Larger temperature response of autumn leaf senescence than spring leaf-out phenology

Running title: temperature response of autumn leaf senescence

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Keywords: climate change, summer and autumn warming, leaf phenology, leaf senescence, leaf-out, temperature sensitivity

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Paper type: Primary Research Articles

Manuscript for *Global Change Biology*

Abstract

Climate warming is substantially shifting the leaf phenological events of plants, and thereby impacting on their individual fitness and also on the structure and functioning of ecosystems. Previous studies have largely focused on the climate impact on spring phenology, and to date the processes underlying leaf senescence and their associated environmental drivers remain poorly understood. In this study, experiments with temperature gradients imposed during the summer and autumn were conducted on saplings of European beech to explore the temperature responses of leaf senescence. An additional warming experiment during winter enabled us to assess the differences in temperature responses of spring leaf-out and leaf senescence. We found that warming significantly delayed the dates of leaf senescence both during summer and autumn warming, with similar temperature sensitivities (6 - 8 days delay per °C warming), suggesting that, in the absence of water and nutrient limitation, temperature may be a dominant factor controlling the leaf senescence in European beech. Interestingly, we found a significantly larger temperature response of autumn leaf senescence than of spring leaf-out. This suggests a possible larger contribution of delays in autumn senescence, than of the advancement in spring leaf-out, to extending the growing season under future warmer conditions.

Introduction

Plant phenology is the study of periodic plant life cycle events, and how these are influenced by seasonal and interannual variations in climate (Lieth, 2013). Plant phenology is one of the most reliable biological indicators of anthropogenic climate change (Parmesan & Yohe, 2003, Root *et al.*, 2003, Walther *et al.*, 2002), and changes in plant phenology impact on individual fitness, species distribution, interspecific interactions, ecosystem structure and function, as well as on feedbacks to the climate system (Chuine *et al.*, 2010, Peñuelas & Filella, 2009, Piao *et al.*, 2007, Thackeray *et al.*, 2016, Zeng *et al.*, 2017). Therefore, understanding the processes underlying plant phenology is essential to improve our understanding of plant and ecosystem responses to the ongoing climate change.

Plant phenology research has grown tremendously over the past four decades (Hänninen, 2016, IPCC, 2014, Wolkovich & Ettinger, 2014). Most studies, however, have addressed spring phenological events, such as budburst, leaf-out and flowering (Fu *et al.*, 2015, Richardson *et al.*, 2013), while autumn phenological events, such as leaf senescence, have been paid comparatively less attention (Gallinat *et al.*, 2015, Panchen *et al.*, 2015). One probable reason for this is the difficulty to accurately acquire leaf senescence observations in natural conditions. However, as the final stage of the leaf's life cycle and as adaptive strategy to unfavorable environmental conditions of temperate and boreal plant species (Chabot & Hicks, 1982), leaf senescence is critical to plants' fitness as well as to ecosystem functions (Estiarte & Peñuelas, 2015, Piao *et al.*, 2008, Rohde & Bhalerao, 2007).

The main function of autumn leaf senescence is to recycle nutrients from senescing leaves and transport them to other plant tissues to support growth during the following spring (Chapin III, 1980, Killingbeck, 1996, Maillard *et al.*, 2015). This nutrient-conservation mechanism increases the fitness of individual plants, especially in nutrient poor environments (Chapin III, 1980, May & Killingbeck, 1992). Generally, more than half of the leaf macro-nutrients, such as N and P, are being resorbed during the leaf senescence process, although the nutrient resorption efficiency varies widely among species and elements (Aerts, 1996, Freschet *et al.*, 2010, Wright & Westoby, 2003). Apart from its influence on nutrient cycles, the timing of leaf senescence influences the ecosystem carbon balance by modulating the length of the photosynthetically active period (Myneni *et al.*, 1997, Richardson *et al.*, 2010). Leaf senescence may even play a more critical role than spring phenology in determining the length of the photosynthetically active period (Garonna *et al.*, 2014, Wu *et al.*, 2013). Understanding the response of leaf senescence to climate change is therefore important. However, to date, the processes underlying autumn leaf senescence, their associated environmental controls and the response of leaf senescence to climate change are still poorly understood.

