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ORIGINAL ARTICLE

High autumn temperatures increase the depth of bud dormancy in the subtropical *Torreya grandis* and *Carya illinoinensis* and delay leaf senescence in the deciduous *Carya*

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Abstract

Key message **Autumn phenology and physiology in the subtropical tree species *Torreya grandis* and in a subtropical provenance of *Carya illinoinensis* are affected by air temperature rather than photoperiod.**

Abstract Though leaf phenology is a key tree trait affecting several ecological processes in forested ecosystems, its environmental and genetic regulation in subtropical trees is poorly understood. A few recent studies have addressed the spring phenology of subtropical trees, but the regulation of autumn leaf senescence in these trees remains unexplored. Here we carried out an experimental study of the effects of air temperature and photoperiod on autumn phenology and physiology of seedlings of two tree species growing in subtropical southeastern China: the native torreya (*Torreya grandis*) and a subtropical provenance of the non-native pecan (*Carya illinoinensis*). Our first-time results, still limited, suggest a major role of air temperature in the degradation of leaf chlorophyll and leaf senescence in the deciduous pecan: low air temperature accelerated and high air temperature delayed these processes. As expected, no leaf senescence and only minor degradation of leaf chlorophyll was observed in the evergreen torreya. In both species, the depth of bud dormancy was increased by high temperatures during dormancy induction. Our results suggest that in torreya, the depth of both endo- and ecodormancy is increased by high temperatures. As predicted by our experimental results from autumn only, an apparent legacy effect of autumn leaf senescence on bud burst in the next spring was found in an analysis of observational phenology data on adult pecan trees growing in southern USA: late leaf senescence in the autumn was followed by a late bud burst the next spring, and vice versa.

Keywords Air temperature · Chlorophyll degradation · Dormancy induction · Leaf senescence · Legacy effect · Photoperiod

Introduction

The leaf phenology of woody plants plays a crucial role in several ecological processes, such as carbon balance, forest productivity, and determination of the geographical ranges of tree species (Richardson et al. 2009; Chuine 2010; Keenan et al. 2014). Many studies have shown that climatic warming has lengthened the growing season by advancing spring bud burst and delaying leaf senescence (Menzel and Fabian 1999; Peñuelas and Filella 2001; Menzel et al. 2006). It has also been found, however, that the advancing of spring phenology caused by climatic warming is levelling off in many tree species because the warming may also cause a failure to meet the chilling requirement of bud dormancy release (Fu et al. 2015; Chen et al. 2019).

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For trees growing in the boreal and temperate zones, the environmental regulation of tree phenology has been studied for a long time (Fuchigami et al. 1982; Hänninen 2016). Considerable uncertainties still exist in our understanding of the environmental regulation of tree spring phenology (Körner and Basler 2010a, b; Chuine et al. 2010; Fu et al. 2019a, b), but it is relatively well understood in comparison with autumn phenology, where there is much more uncertainty in our understanding of the effects of environmental cues on leaf senescence (Delpierre et al. 2009; Liu et al. 2020). This is unfortunate, for leaf senescence is in several ways ecologically essential for deciduous trees growing in the boreal and temperate zones. It is one visible manifestation of the shift from the active susceptible growth phase to the dormant frost-tolerant phase; also, physiological changes in the leaves, such as the degradation of chlorophyll and the decline in photosynthetic efficiency (Aikio et al. 2019), occur well before the visible change of leaf colour observed in both ground-based and remote-sensing phenological studies (Keenan and Richardson 2015).

In boreal and temperate trees, leaf senescence is influenced by environmental cues such as photoperiod, temperature, and precipitation (Gill et al. 2015). The roles of environmental cues in leaf senescence are species-specific. In European aspen (*Populus tremula*), the initiation of leaf senescence depends only on photoperiod (Fracheboud et al. 2009), which has been considered a reliable environmental cue for the approaching winter (Way and Montgomery 2015). In contrast, in species of the Rosaceae family, such as apple (*Malus pumila*) and pear (*Pyrus communis*), leaf senescence is insensitive to photoperiod but is controlled by low temperatures (Heide and Prestrud 2005). In many tree species, however, leaf senescence has been found to be regulated by a joint effect of environmental cues, mainly by photoperiod and temperature (Håbjørg 1972; Delpierre et al. 2009; Aikio et al. 2019; Liu et al. 2020). Recently, Zani et al. (2020) suggested that leaf senescence in temperate trees is regulated not only by the immediate effects of environmental factors, such as air temperature and photoperiod, but also by the constraints caused by the sink limitation of the trees. Accordingly, any environmental factor that increases productivity in the growing season would accelerate leaf senescence in the autumn.

Environmental factors in late summer and autumn affect not only the autumnal phenological events and related physiological processes but the depth of bud dormancy, too. In particular, as shown in several studies, high temperatures during the short-day dormancy induction deepen the subsequent bud dormancy in temperate and boreal trees (Westergaard and Eriksen 1997; Junttila et al. 2003) This phenomenon, referred to as *quantitative dormancy induction* by Hänninen (2016), may delay bud burst in the next spring and thus counteract the accelerating effect of climatic warming on spring bud burst (Heide 2003). In many species, high temperatures also delay leaf senescence (del Rio-Garcia et al. 2015; Fu et al. 2018), so that these two effects may provide a causal explanation for the apparent legacy effect observed in field studies, in which delayed leaf senescence has been followed by delayed spring bud burst (Delpierre et al. 2017; Marchand et al. 2020).

Though a few recent studies have examined spring phenology in subtropical trees (Du et al. 2019; Song et al. 2020; Zhang et al. 2021a, b; Jewaria et al. 2021; Pan et al. 2021) the environmental and genetic regulation of autumn phenology in subtropical trees remains largely unexplored. Contrary to the boreal and temperature zones, where photoperiod shows wide seasonal variation, its seasonal variation in low-latitude subtropical areas is limited. It remains unclear whether subtropical trees might react to the small variation in photoperiod, making photoperiod a seasonal cue for leaf senescence. Furthermore, autumn temperatures are generally quite high in subtropical areas, and many subtropical trees may have a second flush in early autumn, after growth cessation and bud set have taken place in late summer. In some exceptionally warm autumns, the average daily temperature may even be as high as +20 °C in early November, so that similarly to photoperiod, the role of air temperature as a seasonal cue in autumn may also be questioned.

