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Daylength helps temperate deciduous trees to leaf-out at the optimal time

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Abstract

Global warming has led to substantially earlier spring leaf-out in temperate-zone deciduous trees. The interactive effects of temperature and daylength underlying this warming response remain unclear. However, they need to be accurately represented by earth system models to improve projections of the carbon and energy balances of temperate forests and the associated feedbacks to the Earth's climate system. We studied the control of leaf-out by daylength and temperature using data from six tree species across 2,377 European phenological network (www.pep725.eu), each with at least 30 years of observations. We found that, in addition to and independent of the known effect of chilling, daylength correlates negatively with the heat requirement for leaf-out in all studied species. In warm springs when leaf-out is early, days are short and the heat requirement is higher than in an average spring, which mitigates the warming-induced advancement of leaf-out and protects the tree against precocious leaf-out and the associated risks of late frosts. In contrast, longer-than-average daylength (in cold springs when leaf-out is late) reduces the heat requirement for leaf-out, ensuring that trees do not leaf-out too late and miss out on large amounts of solar energy. These results provide the first large-scale empirical evidence of a widespread daylength effect on the temperature sensitivity of leaf-out phenology in temperate deciduous trees.

KEYWORDS
climate change, daylength, deciduous trees, spring phenology, temperature response

1 | INTRODUCTION

The timing of leaf-out co-determines the growth, reproductive success and competitiveness of temperate deciduous trees and thus strongly affects their fitness and distribution (Chuine, 2010). Global warming has led to substantially earlier spring leaf-out (Menzel et al., 2006; Parmesan & Yohe, 2003; Peñuelas & Filella, 2001), although this advance is declining (Fu et al., 2015). These changes in spring phenology may influence terrestrial ecosystem fluxes of carbon, water, nutrient and energy in the short term (Keenan et al., 2014; Myneni, Keeling, Tucker, Asrar, & Nemani, 1997; Piao et al., 2017). Mechanistic understanding of the leaf-out process is, however, far from complete (Chuine, Morin, & Bugmann, 2010; Flynn & Wolkovich, 2018; Körner & Basler, 2010; Laube et al., 2014; Zohner, Benito, Svenning, & Renner, 2016), which challenges the projected impacts of climate change on ecosystems by dynamic global vegetation models (Richardson et al., 2012). A better understanding of the ecophysiological processes controlling leaf-out phenology is thus essential for improving our understanding of the responses of ecosystems to the ongoing climate change and the subsequent feedbacks to the climate system, as well as explaining the slow-down of the warming-induced advance in leaf-out.

A species' optimal leaf-out date results from natural selection that optimizes the species' fitness under given environmental conditions, such as avoiding freezing damage (Lenz, Hoch, Körner, & Vitasse, 2016), ensuring flowering synchrony among species (Elzinga et al., 2007; Zohner, Mo, & Renner, 2018) and maximizing the length of the remaining season for light and nutrient resources (competition with other trees) as well as for tissue maturation (Körner et al., 2016). In temperate and boreal regions, temperature, including both cold winter temperatures (chilling requirement) and warm spring temperatures (heat requirement), and daylength interact to realize leaf-out around the optimal date (Flynn & Wolkovich, 2018; Körner & Basler, 2010). Chilling accumulates over autumn and winter, and when the accumulated chilling exceeds the chilling requirement, endodormancy (the first stage of dormancy; Lang, 1987) is broken and buds enter the second dormancy stage: ecodormancy (Chuine & Régnière, 2017; Hänninen, 2016). During ecodormancy, meristem cells begin to grow, a process that is accelerated by warm temperatures and a gradually increasing daylength (Hänninen, 2016). Inter-annual variation of these three environmental drivers is strongly correlated (e.g. a warm winter reduces chilling and increases heat supply, and the earlier leaf-out associates with short daylength). As a result, the direct effect of daylength on spring phenology and its eventual interactions with chilling and the heat requirement remain unclear and highly debated (Chuine et al., 2010; Flynn & Wolkovich, 2018; Körner & Basler, 2010; Laube et al., 2014; Zohner et al., 2016). In this study, based on a large set of in situ phenology observations across Europe (www.pep725.eu), we propose a framework to unravel the effect of daylength on leaf-out phenology of temperate-zone deciduous trees and test the hypothesis that daylength affects the leaf-out process by altering the heat requirement at any given chilling accumulation.