Photoperiod has generally been proposed as the primary driver of leaf senescence, with a critical photoperiodic threshold, i.e., a critical day length below which leaf senescence is triggered (Lagercrantz, 2009, Wareing, 1956, Way & Montgomery, 2015, Welling & Palva, 2006). For example, the autumnal senescence in mature European aspen occurs every year on almost the same date (Fracheboud *et al.*, 2009). However, photoperiod is not consistently important across species and even sites. For example, a recent study reported that leaf senescence is not triggered by photoperiod across 116 European aspen natural genotypes (Michelson *et al.*, 2017), suggesting that other environmental factors must be involved in driving the leaf senescence process. In line with this finding, many studies have suggested that temperature interacts with photoperiod to control the leaf senescence process (Chung *et al.*, 2013, Hänninen & Tanino, 2011, Heide & Prestrud, 2005, Liu *et al.*, 2016a, Tanino *et al.*, 2010), and that temperature can be even the main controlling factor of leaf senescence (Chmielewski & Rötzer, 2001, Estiarte & Peñuelas, 2015, Heide & Prestrud, 2005, Xie *et al.*, 2015), in particular autumn temperature (Delpierre *et al*., 2009). However, these results are not conclusive because other studies have shown that autumnal senescence is only weakly affected by air temperature (Čufar *et al.*, 2012, Olsson & Jönsson, 2015, Sparks & Menzel, 2002). In addition to photoperiod and temperature, also other environmental factors have been reported to influence the leaf senescence process. These include light intensity (Liu *et al.*, 2016b), precipitation and soil water conditions (see review in Estiarte and Peñuelas (2015)) and soil nutrient status (Sigurdsson, 2001, Weih, 2009). Furthermore, a positive correlation was recently reported between spring leaf-out dates and autumn leaf senescence dates, suggesting that the factors regulating the leaf-out days are carried over to affect leaf senescence in the following autumn (Fu *et al.*, 2014, Signarbieux *et al.*, 2017). Thus, the literature remains inconsistent about the determinants of autumn leaf senescence (Estiarte & Peñuelas, 2015), so that well-designed experiments are needed to investigate and better understand the leaf senescence process.

Current studies of leaf senescence are generally based on either species-specific long-term in situ observations (Menzel *et al.*, 2006, Panchen *et al.*, 2015), or on remote-sensing based observations (Garonna *et al.*, 2014, Julien & Sobrino, 2009, Liu *et al.*, 2016b, Shen *et al.*, 2015, Xie *et al.*, 2015, Jeong *et al*.,2011). While manipulation experiments have been conducted, only few have studied the autumn phase in relation to climate change, as opposed to spring (Wolkovich *et al.*, 2012). Furthermore, these few-experimental autumn phenology studies were designed with only one or two warming treatments (Gunderson *et al.*, 2012, Marchin *et al.*, 2015, Morin *et al.*, 2010, Norby *et al.*, 2003). How leaf senescence responds to a temperature gradient, whether summer and autumn warming influence leaf senescence differently, and whether autumn phenology has the same temperature sensitivity as spring phenology, to our knowledge, has not yet been experimentally investigated.

In the present study, we therefore carried out gradient-warming/cooling manipulation experiments using two-year old and one-meter-high saplings of *Fagus sylvatica* L. (European beech), a widespread deciduous forest tree species in temperate Europe. Specifically, we exposed the saplings to either summer or autumn warming. The primary objectives of this study were (1) to quantify the temperature sensitivity of leaf senescence date (St, changes in days per °C warming); (2) to investigate the effect of summer versus autumn warming on leaf senescence dates, and (3) to compare St of autumn senescence with that of spring leaf-out.

Materials and methods

Study site and climate chambers

The experiment was conducted in 12 climate-controlled transparent chambers at the Drie Eiken campus of the University of Antwerp (Belgium, 51º19′N, 4º21′E). The long-term mean annual air temperature is 9.6 ºC, and mean monthly air temperatures vary from 2.2 ºC in January to 17.0 ºC in July. Annual precipitation averages 780 mm, being uniformly distributed throughout the year (Campioli *et al.*, 2012). The chambers could be artificially warmed/cooled by a centralized heating/cooling system ensuring different levels of continuous (day and night) warming or cooling above/below the fluctuating ambient air temperature (Fu *et al.*, 2016). Each chamber could accommodate 12 saplings. Temperature sensors (Siemens, type QFA66, Berlin, Germany) were used to continuously monitor the air temperature inside each chamber, logging every 30 minutes and storing hourly data. Here, we combine the results from three different experiments performed in the climate chambers using beech saplings of the same provenance and size.