We examined the effects of photoperiod and temperature on the autumn phenology and physiology of two nut tree species commonly grown in subtropical China. One of the species is native to our subtropical study area, and the other was represented in our study by a subtropical provenance of a non-native subtropical-temperate species (see "Materials and methods" section). Seedlings were subjected to different photoperiod and temperature conditions for three months, and leaf chlorophyll contents and visible leaf senescence were examined. Subsequently, the depth of bud dormancy was tested by means of a chilling-forcing experiment. Additionally, using observational phenological data, we examined the occurrence of the apparent legacy effect of leaf senescence on bud burst in the next spring. We tested the following hypotheses: (1) A low air temperature is the main factor causing leaf senescence (in deciduous trees) and related degradation of leaf chlorophyll, whereas a high temperature delays leaf senescence and chlorophyll degradation or even stimulates a second flush; (2) Photoperiod plays an additional minor role, so that short days promote leaf senescence and chlorophyll degradation; and (3) High autumn temperatures increase the depth of bud dormancy, thus potentially causing in deciduous species the apparent legacy effect of delayed bud burst in the next spring after an autumn with delayed leaf senescence. As far as we know, the roles of environmental cues on leaf senescence and depth of bud dormancy in subtropical trees have not been addressed in previous studies; therefore, the testing of these three

hypotheses will provide novel results that will facilitate the process-based modelling of tree phenology of subtropical trees under climate change in the long run.

Materials and methods

Study site and plant materials

The experiments were conducted on the campus of Zhejiang A&F University (30° 14′ N, 119° 42′ E), China. We selected two tree species, pecan (*Carya illinoinensis*) and Chinese torreya (*Torreya grandis*, henceforth 'torreya' for brevity's sake), for the experiments. Torreya is an evergreen coniferous species native to subtropical southeastern China, where it has been cultivated for thousands of years by grafting. Pecan is an exotic deciduous broadleaved tree species introduced from the subtropical USA to subtropical China about a hundred years ago (Zhang et al. 2015). In the USA, pecan has a wide range of natural distribution in both subtropical and temperate zones, showing a substantial genetic diversity among genotypes from different climatic conditions (Sparks 1995; Volk et al. 2009). Pecan was introduced to China in the form of seeds, and seedlings produced in nurseries from the imported seeds of subtropical provenances were used in planting the current seminatural pecan stands in subtropical China (Zhang et al. 2015). Both first-year and second-year seedlings of the two species were used in the experiments, providing $2 \times 2 = 4$ *material categories* defined by the tree species and the seedling age (see Supplementary Fig. S1).

The seedlings were propagated by open-pollinated seeds collected from the nearby seminatural forests and were grown using standard management practices in the nearby nursery of Tianmushan National Forest Station (30° 24′ N, 119° 28′ E). In brief, the seedlings were grown in individual 1.2 (first-year seedlings) or 3.7 L (second-year seedlings) containers filled with soil substrate consisting of 5 peat:2 vermiculite:1 perlite:2 organic matter by volume (Universal potting soil, Hangzhou, China). In our area, pecan and torreya generally burst buds in mid to late April. After leaf unfolding, the seedlings were in the active growth phase from May to mid-July. At that time, height growth ceased and the buds were generally set from late July to early August. After growth cessation, a small part of the seedlings of both species in the nursery showed a second flush in early September. Other than that, no subsequent bud burst occurred in the natural conditions before the next spring. The experimental seedlings were transferred from the nursery to the university campus on 10 August 2018, after growth cessation and bud set had taken place in all the seedlings. On the campus, the seedlings were kept outdoors and were watered every day until the start of the experiments on 15 August 2018.

Experimental design

Experiment 1: leaf senescence and chlorophyll degradation. A factorial combination of two levels of air temperature and photoperiod was used: high temperature (HT, +35/+25 °C day/night), low temperature (LT, +25/+15 °C day/night), long day (LD, 13 h), and short day (SD, 10 h). For both temperature and photoperiod, the treatments were designed to represent the typical natural conditions prevailing at our experimental site in August and November, respectively. Additionally, control seedlings kept in natural conditions (N) over the entire experiment were included (see Supplementary Fig. S2). Accordingly, a total of five treatments were included in our experiment: HT-LD, HT-SD, LT-LD, LT-SD, and (N). The experimental treatments were started on 15 August and ended on 15 November 2018.

For the four respective temperature and photoperiod treatments, four computer-controlled walk-in growth chambers (E-lotus Technology Co., Beijing, China) were used. In all chambers, the environmental factors other than air temperature and photoperiod were set as follows: photosynthetic photon flux density 200 μmol s^{-1} m^{-2} during the light period, $[CO_2] = 300–400$ ppm, and RH = 70%. At the beginning of the experiment, fifty seedlings per material category were sampled from the campus outdoor seedling collection for each of the four treatments in the four respective growth chambers. For the N treatment, too, fifty seedlings were sampled, though these seedlings remained in the natural conditions of the outdoor seedling collection. In all, 5 (treatments) × 50 (seedlings per treatment) = 250 seedlings per material category were used in Experiment 1. The seedlings were watered at one to three days' intervals to keep the soil moist.

On 15 September, 15 October, and 15 November 2018, three seedlings per material category were randomly selected from each treatment for leaf chlorophyll measurements. Visible leaf yellowing started around 15 October, which is when we started to determine the stages of leaf senescence, continuing that until the end of the experiment. In addition, the potential second flush of the seedlings was observed and the percentage of seedlings showing a second flush was calculated for each treatment (for details, see below).

Experiment 2: Depth of bud dormancy. In Experiment 2 we examined the depth of bud dormancy in seedlings subjected to the five temperature and photoperiod treatments for Experiment 1. Though the experimental treatments were the same in Experiments 1 and 2, the five conditions (HT-LD, HT-SD, LT-LD, LT-SD, N) are referred to as dormancy-inducing treatments when Experiment 2 is referred to. Due to the limited room available in our growth chambers, we used only first-year seedlings of pecan and torreya for Experiment 2.

On 16 November, 40 seedlings per species were sampled from each of the four dormancy-inducing treatments

and were transferred to natural chilling conditions outdoors (see Supplementary Fig. S2). Similarly, 40 seedlings were sampled from the N treatment, and these stayed outdoors. Then, after 0, 1, 2, 4, and 6 weeks of natural chilling we sampled eight seedlings per species each time to represent each of the previous five dormancy-inducing treatments and transferred them to the forcing conditions in a growth chamber (+20 °C, day length = 12 h, E-lotus Technology Co., Beijing, China). The five durations of chilling represented 0, 24, 118, 340, and 604 chill hours with air temperatures below the threshold of +10 °C (see Supplementary Table S1). The treatment groups representing 0 weeks of chilling were transferred directly from each of the corresponding five dormancy-inducing conditions to the forcing conditions on 16 November. In all, 5 (dormancy-inducing treatments) x 5 (durations of chilling) × 8 (sample size in each combination of dormancy-inducing treatment and chilling duration) = 200 seedlings were used for each of the two species. Environmental factors in the forcing chamber, other than air temperature and photoperiod, were the same as in Experiment 1 (see above).