We start by assuming that trees are characterized by an optimal, climate-dependent, daylength (Figure 1). Occasional late frost events give a competitive disadvantage to individuals that leaf-out earlier than the species' optimal daylength, whereas reduced light harvesting gives a competitive disadvantage to individuals that leaf-out later than the optimum period. As such, an optimal date of leaf-out exists for a given species, determined by a trade-off between maximizing annual carbon and nutrient uptake to ensure competitive advantage by lengthening the duration of the ground cover period (earlier leaf-out is preferred) and reducing the risk of late frost damage after leaf-out (later leaf-out gives more security and is thus preferred) (Allstadt et al., 2015; Liu et al., 2018) (Figure 1a). In the long term, carbon assimilation and competitiveness are determined by the lowest of these two cost functions, and the optimal leaf-out date occurs where the minimum cost yields the highest carbon assimilation and competitiveness. Experimental studies have revealed a nonlinear relation between accumulated chilling and the heat required for leaves to flush (typically quantified as growing degree day [GDD] units) (Figure 1b). Daylength is hypothesized to act as a cue controlling the sensitivity of meristem cell growth to warm temperatures, thereby altering the apparent relationship between chilling and GDD requirement. Their nonlinear relation becomes steeper when days are shorter than optimal (short daylength, Figure 1c) and less steep when days are longer than optimal (long daylength, Figure 1d).

Two substantially different impacts of suboptimal daylength on leaf-out date are thus theoretically possible: (a) Shorter than optimal daylength reduces the temperature sensitivity (increases the GDD requirement), thereby avoiding precocious leaf-out that would increase the risk of frost damage (i.e. the short daylength effect, Figure 1c). (b) Longer than optimal daylength increases the temperature sensitivity (reduces the GDD requirement), effectively avoiding belated leaf-out at a time when solar radiation is high and thus ideal for photosynthesis (i.e. the long daylength effect, Figure 1d).

These two postulated consequences of daylength impacts have not been strongly supported by empirical evidence. The short daylength effect in early spring, to our knowledge, has not yet been empirically documented, whereas the long daylength effect in late spring has been experimentally evidenced in earlier studies, albeit only on cut twigs or saplings (Flynn & Wolkovich, 2018; Körner & Basler, 2010; Laube et al., 2014; Malyshev, Henry, Bolte, Khan, & Kreyling, 2018) and not yet on mature trees. We therefore set out to determine the consequences of both a short and a long daylength on spring leaf-out of mature trees of temperate deciduous tree species, to assess how widespread these two effects are across these species, to quantify the sensitivities of the GDD requirement to suboptimal and supra-optimal daylength and, finally, to determine the relative importance of chilling and daylength as controls of the leaf-out process.
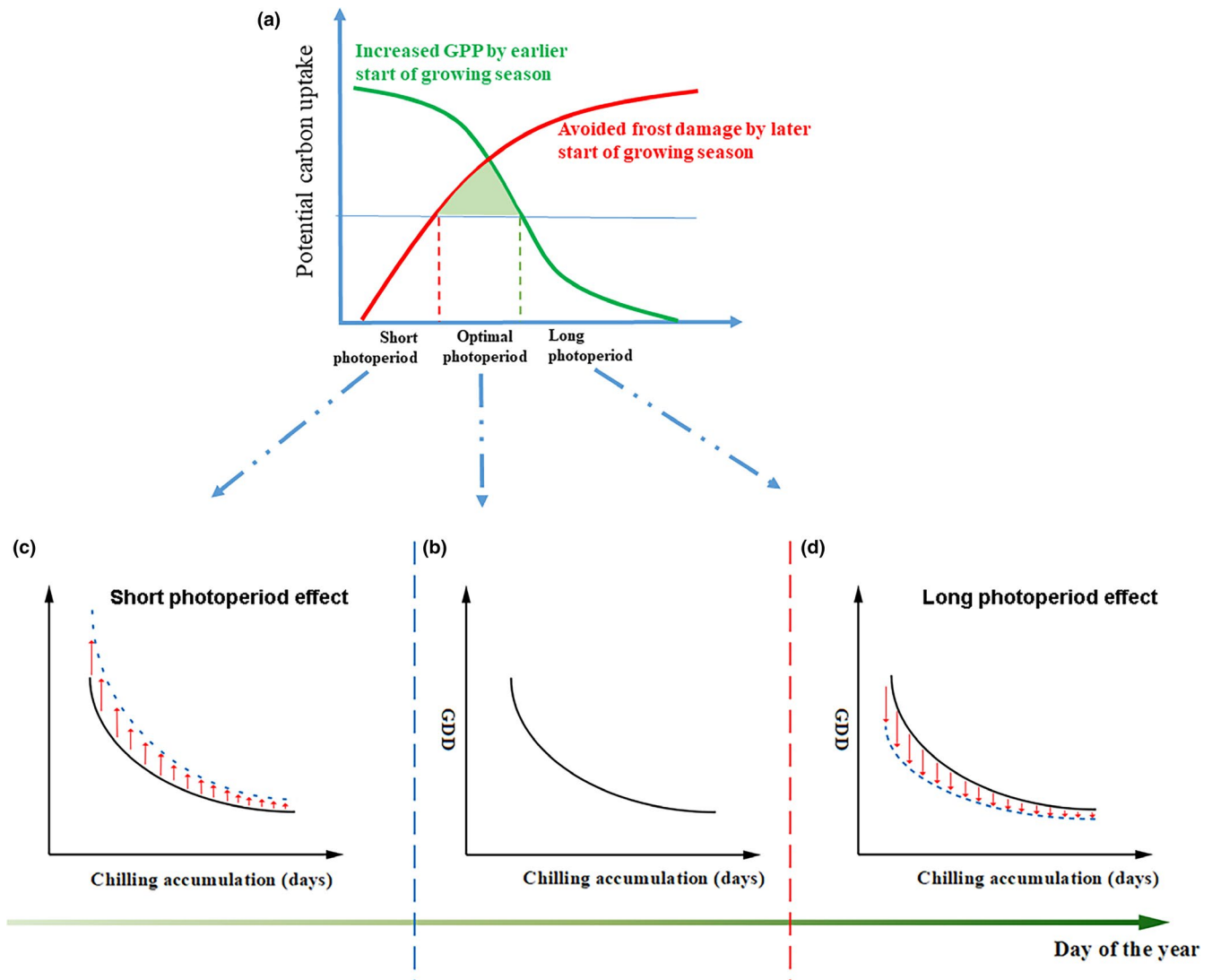
FIGURE 1 Conceptual scheme of daylength effect on the leaf-out process. (a) Conceptual scheme depicting why an optimal daylength for tree leaf-out exists within which the competitiveness of a species is maximized and how this is realized. Tree competitiveness is increased by earlier start of the growing season, which maximizes annual carbon and nutrient uptake and reduces that of the neighbours, but is subject to a trade-off with avoiding the risk of late frost-induced damage for which a later start of growing season is preferred. The green filled area represents the leaf-out period that ensures the most secure, high competitiveness and carbon uptake. This study provides evidence that the spring leaf-out process requires less warm temperatures (lower heat requirement; growing degree day [GDD]), and thus becomes more temperature responsive, as daylength increases. As such, daylength aids in constraining leaf-out within the optimal period in both cold and warm springs. (b) In very warm springs, when leaf-out is early, trees minimize the advance of leaf-out because their temperature sensitivity is low under short daylength. This is reflected in an increased GDD requirement and results in trees being protected against late frost events, that is, the 'short daylength effect'. (c) Under optimal daylength, the GDD required for leaf-out is mainly determined by the chilling accumulated during endodormancy. (d) In very cold springs, when leaf-out is late, trees minimize the delay of leaf-out because their temperature sensitivity becomes greater under increasing daylength. This high temperature sensitivity is reflected in the reduced GDD requirement, and protects trees against leafing-out too late, that is, the 'long daylength effect'