Experimental design and leaf senescence measurements

Tree material. The experiments used 2-year-old and one-meter-high saplings of *Fagus sylvatica* L. grown from seeds of the same origin and cultivated in the same field for one year at a commercial nursery. We transplanted the saplings into plastic pots (diameter 25 cm, depth 40 cm). The pots were moved into the climate-controlled chambers during early summer, late summer or winter (see below). The pots were filled with a substrate that was created by combining potting soil and Lommel sand (grain size <1 mm diameter), bought from commercial suppliers (Van den Broeck and Jos Meeussen & Zoon bvba) in Belgium. In experiment 1 and 2, slow release fertilizer (100 $g \cdot m^{-2}$, 13–10–20 for N, P, and K, respectively, all in percentage) was added in end of May to each sapling. Over the growing period, the saplings were watered at least three times per week to ensure no water limitation.

Experiment 1 (temperature treatment during summer, targeting leaf senescence) (Fig. 1). In this experiment, one control treatment (+0°C) and three temperature treatments were applied: +1°C, +3°C and +4°C. Two to four replicate chambers were used, except for the +4°C treatment, for which data from only one chamber were available because one chamber failed. At summer solstice (21 June 2016), four saplings were placed in each chamber. The saplings were moved out at the “end of summer”, i.e., on 15 August 2016. In total, 9 chambers and 36 saplings were used in this experiment.

Experiment 2 (temperature treatment during autumn, targeting leaf senescence) (Fig. 1). In this experiment, we applied one control treatment (+0°C), one cooling treatment (-1°C) and one warming treatment (+1°C), using three replicated chambers for each treatment. Four saplings were exposed to the treatment in each chamber during the autumn period, i.e. from 15 Aug 2016 to leaf senescence. In total, 9 chambers and 36 saplings were used in this experiment.

Experiment 3 (temperature treatment during winter-spring, targeting leaf-out). In winter-spring 2016, we conducted a separate warming experiment on the spring leaf-out phenology. Four saplings were moved into each of the twelve climate-controlled chambers on 1 January 2016. During the experiment, five warming temperature treatments, i.e. +1°C, +2°C, +3°C, +4°C and +5°C (two chambers per treatment) and a control treatment (+0°C) were applied. In total, 12 chambers and 48 saplings were used in this experiment.

The warming/cooling provided was generally stable for the experiments 1 and 3 (actual warming was on average ± 10% of the prescribed value; see below for description of the experiments). However, for experiment 2 (see below) the warming during autumn was less stable (within ± 20%). This inaccuracy was not considered crucial, because our main analyses were based on the actually realized warming/cooling (e.g. regression analysis, see below), not the envisaged warming.

Observation of leaf senescence and leaf-out

Leaf senescence was monitored following Vitasse *et al.* (2009). In detail, the number of leaves with autumn colour was determined visually and the percentage of them, out of the total number of leaves, was calculated. The senescence date was defined as the date when 50% of the leaves had autumn colour. Leaf-out date was defined as the day when the entire leaf blade and the leaf stalk were visible on the terminal buds (Fu *et al.*, 2016).

Cooling degree hours

To evaluate the relationships between leaf senescence and air temperature, we calculated cooling degree hours (CDH) as the sum of hourly temperature below a temperature threshold (T_{base}) during the study period, i.e., from summer solstice (21 June) to the day of leaf senescence (LS) (Dufrêne *et al.*, 2005). The T_{base} was set at 25°C, according to a previous study on *Fagus sylvatica* (Delpierre *et al.*, 2009):

$$CDH = \sum_{start}^{LS} (\mathrm{T}_{base} - \mathrm{T}_{hourly}) \text{ if } \mathrm{T}_{hourly} < \mathrm{T}_{base}$$

We also tested the use of a higher T_{base}, i.e. 30°C, but found very similar results, and therefore only reported the results based on 25°C in the main text.

Data analysis

The temperature responses of leaf senescence and leaf-out were evaluated using linear regression based on the average dates obtained from the four saplings per chamber. The temperature sensitivity of leaf senescence and leaf-out were defined as the slopes of the linear regression between dates and the actual temperature change in the chambers. Independent samples *t*-tests were used to evaluate the difference between leaf senescence, or leaf-out dates, as well as the accumulated CDH, among different temperature treatments. Differences in the temperature sensitivity of leaf senescence between autumn cooling and autumn warming, and between summer and autumn, as well as in the temperature sensitivity between leaf senescence and leaf-out, were tested using ANCOVA, i.e. testing the slopes and intercepts. All statistical analyses were conducted using SPSS 16.0 (SPSS Inc., Chicago, IL, USA).