In the forcing conditions, the seedlings were watered every three or four days to keep the soil moist. The occurrence and timing of bud burst were investigated every two or three days (for details, see below). Bud burst percentage (BB%) and the days to bud burst (DBB) were calculated for each treatment group. The depth of bud dormancy was evaluated by means of BB% and DBB, so that a low BB% and/or a high DBB indicated deep dormancy, and vice versa.

Throughout the two experiments, air temperature was recorded hourly in all the growth chambers used and in the natural outdoor conditions with iButton Data Loggers (Model DS1912L, Embedded Data Systems Co., Ltd, KY, USA).

Occurrence of a second flush and visible leaf senescence

In Experiment 1, we counted the number of seedlings showing a second flush, and the second-flush percentage was calculated for each treatment. For visible leaf senescence in pecan, we discerned the following four developmental stages: (1) all leaves green, (2) < 10% leaves turned yellow, (3) 10–50% of leaves turned yellow, and (4) > 50% leaves turned yellow or fallen. For the evergreen torreya, no visible leaf senescence was observed.

Degradation of leaf chlorophyll

In Experiment 1, the total chlorophyll content was examined on 15 September, 15 October, and 15 November 2018. For each of the five treatments, three replicated seedlings per material category were randomly sampled on each of the above dates. From each seedling, penultimate current-year leaves were collected. About 0.1 g of finely cut and well-mixed samples were put on glass vials with 8 mL of 95% (v/v) ethanol at 25 °C in the dark for 24 h until they were blanched. After centrifugation of the mixture on standing, the absorbance of the supernatant was measured with a spectrophotometer (UV-2550, Shimadzu, Kyoto, Japan) at 646 and 663 nm. The total chlorophyll content was determined following Lichtenthaler (1987).

Determination of bud burst

In Experiment 2, all of the seedlings transferred to the forcing conditions were inspected for occurrence of bud burst every two or three days. For both species, we discerned the following four developmental stages: (1) bud closed, (2) bud swelling, (3) leaf emergence, and (4) leaf unfolding. The timing of bud burst was determined by the date when 50% of the buds achieved the developmental stage of leaf unfolding. The first three developmental stages were observed to improve the precision of observing the fourth stage, which was used for determining bud burst (Zhang et al. 2021a).

Legacy effect of autumn leaf senescence on spring bud burst in pecan

The legacy effect of autumn leaf senescence on spring bud burst in adult pecan trees was examined with observational data from four locations in the USA (30° 24′ N, 84° 16′ W), (35° 48′ N, 78° 42′ W), (34° 52′ N, 82° 21′ W), and (34° 46′ N, 96° 39′ W) for the years 2012 to 2019. The data were downloaded from the website of the USA National Phenology Network (http://www-dev.usanpn.org). The legacy effect was tested by plotting the date (Day of Year, DOY) of spring bud burst against that of leaf senescence in the previous autumn and then examining whether there was a positive correlation between these two dates as predicted by the legacy effect.

Statistical analyses

All statistical analyses were conducted separately for the two species. Differences in the second-flush percentage among the treatments were analyzed by means of logistic regression with a binary response, with air temperature, photoperiod, and seedling age (first-year vs. second-year seedlings) as the explaining factors. A four-way ANOVA was applied to test the effects of air temperature, photoperiod, seedling age, and the examination date on the total chlorophyll content and the stage of leaf senescence. Following ANOVA, post hoc analyses were done with Tukey's HSD (honestly significant difference) test. In pecan, the relationship between total chlorophyll content and stage of visible leaf senescence was

examined with the Pearson correlation analysis. Pooled data for both first-year and second-year seedlings sampled from all treatments on two dates (15 October and 15 November) were used in the test. In testing the effects of air temperature and photoperiod on the depth of bud dormancy, the duration of chilling was taken as an additional explaining factor because it was the driving force of endodormancy release in the chilling-forcing experiments. In particular, the effects of the three factors on bud burst percentage, BB%, and days to bud burst, DBB, were tested with logistic regression with a binary response and a three-way ANOVA, respectively. All statistical tests were conducted with SPSS (version 16.0, SPSS Inc., Chicago, USA).

Table 1 A logistic regression analysis with a binary response of factors affecting the second-flush percentage of pecan and torreya seedlings in autumn

	Pecan	Torreya
	P	*P*
Age (A)	1.000	**0.001**
Photoperiod (P)	0.196	0.123
Temperature (T)	**0.001**	**<0.001**
A * P	**0.459**	**0.002**
A * T	**0.026**	**<0.001**
P * T	**0.001**	**<0.001**
A * P * T	**0.011**	**<0.001**

'Age' stands for the differences observed between the first-year and the second-year seedlings. The *P* values in bold indicate statistical significances with at least $P < 0.05$

Results

Occurrence of a second flush

After growth cessation and bud set had already set in, some of the seedlings of both species showed a second flush (Fig. 1). Whenever a second flush was seen, it occurred in September or early October. The subsequent second growth cessation and bud set occurred one or two weeks after the second flush. The second flush percentage was higher in torreya than in pecan (Fig. 1).

Our results show a dominant role for high air temperature in causing the second flush: under LT no second flush was seen in either species, whereas under HT the second-flush percentage varied from 3.3 to 53.3% (Fig. 1; Table 1). In all material categories, photoperiod interacted with temperature, so that under HT, a higher second-flush percentage was seen in LD than in SD (Fig. 1; Table 1); but as stated above, no second flush was seen under LT regardless of the photoperiod. In addition, a significant age effect was found in torreya, with a higher second-flush percentage in the second-year (Fig. 1d) than in the first-year (Fig. 1c) seedlings. Some of the torreya seedlings showed a second flush in the natural conditions (Fig. 1c, d) as well, whereas pecan seedlings showed no second flush in the natural conditions (Fig. 1a, b).

