculus hippocastanum* L., *Betula pendula* Roth*, Fagus sylvatica* L.*,* and *Quercus robur* L.

Fig. 4 Growing degree days (GDD) at different site groups in Europe during 1951 – 2013. The site groups represent a climatic gradient from cold (G1) to warm (G4) observation sites (see Table S1). The results are presented separately for cold (blue) and warm (red) autumn seasons (1st August – 31st October), based on whether mean daily T_{max} during the autumn season of the particular year was below or above its long-term average for 1951 – 2013, respectively. The growing degree days were calculated based on the optimized preseason of leaf senescence. (a) GDD5 and (b) GDD10 represent accumulated GDDs calculated with base temperatures T_{base} = +5 ºC and T_{base} = +10 ºC, respectively. Different letters indicate significant differences between site groups based on Tukey's honest significant difference (HSD) test ($P<0.05$).

Fig. 5 Climatic responses of leaf senescence of four temperate tree species in Europe during 1951-2013. (a) Climatic sensitivity and (b) climatic signal. Climatic signal is defined as the absolute value of climatic sensitivity. Unlike climatic sensitivity, climatic signal does not address direction of the effect of climatic factor on leaf senescence. The values of both indicators are calculated for daily maximum temperature, T_{max} (days per ºC), daily minimum temperature, T_{min} (days per ºC), daily sunshine duration, Sun (days per h), and daily precipitation, Prec (days per mm) during the optimal preseason (see Methods for details). The climatic sensitivities reported were calculated using normalized response and predictor variables. 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 black points outside the boxes represent outliers. The four temperate tree species addressed are *Aesculus hippocastanum* L., *Betula pendula* Roth*, Fagus sylvatica* L.*,* and *Quercus robur* L. Different letters indicate significant differences among the climatic factors based on Tukey's honest significant difference (HSD) test (*P* <0.05).