Results

Leaf senescence response to experimental warming and cooling

Leaf senescence dates were significantly delayed by the warming treatments, but were significantly advanced by cooling (both $P<0.05$), as compared to the control treatment (Fig. 1a). Although both summer and autumn warming significantly delayed the leaf senescence dates, compared to the control, a larger delay (14 days on average) was found under summer warming treatments than under autumn warming treatments (11 days on average) (Fig. 1a). As opposed to the warming treatments, cooling significantly advanced the dates of leaf senescence, by 3 days on average ($F=9.8$; $P=0.005$; Fig. 1a).

Temperature sensitivity of leaf senescence and leaf-out

In the previous paragraphs the phenology responses were given, independent of the intensity of the warming or cooling. This paragraph aims to render these treatments more comparable by expressing all phenology changes on a per °C basis. By using a relative variable, we aim to removing the influence of different periods (summer vs. autumn) and exposure times to warming. On average, a rise of air temperature by one degree delayed the leaf senescence date by 6.4 ± 1.1 days, and the difference in the temperature sensitivity of leaf senescence (St, delay in days per °C warming) between autumn warming treatment (St_autumn, 8.3 ± 1.1 days °C-1) and summer warming treatment (St_summer, 6.1 ± 0.8 days °C^{-1}) was not statistically significant (P=0.75, Fig. 1b). The absolute St values of leaf senescence during autumn warming and autumn cooling (-6.7 ± 1.0 days °C^{-1} for cooling treatments) also did not differ statistically significantly (Fig. 2).

Warming significantly advanced the date of leaf-out in spring, with 4.5 ± 0.5 days advancement per degree Celsius warming (Fig. 3a). Compared to the autumn leaf senescence (delay of 8.3 ± 1.1 days °C^{-1}), the temperature sensitivity of leaf-out was thus significantly lower (Fig. 3b), suggesting a larger effect of climate warming on autumn leaf senescence than on spring leaf-out phenology.

Correlation between leaf senescence and cooling degree hours

No significant correlation was found between leaf senescence dates and CDH that were accumulated from 21 June to the day of leaf senescence across the temperature treatments (R^2=0.09, P=0.12, Fig. 4). In addition, the CDH requirement was not significantly different between the two autumn treatments, i.e., 14677K and 13067K for autumn warming treatment and autumn cooling treatment, respectively. However, the CDH requirement of saplings in the summer warming treatment was statistically significantly lower than in the autumn warming and autumn cooling treatments (P<0.05).

Discussion

Previous studies have highlighted the ambiguous nature of the warming response of leaf senescence (Gunderson *et al.*, 2012, Heide & Prestrud, 2005, Menzel *et al.*, 2006), and attributed this to the limited availability of long-term datasets, the difficulty of quantifying the exact date of leaf senescence under natural conditions, and the lack of focused experimental studies designed to understand the leaf senescence response to temperature. For temperate trees under favorable conditions, i.e., without water or nutrient stress, it is generally assumed that the leaf senescence process is mainly triggered by photoperiod and temperature (Lieth, 2013, Way & Montgomery, 2015). Some studies reported a delayed trend of leaf senescence with climate warming, based on in situ observations (Delpierre *et al.*, 2009, Vitasse *et al.*, 2011), remote sensing observations (Liu *et al.*, 2016b, Reed *et al.*, 2009, Stöckli & Vidale, 2004), as well as open top chamber-based field warming experiments (Gunderson *et al.*, 2012). In contrast, other studies reported insignificant responses or even advanced senescence with climate warming (Norby *et al.*, 2003, Xie *et al.*, 2015), which may be related to warming-induced drought stress (Xie *et al.*, 2015). Based on gradient warming experiments, in which drought was excluded, our study clearly revealed that warming significantly delays the timing of leaf senescence in European beech saplings in both summer and autumn warming, with even more than 30 days delay under the +4°C treatment (4°C higher than ambient). This suggested that, under sufficient water and nutrient conditions, temperature may be more important than photoperiod in controlling the leaf senescence process under temperate latitudes. In fact, if there was a photoperiod threshold, this would have been overpassed by up to 30 days. Note that we found a larger delay (14 days on average) under summer warming treatments than under autumn warming treatments, this was, however, maybe largely attributed to the more intensive warming treatment that was applied during summer (warmed up to ca. 4°C) than during autumn (warmed up to ca. 1°C) (see Fig. 1b). We also did not find a statistical difference of the temperature sensitivity of leaf senescence between autumn warming and autumn cooling treatments. This may be due to the limited sample size in this study, i.e. only one cooling treatment and one warming treatment during autumn, and therefore this conclusion needs to be further studied. In addition, we found a larger temperature sensitivity of leaf senescence, with 6-8 days delay per degree Celsius warming, as opposed to 2-7 days delay per °C warming found in earlier experimental studies (Gunderson *et al.*, 2012, Han *et al.*, 2014, Nakamura *et al.*, 2010). This difference might be related to species differences, to differences in the local environment, as well as to the different experimental designs, i.e., only one or two warming treatments in the previous studies versus gradient warming/cooling in the present study.