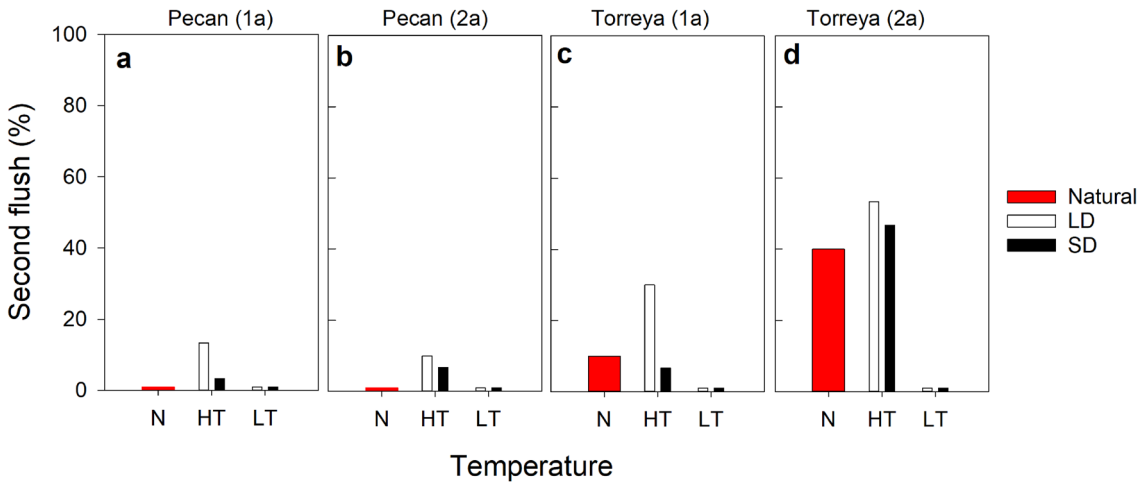

Fig. 1 Effects of temperature and photoperiod in autumn on the second-flush percentage in first-year ('1a') and second-year ('2a') seedlings of pecan (**a**, **b**) and torreya (**c**, **d**). From 15 August to 15 November, the seedlings were exposed to four factorial combinations of two levels of temperature and photoperiod: high temperature (HT, +35/+25 °C day/night), low temperature (LT, +25/+15 °C day/night), long day (LD, 13 h), and short day (SD, 10 h). Additionally, the experiment included control seedlings in natural conditions (N, red bars)

Visible leaf senescence

Visible leaf senescence was studied in both first-year and second-year seedlings of the deciduous pecan. The first visible signs of leaf senescence were seen in early October, which was about two months after the start of the treatments (Fig. 2). Our results showed a dominant role for low air temperature in causing leaf senescence: under LT a continuous and significant progress of leaf senescence was seen, whereas under HT all leaves remained green (Fig. 2; Table 2). Photoperiod showed an interaction with the age of the seedlings: under LT, SD further accelerated leaf senescence in the second-year (Fig. 2b) but not in the first-year (Fig. 2a) seedlings. Overall, leaf senescence advanced more rapidly in the second-year (Fig. 2b) than in the first-year (Fig. 2a) seedlings. The progression of leaf senescence in the natural conditions was basically similar to that in the LT condition (Fig. 2).

Degradation of leaf chlorophyll

The degradation of leaf chlorophyll showed more clearly in the deciduous pecan than in the evergreen torreya (Fig. 3). In both first-year and second-year pecan seedlings, the total chlorophyll content declined from September to November (Fig. 3a, b; Table 2). In pecan, the main factor causing degradation of leaf chlorophyll was low temperature: the total chlorophyll content was consistently lower under LT than under HT (Fig. 3a, b; Table 2). Photoperiod showed no effect on the total chlorophyll content in most cases, but under HT, SD accelerated the decline of the chlorophyll content at the late stage of leaf senescence in November (Fig. 3a, b). As expected, the total chlorophyll content in the pecan seedlings was negatively correlated with the stage of visible leaf senescence (Fig. 4).

Depth of bud dormancy induced by autumn temperatures and photoperiod

In an experiment carried out after exposing the seedlings to the five dormancy-inducing treatments, BB% increased and DBB decreased significantly with increased duration of chilling in both pecan and torreya seedlings (Fig. 5; Table 3). This finding confirms that both species show endodormancy and a chilling requirement. In torreya, the BB% values were 100% with the longest duration of chilling (Fig. 5b), and the DBB-values showed signs of levelling off (Fig. 5d). These findings suggest that the chilling requirement is met, by and large, by the longest duration of chilling (6 weeks), but this result remains inconclusive due to the uncertainty related to the levelling off of the DBB curve (Fig. 5d). Under the same

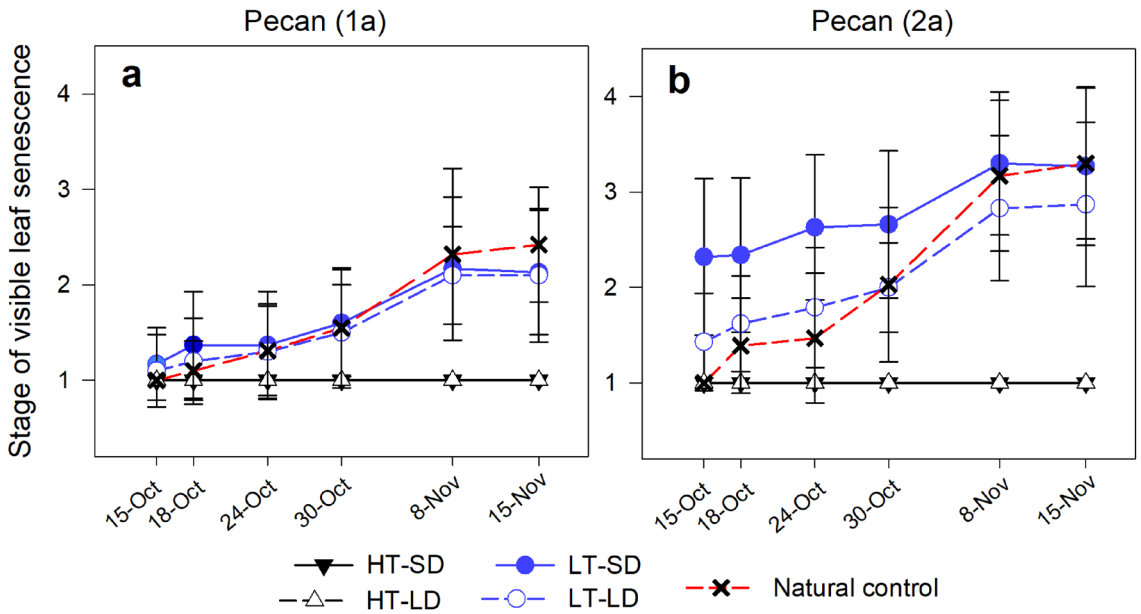

Fig. 2 Effects of temperature and photoperiod in autumn on the stage of visible leaf senescence (mean ± SE) in first-year ('1a', **a**) and second-year ('2a', **b**) seedlings of pecan. From 15 August to 15 November, the seedlings were exposed to four factorial combinations of two levels of temperature and photoperiod: high temperature (HT, +35/+25 °C day/night), low temperature (LT, +25/+15 °C day/night), long day (LD, 13 h), and short day (SD, 10 h). Additionally, the experiment included control seedlings in natural conditions ('Natural control'). Visible leaf senescence was assessed in terms of four stages: (1) all leaves green, (2) < 10% of leaves turned yellow, (3) 10–50% of leaves turned yellow, and (4) > 50% of leaves turned yellow or dropped. Some of the overlapping data points have been moved slightly apart for better visibility

Table 2 A four-way analysis of variance of factors affecting the degradation of chlorophyll in leaves of torreya and pecan seedlings and visible leaf senescence in pecan seedlings in autumn