487 Figure 1

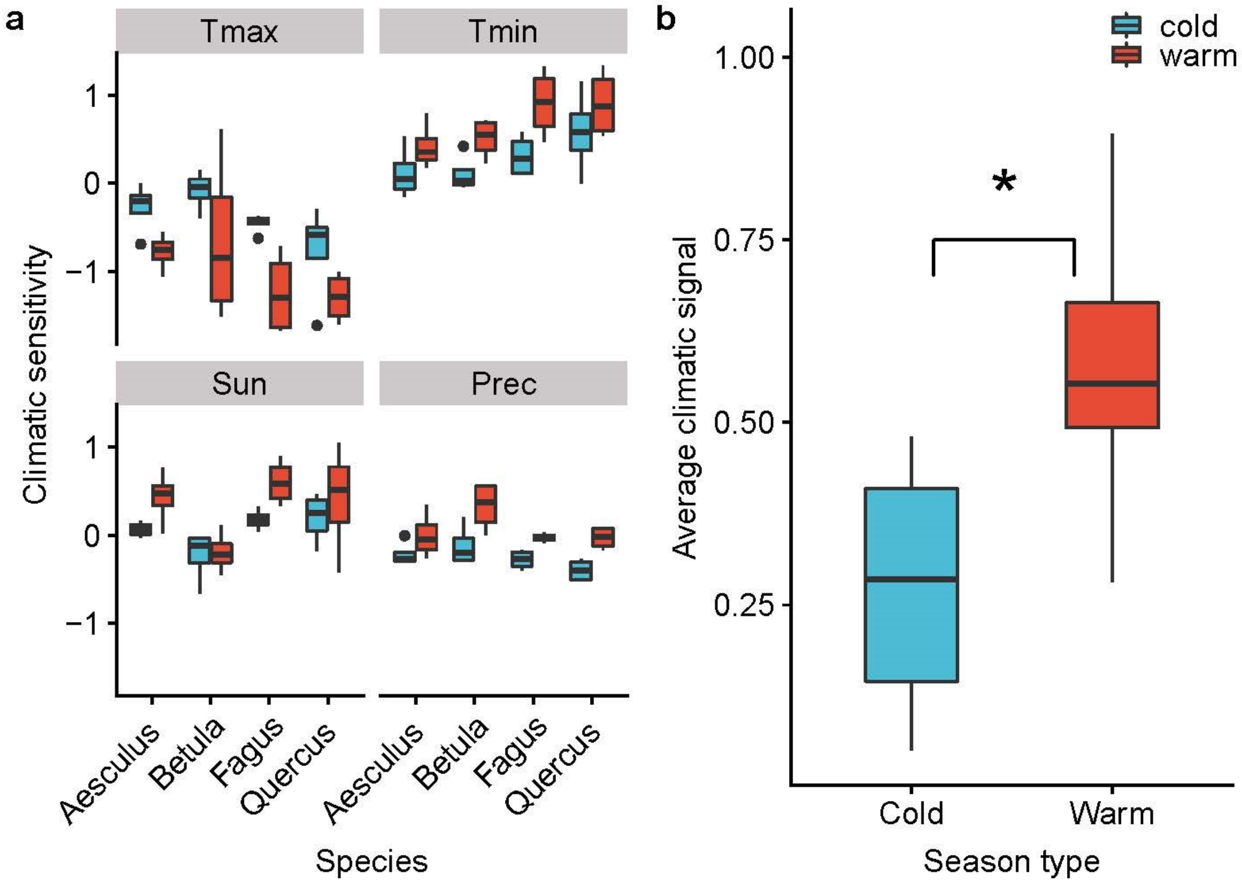

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Figure 2

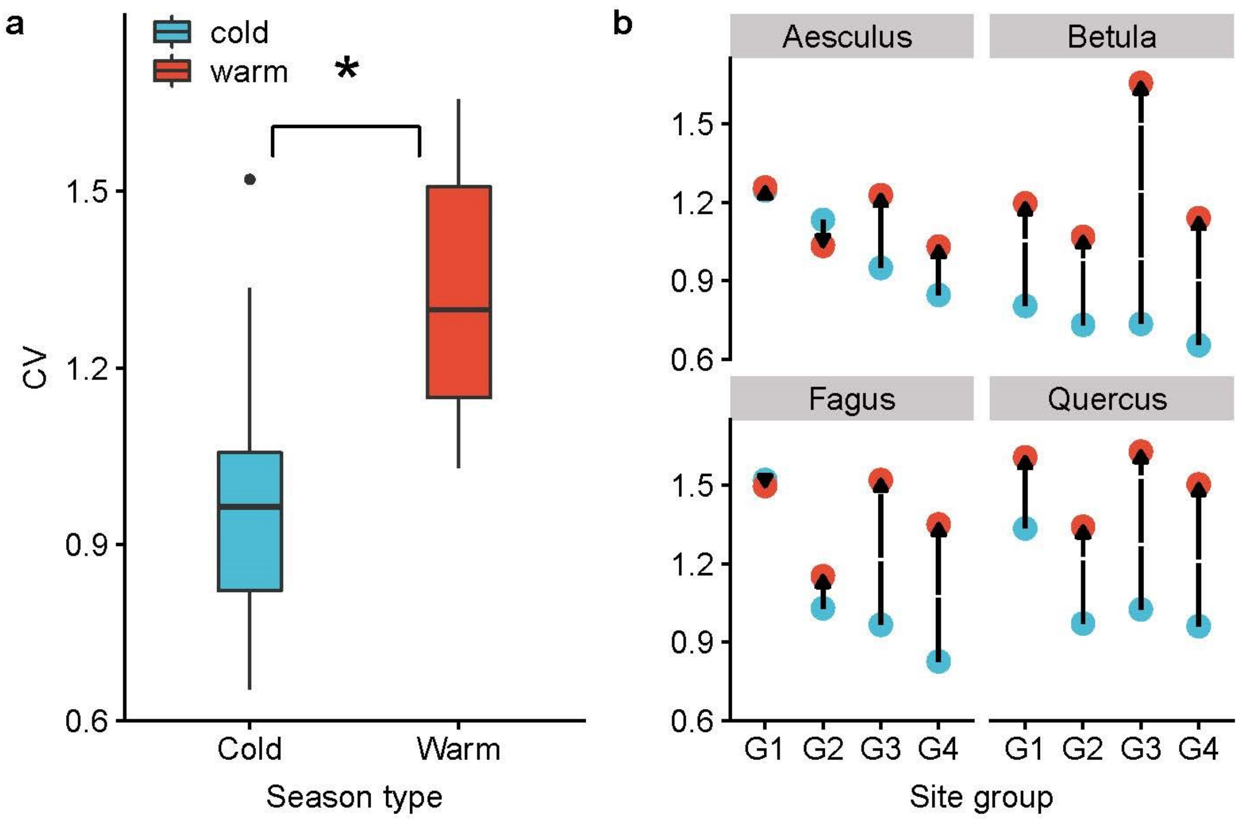

a
cold
warm
*
CV
1.5
1.2
0.9
0.6
Cold
Warm
Season type
b
Aesculus
Betula
Fagus
Quercus
1.5
1.2
0.9
0.6
G1
G2
G3
G4
G1
G2
G3
G4
Site group