Surprisingly, there were no statistically significant differences in the sensitivity of the leaf senescence process to summer and autumn warming. This implies that the positive impacts of warming on leaf physiology, such as delayed chlorophyll degradation (Fracheboud *et al.*, 2009), leading to delayed leaf senescence at the end of the growing period, does not depend on the seasonal timing of the temperature elevation. Nonetheless, warming may affect different processes during summer (e.g. predominantly cell division and expansion) than during autumn (cell maturation and lignification). Furthermore, warming might affect different phases of the leaf senescence process when applied in summer versus autumn. During summer, warming might delay the leaf senescence onset, whereas autumn warming might slow down the progression rate of the leaf senescence (Fracheboud *et al.*, 2009). These different aspects (delay in leaf senescence onset vs. slowdown of leaf senescence rate) cannot be independently assessed with the coloration method we used.

The lower CDH requirement associated with the summer treatment should be related to more intense warming in summer than in autumn. We do not believe that the low CDH requirement in summer is related to differences in the leaf senescence date as summer warming elicited, on average, later leaf senescence than autumn warming, which should have caused a larger CDH. The timing of leaf senescence simulated by cooling degree days-based models has been compared in earlier studies with in situ observations (Archetti *et al.*, 2013, Delpierre *et al.*, 2009, Jolly *et al.*, 2005, Vitasse *et al.*, 2011). Consistent with the assumption of degree days-based models, we found that the differences in the cooling degree hours (CDH) required for leaf senescence between the two autumn treatments were statistically insignificant. Furthermore, good model performances were found in boreal tree species (Koski & Selkäinaho, 1985, Partanen, 2004, Viherä-Aarnio *et al.*, 2005). However, contrary to the results of the present study, these studies found that warming during summer and autumn would advance, not delay, the timing of leaf senescence. Possibly, this opposite temperature response is attributable to differences among boreal and temperate-zone species. Jeong and Medvigy (2014) reported a nonlinear temperature sensitivity of leaf senescence using many ground observations and suggested that warmer regions may have a larger temperature sensitivity than cooler regions. In addition, recent studies have reported a positive correlation between spring leaf-out and leaf senescence dates in trees (Fu *et al.*, 2014, Signarbieux *et al.*, 2017), delayed senescence following exceptionally late spring greening in sub-arctic grasslands (Leblans *et al.*, 2017), and the performance of senescence models was substantially improved by incorporating this legacy effect.

Interestingly, we found a larger temperature sensitivity (St) of autumn leaf senescence than spring leaf-out using European beech saplings of the same age. Contrasting conclusions were obtained from a meta-analysis of observations on mature trees from the European phenology network, which reported a larger St of spring leaf-out (4.6±0.07 days $°C^{-1}$) than of autumn leaf colouring (1.0±0.4 days $°C^{-1}$) across plant species (Menzel *et al.*, 2006). This difference may be attributable to the species-specific differences in the phenology response to temperature (Panchen *et al.*, 2015, Richardson *et al.*, 2006, Vitasse *et al.*, 2009). However, similar finding was reported on *Quercus variabilis* seedlings in an open-field warming experiment (Han *et al.*, 2014), and on mature beech trees in an altitude gradient (Vitasse *et al.*, 2009). The difference in temperature sensitivity of leaf-out and leaf senescence are likely related to the differential processes between spring and autumn phenology. Concerning spring leaf-out (particularly for diffuse porous species like beech), temperature impacts the end of bud dormancy and the speed of leaf unfolding but no other trees organ (which are inactive before budburst) (*Delpierre et al.*, 2016). On the other hand, in autumn, temperature impacts both the leaf physiological status (chlorophyll content, photosynthesis, pigment degradation etc) and tree growth (e.g. wood lignification, fine root growth). The latter reduction of carbon sink activity at the tree scale may be an additional, overlooked trigger of leaf senescence. These interactions might affect leaf senescence onset, in other words not only leaf status but also (and maybe primarily) a lack of sink activity might trigger leaf senescence (see hypothesis in Fu et al., 2014). Therefore, it is logical that temperature has a strong effect on autumn phenology, which, as showed by our data, and even can be stronger than that on spring phenology.