	Torreya		Pecan		Pecan	
	Total Chl		Total Chl		Leaf senescence stage	
	F	*P*	*F*	*P*	*F*	*P*
Age (A)	**5.156**	**0.028**	**20.60**	**<0.001**	**194.98**	**<0.001**
Photoperiod (P)	**8.246**	**0.006**	3.11	0.085	**59.73**	**<0.001**
Temperature (T)	2.688	0.108	**395.33**	**<0.001**	**1180.42**	**<0.001**
Date (D)	**5.212**	**0.009**	**119.28**	**<0.001**	**58.11**	**<0.001**
A * P	**4.190**	**0.046**	2.34	0.134	**53.86**	**<0.001**
A * T	2.467	0.124	0.68	0.415	**202.30**	**<0.001**
A * D	0.745	0.481	1.07	0.352	0.96	0.429
P * T	0.004	0.952	**6.37**	**0.015**	**59.73**	**<0.001**
P * D	2.221	0.121	**13.47**	**<0.001**	0.27	0.899
T * D	0.002	0.998	**4.53**	**0.017**	**54.58**	**<0.001**
A * P * T	0.114	0.737	1.23	0.273	**53.86**	**<0.001**
A * P * D	0.506	0.606	1.51	0.233	0.74	0.562
A * T * D	2.05	0.141	**9.89**	**<0.001**	1.41	0.230
P * T * D	0.88	0.422	**3.64**	**0.035**	0.27	0.899
A * P * T * D	0.66	0.523	0.04	0.962	0.74	0.562

'Age' stands for the differences observed between the first-year and the second-year seedlings. 'Total Chl' stands for the total chlorophyll content of the leaves. For determination of the stage of leaf senescence, see "Materials and methods" section. The *P* values in bold indicate statistical significances with at least $P < 0.05$

criteria, the longest duration of chilling was not sufficient to meet the chilling requirement of pecan (Fig. 5a, c).

The BB% values were generally lower and the DBB values higher after dormancy induction under HT than under LT (Fig. 5). Over all treatments and regardless of the photoperiod, this result was consistent for BB% in torreya (Fig. 5b) and for DBB in both species (Fig. 5c, d). Regarding BB% in pecan, the result was consistent within limits of the results obtained for each of the two dormancy-inducing photoperiods: in both LD and SD treatments, BB% was higher after HT than after LT dormancy induction, with the longest duration of chilling (6 weeks) as the only exception (Fig. 5a). These results indicate that deeper dormancy was generally induced under HT than under LT. Photoperiod did not have a similar effect on the depth of bud dormancy (Fig. 5; Table 3), except that for pecan, LT dormancy induction produced higher BB% values under SD than under LD (Fig. 5a).

Legacy effect of autumn leaf senescence on spring bud burst in pecan

For adult pecan trees growing in the southern USA, a clear positive correlation was found between the timing of autumn leaf senescence and of bud burst in the next spring. A one-day delay in senescence corresponded to a 0.63-day delay in bud burst (Fig. 6). This finding suggests that pecan shows an apparent legacy effect of autumn senescence on bud burst in the next spring.

Discussion

Effects of air temperature and photoperiod on leaf senescence and pigment degradation

The effects of air temperature and photoperiod on leaf senescence have been studied earlier in boreal and temperate trees (Gill et al. 2015). Our study provided first-time experimental results for these effects in subtropical trees. In support of our first hypothesis, our results show that low air temperatures play a dominant role in the leaf senescence and pigment degradation of the deciduous pecan. Both of these processes were accelerated by a three-month exposure to low air temperatures (LT, +25/+15 °C day/night). Under high temperatures (HT, +35/+25 °C day/night) no visible leaf senescence was observed regardless of the photoperiod applied in the treatment. These results are in line with the earlier findings of Heide and Prestrud (2005), del Rio-Garcia et al. (2015), and Fu et al. (2018). Our first hypothesis on the role of low air temperatures in causing the autumn development related to the approaching winter is also supported indirectly by the observation that in both species examined, high temperatures, rather than causing leaf senescence and/or pigment