2 | MATERIALS AND METHODS

We tested the daylength effect on mature trees using data from 2,377 sites of the European phenological network (http://www.pep725.eu/) (Templ et al., 2018). The date of leaf-out had been recorded at each site for at least 30 years between 1950 and 2016, but in most cases, observations were available for many more years. Six deciduous tree species were selected (for which sufficient observational data were available): *Fagus sylvatica* (beech), *Aesculus hippocastanum* (horse

chestnut), *Betula pendula* (birch), *Fraxinus excelsior* (ash), *Quercus robur* (oak) and *Tilia cordata* (lime). In total, 509,284 individual observations from 12,348 site–species combinations at 2,377 sites were used. The sites mainly occurred in moderate climates in Central Europe (Figures S1 and S2). The leaf-out dates were defined based on the BBCH code (Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie, BBCH = 11, first visible leaf stalk) (Templ et al., 2018). We first determined the preseason length for each species at each site as the period before leaf-out for which the partial correlation coefficient

between leaf-out and air temperature was highest (Fu et al., 2015). Using this optimal preseason, we then calculated the GDD requirement for each species at each site and in each year. We defined the GDD requirement as an integration of daily mean temperature (T_t) above a temperature threshold (T_{th}) throughout the preseason with the mean leaf-out dates as the end:

$$GDD = T_t - T_{th}, \quad if \quad T_t > T_{th} \tag{1}$$

where T_{th} is the threshold temperature for GDD accumulation and T_t is the mean daily temperature. We used a threshold T_{th} of 5°C. We also tested a temperature threshold of 0°C, which produced very similar results. To best the robustness of the results, we further calculated the GDD from 1 December to the date of leaf-out for each species at each site, and found very similar results (Figure S3). We therefore only report results using the threshold of 5°C and the preseason.