Given the larger warming response of leaf senescence than of spring leaf-out found in the present study, under future climate warming conditions we can expect a larger contribution of the delay in autumn senescence dates to the extension of photosynthetic season than of the earlier spring leaf-out. Thus, warming induced changes in leaf senescence could play an important role in the ecosystem carbon balance (Keenan *et al.*, 2014, Piao *et al.*, 2008). However, delayed leaf senescence in response to warmer summers-autumns may increase the risk of extreme events such early-frost damage to leaves (Augspurger, 2013, Hänninen, 2016, Inouye, 2008), which would hamper the nutrient resorption. This can lead to reduced nutrient reserves to support next season's growth, and subsequentially impact the ecosystem carbon and nutrient cycles (Estiarte & Peñuelas, 2015, Fracheboud *et al.*, 2009). Finally, note that considering the legacy effect of leaf-out on the leaf senescence dates (Fu *et al.*, 2014), the delays in leaf senescence as observed in our experiments might be partially offset by the earlier spring leaf-out in response to warmer winters.

The underlying physiological processes of leaf senescence and their environmental cues, especially the interactive effect of temperature and photoperiod, are still unclear. Moreover, warming responses of leaf senescence largely differ between natural observations and warming experiments (Wolkovich *et al.*, 2012), ontogenetic differences have been reported between saplings and mature trees (Mediavilla *et al.*, 2014, Vitasse, 2013), and species variability exists in response to warming (Parmesan & Hanley, 2015, Primack *et al.*, 2015). Nonetheless, our study provides important insights. Taking advantage of temperature manipulative experiments, we found that, in the absence of water and nutrient limitation, temperature is a dominant factor controlling the leaf senescence process in European beech, and warming during summer and autumn both significantly delay the date of leaf senescence. Furthermore, we found a larger temperature response of leaf senescence than spring leaf-out. These findings enhance our understanding of leaf phenology response to the climate change, and potentially improve our understanding of phenological impacts on ecosystem carbon and nutrient cycles.

Acknowledgments

This study is supported by the General program of National Nature science foundation of China (No. 31770516), the National Key Research and Development Program of China (2017YFA06036001) and the Thousands Talents Program for Young Professionals. Matteo Campioli is a Postdoctoral Fellow of the Research Foundation–Flanders (FWO) and acknowledges ERC for support through ERC-2016-StG-714916 “LEAF-FALL”. Ivan A Janssens acknowledges support from the European Research Council (ERC) through Synergy grant ERC-2013-SyG-610028 “P-IMBALANCE” and support from the University Of Antwerp.

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Figure captions

Fig 1. (a) The distribution, mean, and standard deviation (plot box) of the leaf senescence dates of European beech saplings under different temperature manipulations and the control. Each grey dot indicates the result for one sapling. (b) Relationship between leaf senescence dates of European beech saplings and the mean temperature change in the treatments, as compared with the ambient temperature. Open circles: Experiment 1, i.e. temperature treatment over the summer period (from summer solstice to 15 August 2016); Grey squares: Experiment 2, temperature treatment over the autumn period (from 15 August 2016 to the date of leaf senescence). The grey line and shaded areas represent linear regression fits (with 95% confidence intervals) across summer and autumn treatments.

Fig 2. Temperature sensitivities of leaf senescence to autumn (from 15 August 2016 to the date of leaf senescence) cooling and warming. The temperature sensitivity was calculated using simple linear regression. The difference in the sensitivity between autumn cooling and warming is not statistically significant

.

Fig 3. (a) Experiment 3: temperature treatment during winter-spring 2016. The temperature sensitivity of leaf-out, in relation to the mean temperature change in the treatments, as compared with the ambient temperature. (b) A comparison of the temperature sensitivity of leaf-out and leaf senescence. The asterisk indicates a statistically significant difference ($P < 0.05$).

Fig 4. Correlation between leaf senescence dates and cooling degree hours accumulated in the different treatments. Each dot denotes one climate-controlled chamber. The color bar shows the temperature anomalies in the temperature treatments (blue is control). Treatment of summer warming (squares) refers to the period from summer solstice to 15 August 2016; autumn warming (circles) and autumn cooling (diamonds) refer to the period from 15 August 2016 to the date of leaf senescence.