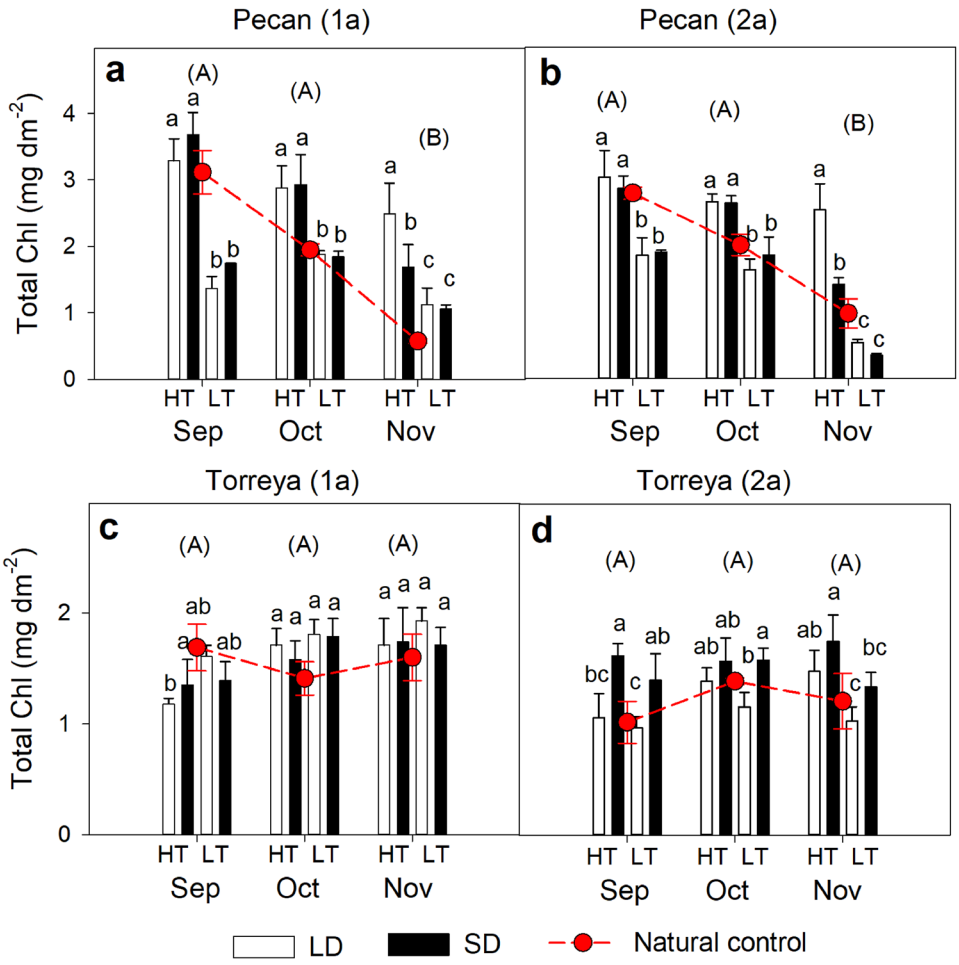

Fig. 3 Effects of temperature and photoperiod in autumn on the total chlorophyll content (Total Chl) in leaves of first-year ('1a') and second-year ('2a') seedlings of pecan (**a**, **b**) and torreya (**c**, **d**). From 15 August to 15 November, the seedlings were exposed to four factorial combinations of two levels of temperature and photoperiod: high temperature (HT, +35/+25 °C day/night), low temperature (LT, +25/+15 °C day/night), long day (LD, 13 h), and short day (SD, 10 h). Additionally, the experiment included control seedlings in natural conditions ('Natural control'). The measurements indicated on the horizontal axis were carried out on the 15th day of each of the 3 months. The bars with different lower-case letters indicate significant differences among the four treatments, and the groups of bars with different upper-case letters in parentheses indicate significant differences among the three measurement dates ($\alpha = 0.05$ in post-hoc one-way ANOVA combined with Tukey's HSD test)

degradation, sometimes caused a second flush, which was not observed at all under low-temperature treatments.

In emphasising the role of low air temperatures, our results differ from the earlier findings that in many temperate and boreal trees, photoperiod plays a greater role than air temperature in leaf senescence (Fracheboud et al. 2009; Liang 2019). This discrepancy may be explained by the differences between boreal and subtropical regions in the seasonality of day length. In the subtropical zone, contrary to the boreal zone, the change in photoperiod in autumn may be too small to provide a robust environmental cue about the progress of autumn (Jewaria et al. 2021). On the contrary, the subtropical autumn is generally long and warm, so that when leaf senescence depends on low temperatures, photosynthesis can continue regardless of the shortening days.

Our second hypothesis suggested an additional minor role for short photoperiod in causing leaf senescence and degradation of leaf pigments. Concerning pecan leaf senescence, the hypothesis received support for the second-year seedlings but not for the first-year seedlings. For the second-year seedlings, photoperiod interacted with the major factor, air temperature, so that SD further accelerated leaf senescence under LT but had no effect under HT, where no leaf senescence was seen (Fig. 2a). In fact, SD appeared to accelerate the degradation of leaf pigments in the first-year seedlings, too, but this occurred only in the last measurement, carried out in November after the seedlings had been exposed to three months of experimental treatments (Fig. 3a, b). In all, our results do not warrant any general conclusions on the potential effects of photoperiod on leaf senescence and chlorophyll degradation in pecan.

Overall, our results suggested a major role for low air temperature and a minor role—if any—for short photoperiod in the leaf senescence of the subtropical pecan. This is well in line with the meta-analysis of Gill et al. (2015), carried out with boreal and temperate trees. They concluded that at low latitudes leaf senescence in temperate trees is sensitive to temperature but at high latitudes to photoperiod.

Our results show a strong correlation between the chlorophyll content according to quantitative laboratory measurements and the stages of leaf senescence estimated by visual inspection and expressed as an ordinal scale variable (Fig. 4). This correlation is not surprising as such, but it

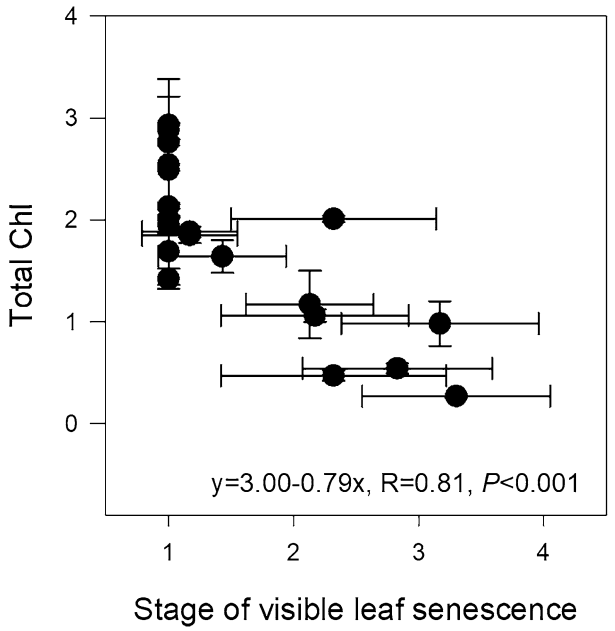

Fig. 4 Relationship between the total leaf chlorophyll content and the stage of visible leaf senescence in pooled data for first-year and second-year pecan seedlings sampled on 15 October and 15 November 2018 from all the five treatments included in the study. For details, see "Materials and methods" section

justifies the somewhat subjective method we used in the visual inspection of leaf senescence.

As expected for the evergreen torreya, no visible leaf senescence was observed. Furthermore, neither the natural nor the experimental conditions brought out any clear degradation of chlorophyll, either. One possible reason is that evergreen torreya leaves generally have a lifetime of three to five years, so that the first-year leaves tested in our study remained vigorous and the chlorophyll content did not degrade. Similar results were reported by Hu et al. (2018).

Quantitative dormancy induction

Recent research has shown that several subtropical trees (Du et al. 2019; Song et al. 2020; Pan et al. 2021), including torreya (Zhang et al. 2021a,b), evince endodormancy and a chilling requirement. For pecan, which has a wide geographical range in both the temperate and the subtropical zone in the USA, the existence of endodormancy and a chilling requirement has already been established earlier (Sparks 1993). Our results further confirm that both the subtropical species torreya and the subtropical provenance of pecan that we examined show endodormancy and a chilling requirement.

In support of our third hypothesis, we found that deeper bud dormancy was generally induced under high rather than low temperatures: in general, the BB% values were lower and the DBB values higher after dormancy induction under HT rather than LT. This is in line with several earlier findings reported for boreal and temperate trees (Westergaard and Eriksen 1997; Junttila et al. 2003; Heide 2003; Søgaard et al. 2008; Kalcsits et al. 2009).

Bud dormancy is classically subdivided into two physiologically distinct phases, i.e., endodormancy and ecodormancy (Lang et al. 1987). During endodormancy, bud burst is prevented (low BB%) or delayed (high DBB), even under growth-promoting conditions, by physiological factors within the bud (Cooke et al. 2012; Hänninen 2016). The main driving force of endodormancy release is long-term exposure to low chilling temperatures (Perry 1971; Sarvas 1974; Fuchigami et al. 1982; Baumgarten et al. 2021). Accordingly, if there is any difference in the depth of endodormancy between two dormancy-inducing treatments, then there should be a difference in BB% and/or DBB values between the two treatments with relatively short durations of chilling, but with prolonged chilling the difference should vanish and the curves representing the two dormancy-inducing conditions should converge. In our results, such an interaction was seen for BB% in both species (Fig. 5a, b; Table 3) and for DBB in torreya (Fig. 5d; Table 3). In all, then, these findings suggest that in both pecan and torreya, a greater depth of endodormancy was induced by HT rather than LT dormancy induction.