Chilling occurs at low, yet non-freezing temperatures and the number of days with mean temperature between 0 and 5°C was suggested as a good proxy for chilling accumulation, although inter-species variation in the chilling efficiency of different temperatures is probably high. Chilling requirement is a physiological parameter that corresponds to the amount of chilling needed to break endodormancy and enter ecodormancy. In the present study, chilling was calculated as the number of days (CD) when daily temperature was between 0°C and 5°C from 1 September in the previous year until the day of leaf-out (DL). We tested another approach, using 0°C and 10°C as temperature thresholds counting all days with mean temperatures between these thresholds, which produced very similar results. Similar results were also obtained when below-freezing temperatures were included, calculating as the number of days when daily temperature below 5°C (Figure S4) or 7°C (Figure S5). We therefore only report the results based on the chilling accumulation using the 0–5°C temperature range.

Daylength at the DL was calculated as a function of latitude and day of the year (DOY):

$$DL = 24 - \frac{24}{\pi} \cos^{-1} \left[\frac{\sin \frac{0.8333\pi}{180} + \sin \frac{L\pi}{180} \sin \varphi}{\cos \frac{L\pi}{180} \times \cos \varphi} \right] \tag{2}$$

$$\varphi = \sin^{-1} (0.29795 \times \cos \theta) \tag{3}$$

$$\theta = 0.2163108 + 2 \times \tan^{-1} \tag{4}$$
$$(0.9671396 \times \tan (0.0086 \times (DOY - 186)))$$

where L is the latitude of the phenological site.

The daily mean air temperature at each site was derived from a gridded climatic data set of daily mean temperature at 0.25° spatial resolution (approximately 25 km, ERA-WATCH) (Fu et al., 2014).

3 | THE SENSITIVITY OF GDD REQUIREMENT TO CHILLING AND DAYLENGTH

We calculated cumulative chilling, the GDD requirement and daylength at the DL for each year at each site. For each individual

tree, we divided the data into four subsets according to chilling accumulation, that is, case 1: lowest chilling accumulation: CD < CDmean − 1 standard deviation of CD (CDsd); case 2: low chilling accumulation: CDmean − CDsd < CD < CDmean; case 3: high chilling accumulation: CDmean < CD < CDmean + CDsd; and case 4: highest chilling accumulation: CD > CDmean + CDsd. Within each CD subset, we subsequently calculated the GDD requirement for three daylength conditions, that is, leaf-out under short-daylength conditions (DL < DLmean − 0.75 DLsd), under long-daylength conditions (DL > DLmean + 0.75 DLsd) and under average-daylength conditions (DLmean − 0.5 DLsd < DL < DLmean + 0.5 DLsd). The differences in mean GDD requirement for leaf-out among the DL groups were tested using independent t tests for each chilling case and each species. Furthermore, we calculated the daylength sensitivity of GDD as the slope of the linear regression between GDD and DL, and then the average of the four daylength sensitivities was determined for each species at each site. Using a similar methodology, we divided the data into four subsets according to DL for each individual tree, that is, case 1: shortest daylength: DL < DLmean − DLsd; case 2: short daylength: DLmean − DLsd < DL < DLmean; case 3: long daylength: DLmean < DL < DLmean + DLsd; and case 4: longest daylength: DL > DLmean + DLsd. We then calculated the chilling sensitivity of GDD for each species at each site. To compare the relative importance of chilling versus that of daylength as determinants of the GDD requirement for leaf-out, we first normalized the daylength and chilling sensitivity, respectively, using a min–max normalization for each species:

$$Si = \frac{(Si - Smin)}{(Smax - Smin)} \tag{5}$$

where Si is the daylength or chilling sensitivity at site i, $Smin$ and $Smax$ are the minimum and maximum observed values of the daylength or chilling sensitivity across all trees of that species. The mean and standard deviation of all normalized sensitivities were then calculated for each species. Histograms were used to show the distribution of sensitivities across all trees for each species.

4 | RESULTS AND DISCUSSION

In agreement with a multitude of previous studies (Cannell & Smith, 1983; Fu et al., 2016; Laube et al., 2014), we found that all studied tree species showed lower GDD requirement under higher chilling conditions (Figure 2 and Table S1). Interestingly, we also observed that in all six species and within each CD group, the GDD requirement for leaf-out was statistically significantly higher under short- than average-daylength conditions, and significantly lower under long- than average-daylength conditions (using paired t test, $p < 0.001$, Figure 2, and Figure S6 and Table S2 as an example at high chilling accumulation).