Figure 3

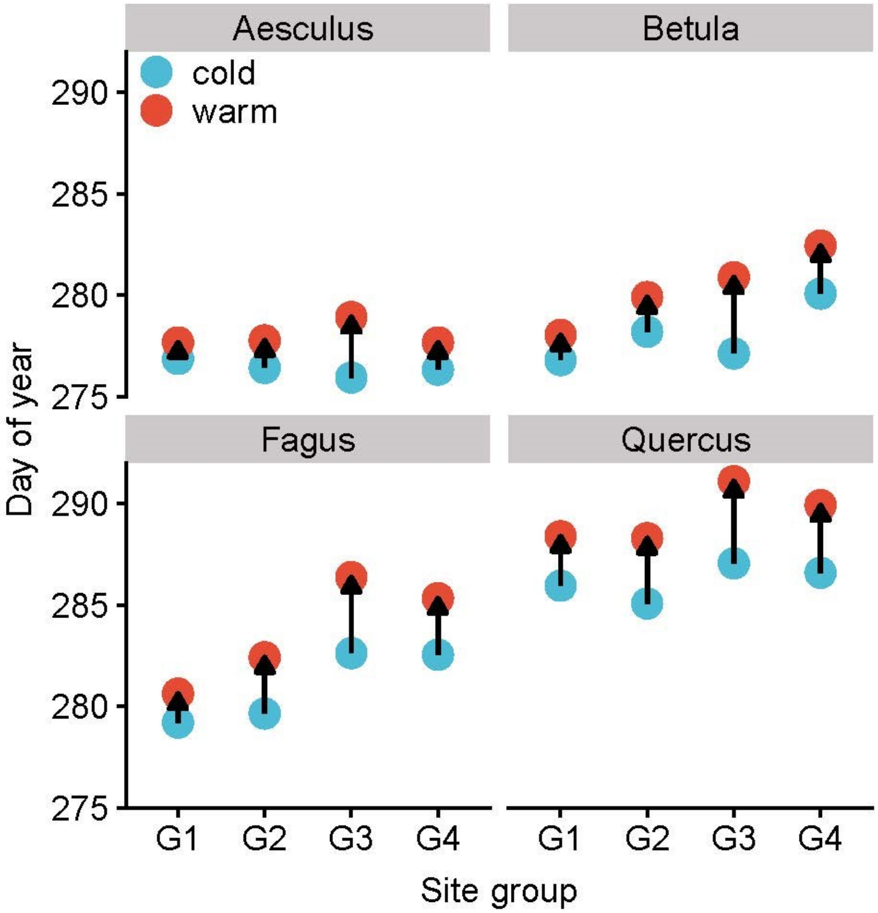

Aesculus
Betula
Fagus
Quercus
cold
warm
Day of year
290
285
280
275
G1
G2
G3
G4
Site group