FIGURE 1

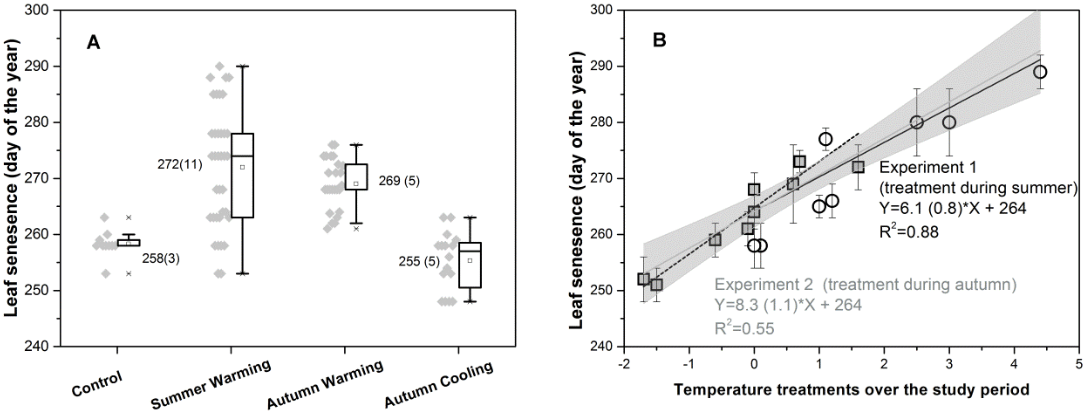

A
Leaf senesence (day of the year)
300
290
280
270
260
250
240
258(3)
272(11)
269 (5)
255 (5)
Control
Summer Warming
Autumn Warming
Autumn Cooling
B
Leaf senesence (day of the year)
Experiment 1
(treatment during summer)
Y=6.1 (0.8)*X + 264
R^2=0.88
Experiment 2 (treatment during autumn)
Y=8.3 (1.1)*X + 264
R^2=0.55
-2
-1
0
1
2
3
4
5
Temperature treatments over the study period

FIGURE 2

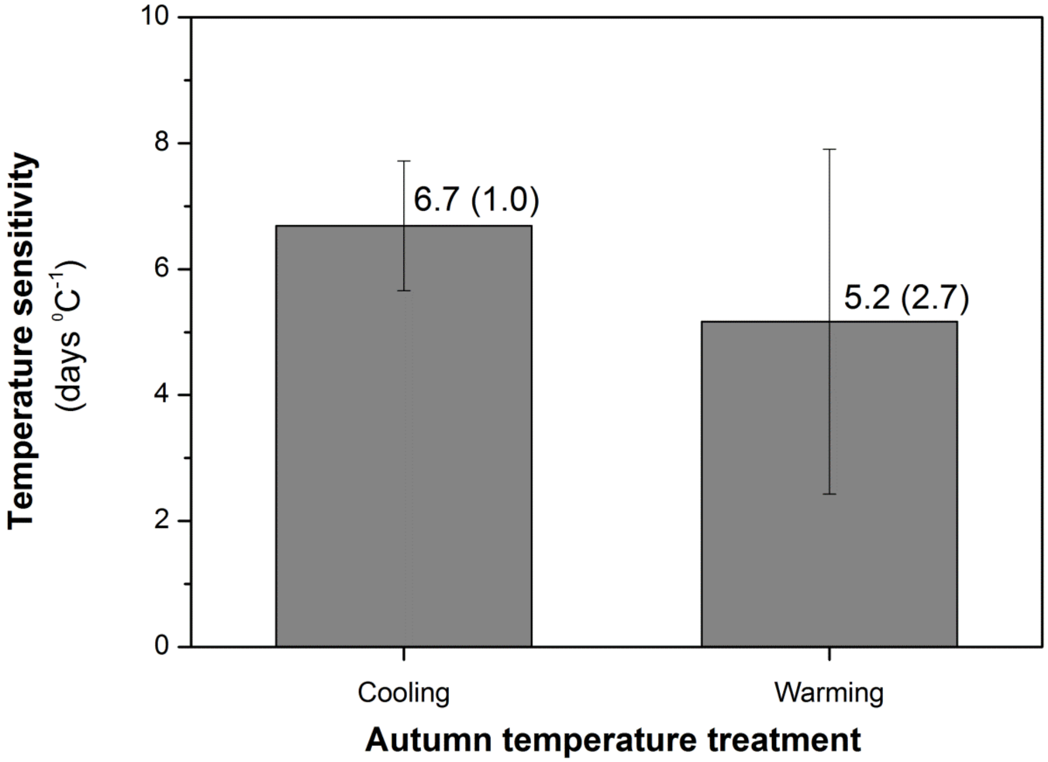

10
8
6
4
2
0
Temperature sensitivity
(days $^0C^{-1}$)
6.7 (1.0)
5.2 (2.7)
Cooling
Warming
Autumn temperature treatment