Contrasting results of the photoperiod effect were reported in experimental studies (Heide, 1993; Laube et al., 2014). However,
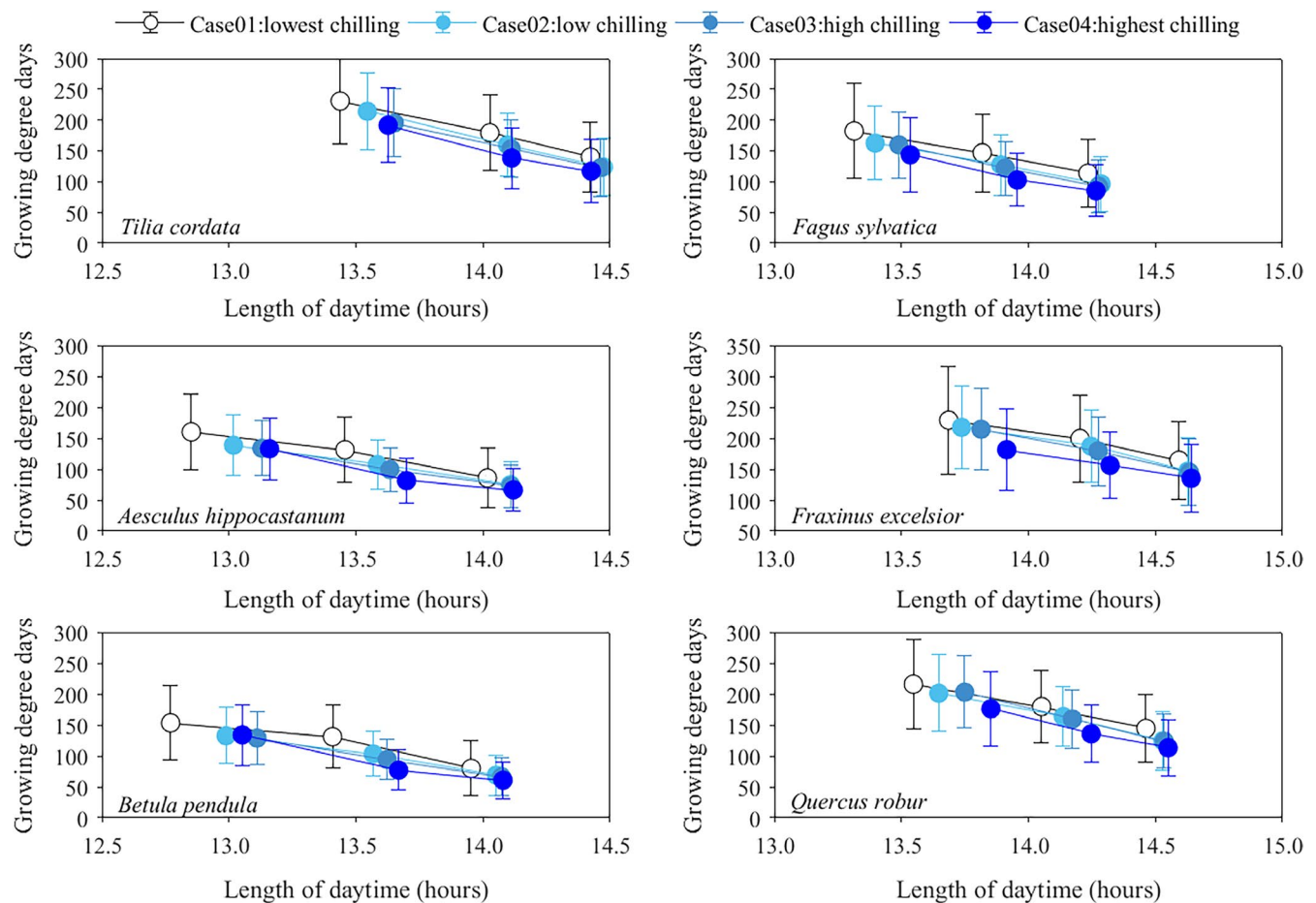
FIGURE 2 Dependence of growing degree day requirement of leaf-out on daylength under constant chilling conditions for six tree species. Dependencies are shown for four different chilling intensities (see Materials and Methods)

almost all of these studies are based on cuttings or saplings in manipulative experiments, and using constant daylength rather than natural continuous changes in daylength (e.g. Laube et al., 2014; Zohner et al., 2016, but see Fu et al., 2019), and young trees often behave opportunistically and exhibit earlier leaf-out than mature trees of the same species. Using trees of different ontogenetic stages might thus explain part of the differences among previous studies. In the present study, we selected six species that belong to five families (Fagaceae, Betulaceae, Malaceae, Sapindaceae, Oleaceae), some of which are phylogenetically quite distinct (Figure S7). Because every tested species (all six species for which sufficient observations were available) exhibited very similar daylength responses, we postulate the widespread existence of a daylength effect among temperate-zone deciduous tree species, at least among European temperate-zone tree species. In line with our findings, a recent study found consistent daylength effects on leaf-out phenology exists across 28 woody species in a North American temperate forest (Flynn & Wolkovich, 2018).