Ecodormancy denotes the condition where there is no physiological factor arresting bud burst and growth onset but the bud does not resume growth because of unfavourable environmental conditions, typically a low air temperature (Lang et al. 1987). Accordingly, the depth of ecodormancy is measured by the time or the forcing unit accumulation required for bud burst after the chilling requirement is met (Sarvas 1972, 1974; Hänninen 1990). That implies that if there is any difference in the depth of ecodormancy between two dormancy-inducing treatments, then there should be a difference in the DBB values, also with long durations of chilling after the levelling off of the DBB curve. Our results for DBB in torreya are in line with that prediction, but for a conclusive result, we would have needed treatments with even longer durations of chilling (Fig. 5d). Despite this uncertainty, the findings suggest that in torreya seedlings, high-temperature dormancy induction increases the depth of ecodormancy, too.

In comparison with the effects of temperature, the role of photoperiod in autumn in dormancy induction looked minor in the present study. Still, in the BB% values observed for torreya, photoperiod showed an interaction with air temperature in determining the depth of dormancy such that in dormancy induction under LT, deeper dormancy (lower BB%) was seen after the LD rather than SD treatment (Fig. 5a).

With the exception of the DBB values for torreya (Fig. 5d), the bud dormancy induced in the natural

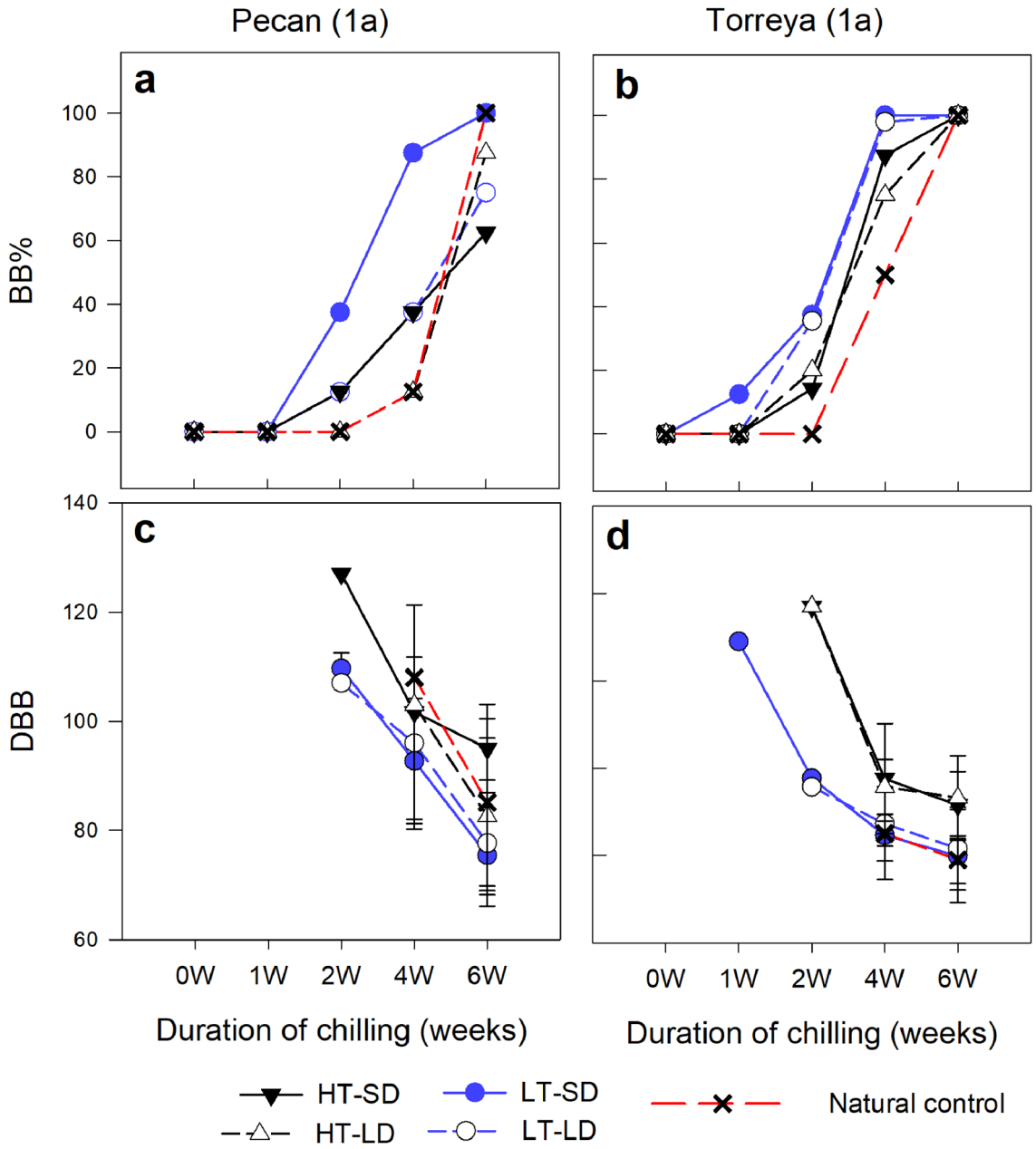

Fig. 5 Effects of temperature and photoperiod in autumn on the induction of bud dormancy in first-year seedlings of pecan (**a**, **c**) and torreya (**b**, **d**). From 15 August to 15 November, the seedlings were first exposed to dormancy induction under four factorial combinations of two levels of temperature and photoperiod: high temperature (HT, +35/+25 °C day/night), low temperature (LT, +25/+15 °C day/night), long day (LD, 13 h), and short day (SD, 10 h). Additionally, the experiment included control seedlings in natural conditions ('Natural control'). After the dormancy-induction period the seedlings were transferred to natural chilling conditions. After different durations of chilling (0, 1, 2, 4 and 6 weeks), indicated on the horizontal axis, the seedlings were transferred into a regrowth test under growth-promoting forcing conditions (20 °C, day length = 12 h). In the forcing conditions, the depth of dormancy was assessed from the values of the bud burst percentage (BB%) (**a**, **b**) and the days to bud burst (DBB, mean ± SE; **c**, **d**). Some of the overlapping data points have been moved slightly apart for better visibility

conditions was either similar to or deeper than the dormancy induced by the HT treatment in the experimental conditions (Fig. 5a–c). During the first half of the experiment, the air temperature fluctuation in the natural conditions was similar, in broad terms, to the fluctuation in the HT treatment, whereas during the second half, the air temperature fluctuation was more similar to that in the LT treatment; during the entire experiment, lower daily minimum air temperatures tended to occur in the natural rather than controlled conditions; see Supplementary Fig. S2). These findings suggest that the first half