Figure 4

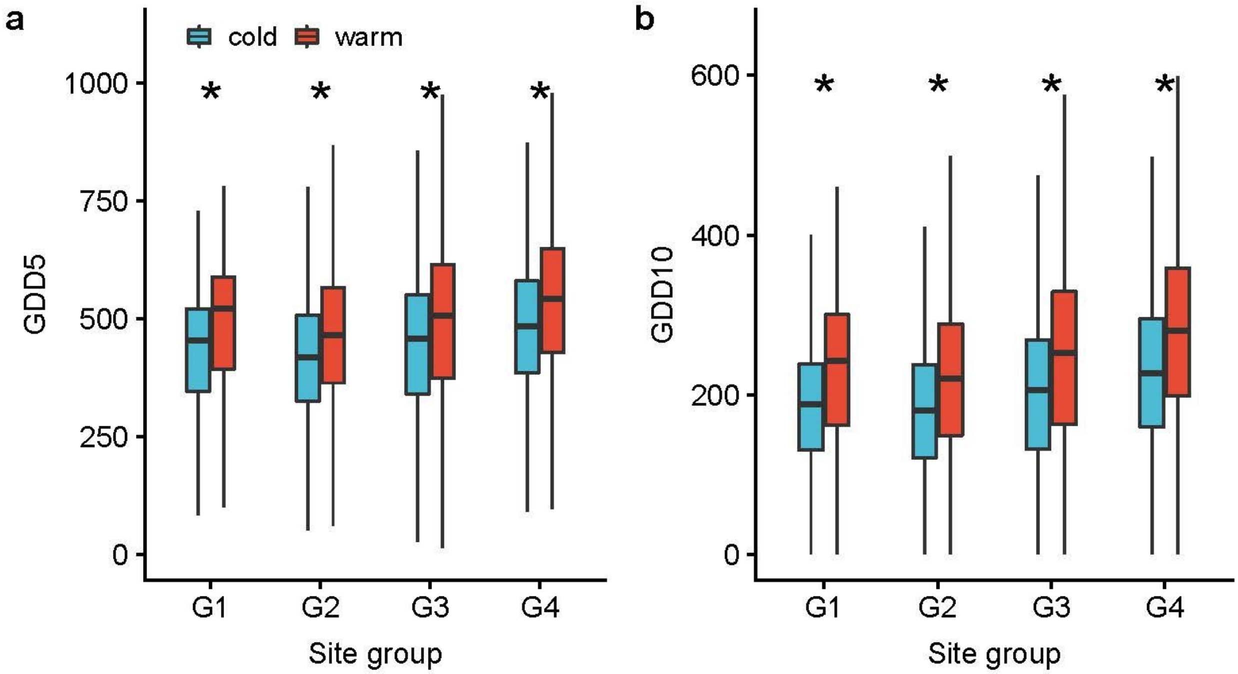
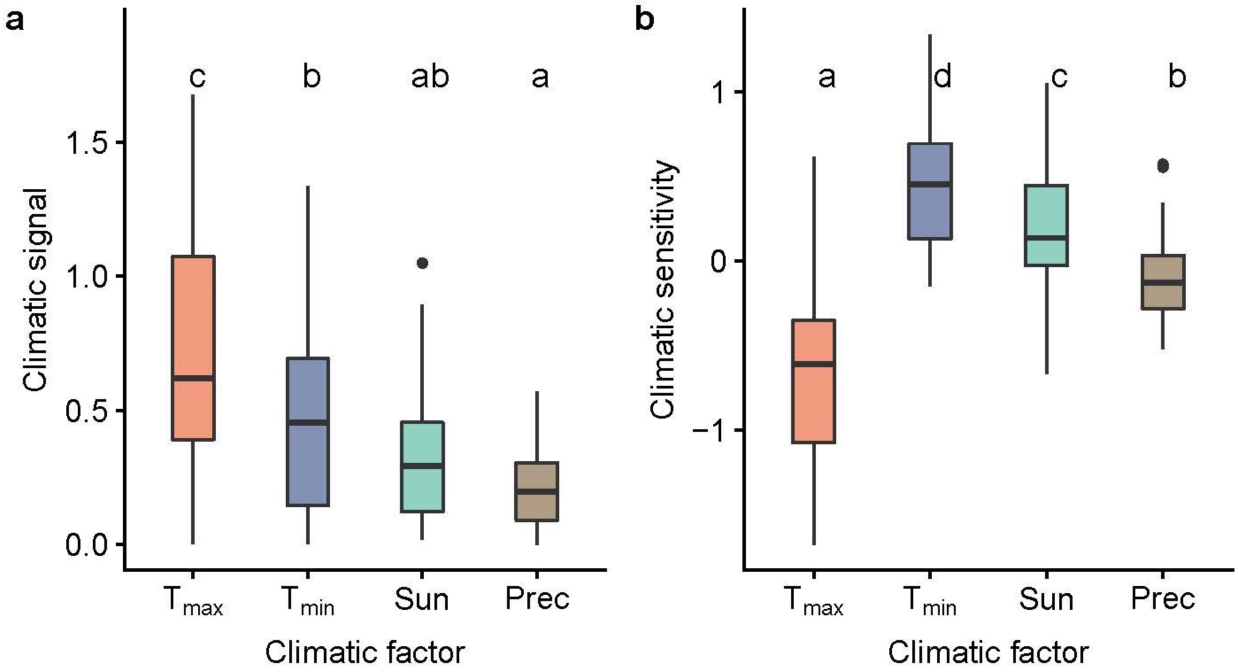

a
cold
warm
GDD5
1000
750
500
250
0
*
*
*
*
G1
G2
G3
G4
Site group
b
GDD10
600
400
200
0
*
*
*
*
G1
G2
G3
G4
Site group

Figure 5


a
Climatic signal
1.5
1.0
0.5
0.0
c
b
ab
a
T_{max}
T_{min}
Sun
Prec
Climatic factor
b
Climatic sensitivity
1
0
−1
a
d
c
b
T_{max}
T_{min}
Sun
Prec
Climatic factor