For each individual tree, we calculated the sensitivity of the GDD requirement for leaf-out to changes in daylength. On average, across all species and averaged over four different chilling intensities, compared to the GDD requirement under average daylength conditions,

each 1-hr decrease in daylength (comparable to the observed inter-annual range) increased GDD by 37°C-days, that is, by 26% (Figure S8a and b), while a 1-hr increase in daylength decreased the GDD requirement by 31°C-days, that is, by 22% (Figures S8a and b). We further compared the relative sensitivity of the GDD requirement for leaf-out to chilling and daylength (comparing the GDD response to 1 *SD* of the observed variation in either chilling or daylength), and observed species-specific sensitivity differences among the six study species (Figure 3).

In detail, sensitivity to daylength was larger than the sensitivity to chilling in four out of six species: *Betula pendula*, *A. hippocastanum*, *T. cordata* and *F. excelsior*, whereas no difference was detected in *Q. robur*. *Fagus sylvatica* also exhibited a pronounced sensitivity to daylength, but its sensitivity to chilling was even greater (Figure 3). *Fagus sylvatica* is indeed known as a highly chilling-sensitive species (Kramer, 1994; Malyshev et al., 2018). Our findings thus confirm that daylength is an important co-regulator of leaf-out in mature temperate deciduous trees (Flynn & Wolkovich, 2018; Körner & Basler, 2010), and further suggest that daylength likely affects the leaf-out process indirectly by altering the nonlinear relationship between chilling and GDD requirement. These results also support the hypothesis that the shorter daylength due to earlier leaf-out in spring
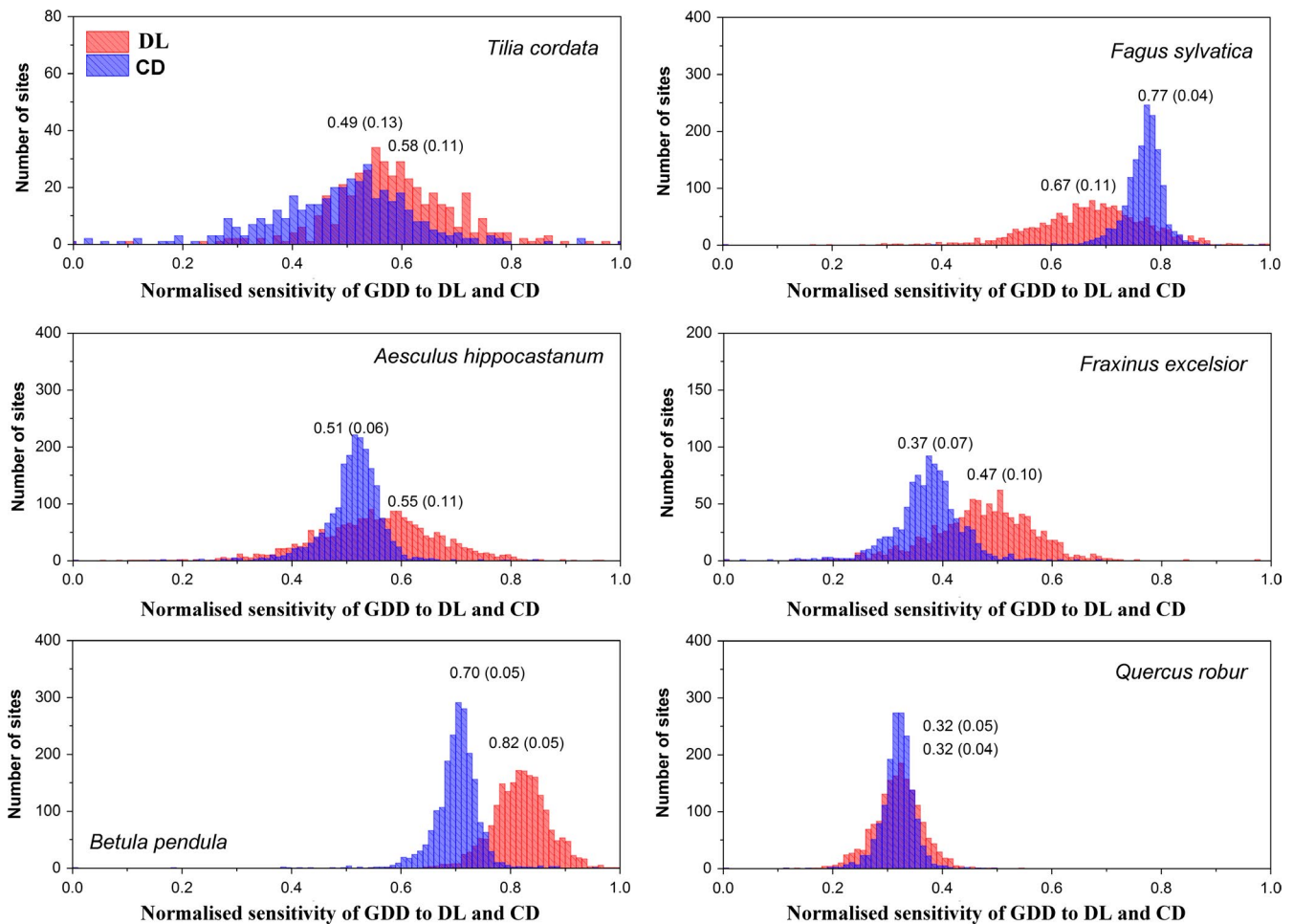
FIGURE 3 Histograms of the growing degree day (GDD) sensitivity to changes in daylength (DL, in red) and in chilling (CD, in blue) across all individual trees of six deciduous tree species. Sensitivity was calculated as the change in GDD per 1 *SD* in the observed DL and CD, respectively, and is therefore coined 'normalized sensitivity'. Mean sensitivities and standard deviations (in brackets) are provided