Table 3 A statistical analysis of the effects of temperature and photoperiod on the depth of bud dormancy in first-year seedlings of pecan and torreya during dormancy induction

	BB%		DBB			
	Pecan	Torreya	Pecan		Torreya	
	P	*P*	*F*	*P*	*F*	*P*
Photoperiod (P)	0.213	0.648	3.99	0.054	0.04	0.841
Temperature (T)	**0.003**	**0.027**	3.24	0.081	**20.59**	**<0.001**
Chilling (C)	**<0.001**	**<0.001**	**18.35**	**<0.001**	**21.15**	**<0.001**
P * T	**0.006**	0.060	2.06	0.16	0.10	0.755
P *C	0.111	0.677	0.28	0.76	0.09	0.915
T * C	**0.013**	**0.027**	0.29	0.753	**6.61**	**0.003**
P * T * C	**0.014**	0.060	0.48	0.492	0.13	0.881

The depth of dormancy is quantified by bud burst percentage, BB%, and days to bud burst, DBB, obtained in a chilling-forcing experiment after the dormancy-inducing treatments. Chilling is included as a factor explaining the values of BB% and DBB because of its role as an endodormancy-releasing factor in the chilling-forcing experiment. The values of BB% were analysed by means of a logistic regression analysis with a binary response of factors and the DBB values by means of a three-way analysis of variance. For details, see "Materials and methods" section. The *P* values in bold indicate statistical significances with at least $P < 0.05$

of the three-month dormancy-inducing treatments affected the depth of dormancy more than the second half did. This is in line with the results of Søgaard et al. (2008), who found that in seedlings of *Picea abies*, extending the dormancy-inducing short-day treatment from 4 to 8 and 12 weeks hastened the subsequent bud burst, indicating that the depth of dormancy was reduced after the first four weeks of the treatment. Our hypothesis remains to be tested in further experimental studies, where the length of the dormancy-inducing treatments is controlled. In more general terms, too, our novel results on the depth of bud dormancy stand to be tested in further studies because of the limited data in our Experiment 2.

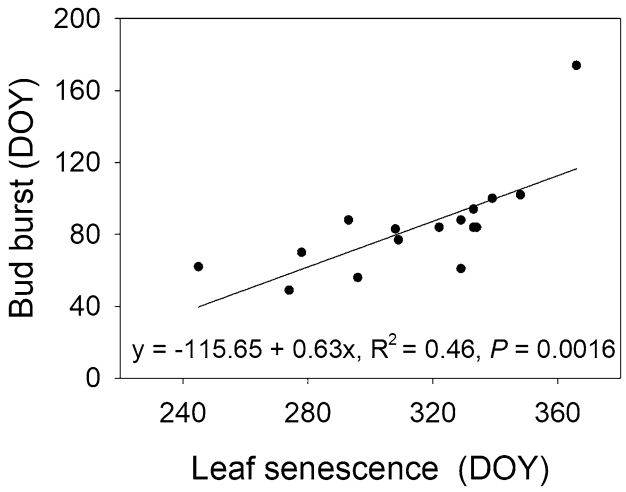

Fig. 6 Relationship between the DOYs (Day of Year) of autumn leaf senescence and the next spring's bud burst in adult pecan trees growing in natural conditions in the southern USA. The data were downloaded from the website of the USA National Phenology Network (http://www-dev.usanpn.org). For details, see "Materials and methods" section

Relationships among the developmental phenomena during the annual cycle

The deep bud dormancy induced by high autumn temperatures may delay bud burst in the next spring. Heide (2003) suggests this is a mechanism counteracting the earlier bud bursts under climatic warming. Such quantitative dormancy induction also provides a causal explanation for the apparent legacy effects of leaf senescence observed in natural conditions: late leaf senescence results in late bud burst the next spring (Delpierre et al. 2017; Marchand et al. 2020). Such a causal explanation is plausible if the high autumn temperatures cause both deeper dormancy and delayed leaf senescence. This was the case in the present study for pecan. On the basis of our experimental results concerning autumn events only, we can thus predict that such an apparent legacy effect will be seen in pecan under the subtropical conditions. The results from our test with observational data on adult pecan trees growing in the southern USA accorded with the prediction, thus providing support for expecting this causal chain of phenomena to occur in pecan: high autumn temperatures delay leaf senescence and deepen dormancy, and the latter results in delayed bud burst the next spring.

We found that high autumn temperatures not only deepened the bud dormancy but also promoted the second flush, especially in torreya. It would have been interesting to examine whether these two phenomena were related to each other, but our restricted results did not facilitate any testing of this hypothesis. Similarly, any potential role of carbon reserves in the spring leaf phenology (Bazot et al. 2013; Roxas et al. 2021) remains to be examined in future studies.

Conclusions

Our experiments provided a first-time evaluation of the effects of temperature and photoperiod on leaf senescence, leaf pigment degradation, and the depth of bud dormancy in subtropical trees. Our experiments were carried out with one native subtropical species, (torreya, *Torreya grandis*) and a subtropical provenance of an exotic subtropical-temperate species (pecan, *Carya illinoinensis*). Our experimental results suggest that chlorophyll degradation and leaf senescence in the deciduous species pecan is mainly caused by relatively low temperatures, but these temperatures are low only in the subtropical context (We used 15-25 °C as the low-temperature treatment). In the evergreen torreya, no clear chlorophyll degradation was seen in the autumn, either in natural or in experimental conditions. Our results also provided first-time evidence for quantitative dormancy induction in subtropical trees, meaning that high temperatures during dormancy induction increase the depth of dormancy. For torreya, our results suggest that in addition to endodormancy, the depth of ecodormancy is also increased by high temperatures during dormancy induction. Put together, our experimental findings on leaf senescence and the depth of dormancy in pecan predicted that the apparent legacy effect of leaf senescence on the timing of bud burst documented in field studies of temperate trees will also occur in the subtropical pecan. Our test results with observational data on bud burst and leaf senescence in adult pecan trees growing in the USA accorded with that prediction. Due to the limited experimental data in our study, further studies are needed to test our first-time results. Such studies will facilitate the development of process-based tree phenology models for subtropical trees, which can be used in climate change impact assessments in the future.

Author contribution statement RZ, JW and HH designed the study. FW and JL carried out the experiments. FW, JZ, and RZ analyzed the data. RZ and FW wrote the manuscript with inputs from HH and JW. All authors approved the final manuscript.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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