FIGURE 3

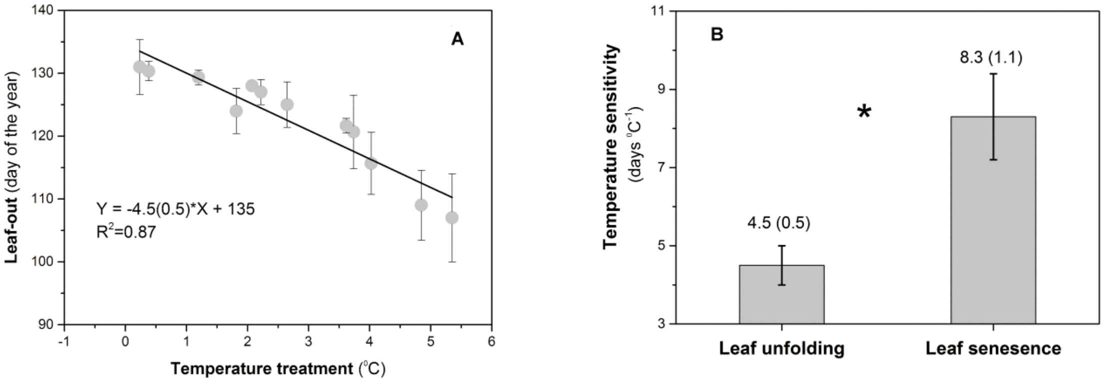
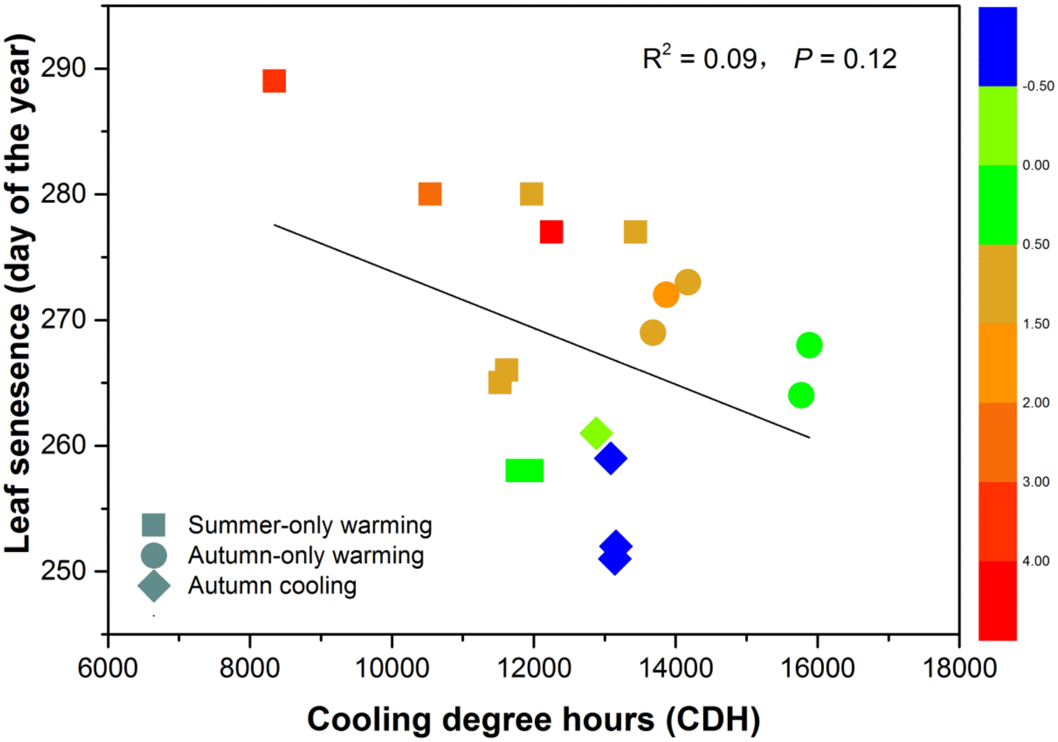

A
Leaf-out (day of the year)
140
130
120
110
100
90
-1
0
1
2
3
4
5
6
Temperature treatment (°C)
Y = -4.5(0.5)*X + 135
R^2=0.87
B
Temperature sensitivity (days °C^{-1})
11
9
7
5
3
*
4.5 (0.5)
8.3 (1.1)
Leaf unfolding
Leaf senesence

FIGURE 4



R^2 = 0.09， P = 0.12
Leaf senesence (day of the year)
250
260
270
280
290
Cooling degree hours (CDH)
6000
8000
10000
12000
14000
16000
18000
Summer-only warming
Autumn-only warming
Autumn cooling
-0.50
0.00
0.50
1.50
2.00
3.00
4.00