contributes to the declining apparent temperature sensitivity of leaf-out in European temperate deciduous trees (Fu et al., 2015). These mechanisms are conceptualized in Figure 4. With climate warming, the GDD requirement increases due to reduced chilling, but GDD supply increases to a great extent (Figure 4, panel a). As a result, GDD supply equals GDD requirement earlier in the year (visualized as an excess GDD supply in Figure 4, panel a), which drives earlier leaf-out. The associated shorter daylength, however, further increases the GDD requirement and thereby restricts the advance of leaf-out (Figure 4, panel b) and reduces the temperature sensitivity of leaf-out with climate warming.

Daylength thus acts as an environmental cue, counteracting the advancing impact of global warming, and helping trees to leaf-out close to their optimal date. As daylength increases from early to late spring, we observed that the GDD requirement also decreases under similar chilling conditions. Similar responses, supporting our findings, were previously reported in experimental studies using cuttings, although the daylength difference among treatments was very large (Zohner et al., 2016). Other studies also reported a decreased photoperiod effect with increasing chilling accumulation (Hänninen,

2016; Laube et al., 2014), which may be because the increasing chilling ensures leaf-out at the optimal daylength, when the photoperiod effect is minimal. We observed that the GDD requirement decreases consistently from very short to very long daylength, suggesting that one single physiological mechanism may suffice to explain the protective effect of daylength against both early and late leaf-out. We speculate that daylength directly impacts on the temperature sensitivity of cell development. By keeping the calculation of GDD constant with daylength, the increase in temperature sensitivity with increasing daylength is mathematically translated into a reduced GDD requirement. However, we acknowledge that the heat signal required by the meristems to initiate leaf-out may not be directly altered by daylength, but that the heat signal reception may become more efficient with increasing daylength. Our data, unfortunately, do not allow unravelling the underlying physiological mechanism.

We further speculate that the daylength control over the GDD requirement depends on the start date of the ecodormancy phase relative to the date when optimal daylength thresholds are reached or passed. When ecodormancy begins late relative to the optimum daylength thresholds, the temperature sensitivity of cell
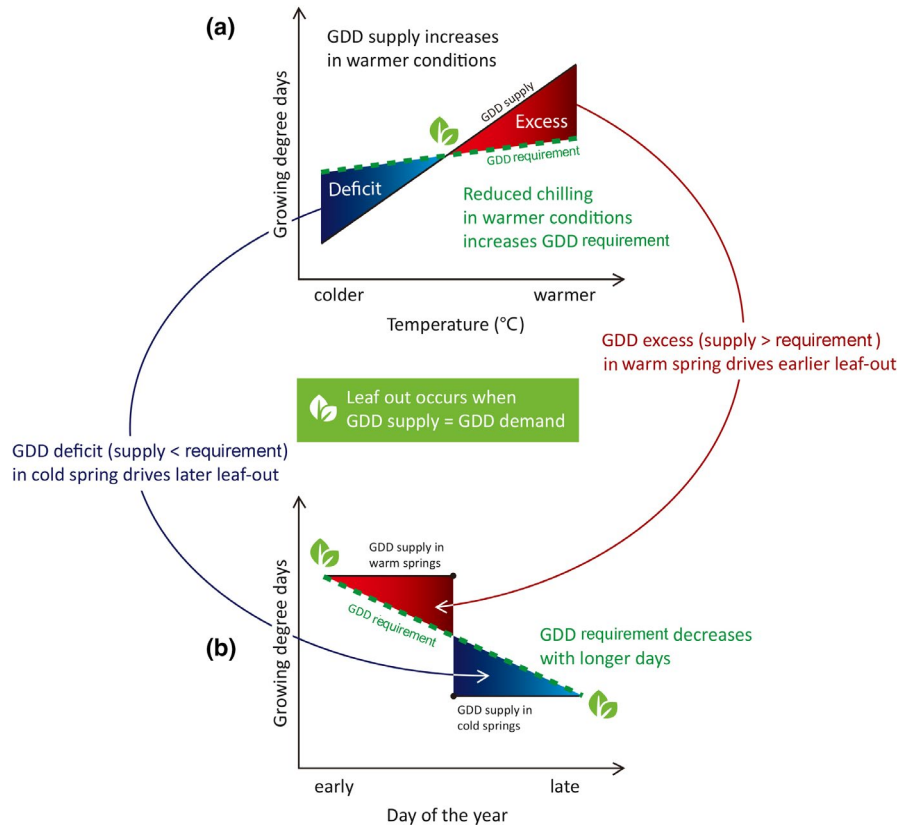
FIGURE 4 Conceptual scheme summarizing how daylength helps deciduous trees to leaf-out within or close to the optimal period. (a) Leaf-out occurs when the supply of warm temperatures (growing degree day [GDD] supply: accumulated daily GDD; black line) equals the GDD requirement (physiological parameter to trigger leaf-out). Note that the X axes indicate the climate from cold to warm spring. The more chilling is accumulated, the lower the GDD requirement (green dashed line; for simplicity reasons we here assume a linear relation). In cold springs, the deficit in GDD supply drives a delay in leaf-out date (blue areas in panels a and b). (b) The associated increasing daylength, however, increases the temperature sensitivity and thereby causes a decline in the GDD requirement, with leaf-out occurring when GDD supply equals the declining GDD requirement. In contrast, in warm springs (red areas in panels a and b), GDD supply typically exceeds the chilling-induced GDD requirement earlier in the year, but the short daylength earlier in spring induces a low temperature sensitivity and thereby an increased GDD requirement, which minimizes the warming-induced advance of leaf-out. Note that the X axes indicate the leaf-out timing from early to late

development is elevated, resulting in reduced GDD requirement to force leaf-out. In contrast, when ecodormancy starts earlier than the target daylength threshold, the temperature sensitivity of cell development may remain low, but not zero, until the date when the optimal daylength threshold is passed. The starting date of eco-dormancy, however, cannot easily be determined empirically and is therefore typically ignored in phenology studies, explaining why the relation between daylength and the start of ecodormancy remains poorly understood (Chuine et al., 2016), despite their importance for pushing the field beyond the state of the art (Hänninen, 2016). To our knowledge, neither the start date of ecodormancy, that is, the start date of GDD accumulation, nor the optimal daylength thresholds have been well studied. As long as dormancy remains poorly understood, the estimations of chilling and forcing units also remain uncertain. For example, the duration of the chilling accumulation period and the start date of the heat accumulation period, as well as their interactions are still unclear. Similarly, the optimal temperature ranges for chilling accumulation and the temperature threshold

above which GDDs start to accumulate, as well as the length of GDD accumulation are poorly understood. Different assumptions can, however, lead to contrasting and sometimes illogical results. For example, an increased GDD requirement is obtained when leaf-out is very late and the GDD is calculated over a fixed number of days prior to leaf-out (see Figure S9). Studies focusing on ecophysiological experiments are thus urgently needed to fully understand spring phenology and enable the development of reliable phenology models (Chuine & Régnière, 2017; Hänninen et al., 2019).

Climate warming–induced spring phenology advances substantially alter regional and global biogeochemical cycles and climate systems (Forzieri, Alkama, Miralles, & Cescatti, 2017; Myneni et al., 1997; Peñuelas & Filella, 2009). However, as the daylength effect reduces the temperature sensitivity of leaf-out in warmer years, slowing down the advancing rate of leaf-out, it thereby also reduces the warming-induced extension of ground cover, and carbon uptake, evapotranspiration and albedo. This study found that all investigated temperate-zone deciduous tree species (the six species for which

sufficient observational data were available) use daylength as a signal to help ensure that leaf-out occurs close to a species-dependent optimal time of the year, by increasing the GDD requirement for leaf-out when daylength is too short, and reducing the GDD requirement as daylength becomes too long.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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