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Research paper

Impact of summer defoliation and winter–spring warming on pre-spring carbon availability and spring phenology in sessile oak and Scots pine saplings

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Seasonal climate warming affects temperate plant phenology differently. Early winter warming can delay dormancy release and budburst due to insufficient chilling, while late winter or spring warming advances budburst. Additionally, the influence of pre-spring non-structural carbohydrate (NSC) availability on leaf phenology remains poorly understood. We explored the effects of previous late-summer defoliation and winter–spring warming on NSC dynamics and spring leaf phenology in two species: deciduous sessile oak with low chilling sensitivity and evergreen Scots pine with intermediate chilling sensitivity. We observed species-specific responses of leaf phenology to warming and defoliation. Winter warming delayed leaf unfolding in pine but not in oak, likely reflecting the greater chilling requirement of the pine. Defoliation significantly reduced pre-spring NSC levels in twigs and roots of both species, and led to earlier needle emergence in pine, with no impact on oak's leaf out date. Our findings indicate a dual dependency of pine leaf unfolding on temperature and internal carbon reserves, suggesting that defoliation, e.g. through herbivory or diseases, affects the following year's spring phenology and leaf growth in evergreen species but not in deciduous trees. These findings are important for understanding the adaptive strategies of different plant functional types under uneven warming conditions.

Keywords: asymmetric warming, chilling, forcing, leaf removal, non-structural carbohydrates, spring leaf phenology.

Introduction

Since the beginning of the industrial revolution, the Earth's average temperature has risen by 1.1 °C due to anthropogenic greenhouse gas emissions (IPCC 2021), and this warming trend has accelerated considerably since the 1950s (Steffen et al. 2015). As temperature is the primary factor controlling plant phenological timing in temperate and boreal regions, numerous phenological shifts have been observed worldwide in relation to global warming in the last decades (Blume-Werry 2022, Vitasse et al. 2022, Marqués et al. 2023). Overall, global warming has resulted in an extension of the growing season due to earlier spring leaf out and, to a lesser extent, later autumn senescence (Wang et al. 2019, Chen et al. 2022, Marqués et al. 2023, Yin et al. 2023). Shifts in timing of spring leaf out directly influence photosynthesis, evapotranspiration rates and carbon cycles. Conversely, plant carbon reserves stored over winter may also affect spring phenology and development early in the season (Blumstein et al. 2024). Plant phenological shifts have major impacts on biogeochemical cycles, productivity, ecosystem functioning and services (Blume-Werry 2022, Shen et al. 2022). It is therefore essential to improve our predictions of future phenological changes in order to anticipate climate feedbacks and better understand how terrestrial ecosystems will be modified by warming.

Most studies focus on the relationship between plant phenology and mean temperature in the months preceding the

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studied phenological event, typically by statistically determining the most correlated period. However, the temperature preceding the start of the growing season can impact spring phenology in different ways depending on the dormancy status and freezing resistance of the buds (Baumgarten et al. 2021, Kovaleski 2022). Exposure to chilling temperatures below ∼10 °C is necessary at the beginning of winter to increase the ability of the buds to respond to warmer temperatures, hereafter referred to as 'forcing temperatures' (Signarbieux et al. 2017, Wenden et al. 2020, Yang et al. 2020, Carteni et al. 2023). Spring phenology is therefore driven by the exposure to chilling and forcing temperatures during winter and early spring. For instance, a climate chamber experiment using cuttings of 28 North American woody species showed that spring warming of 5 °C advanced the average timing of budburst and leaf out by 10 and 19.1 days, respectively (Flynn and Wolkovich 2018). Similarly, green up appeared up to 30 days later than usual in 1983 and 1996 due to abnormal cold spring temperatures derived from satellites data (Liu and Zhang 2020). The impact of temperature depends on the dormancy stage, and a decrease in winter chilling temperatures can slow down spring phenology due to later dormancy release and higher forcing requirements (Cannell and Smith 1983, Murray et al. 1989, Fu et al. 2015). Therefore, a cold spring following a warm winter may drastically delay leaf out due to both inadequate fulfillment of winter chilling and slow accumulation of forcing temperatures. In an experiment where saplings of common European tree species were warmed during October in northeast Germany, leaf unfolding was delayed by, on average, 2.4 days per degree warming (Beil et al. 2021). Similarly, warmer winters from September to December significantly delayed budburst and flowering by 0.9 to 5.6 days per °C in common species including *Betula pendula, Fraxinus excelsior* and *Larix decidua* along elevational gradients in the Alps (Asse et al. 2018). In contrast, some studies reported that warmer winter temperatures advanced spring phenology in herbaceous plants and trees. For instance, one-degree warming of maximum and minimum temperature between December and February advanced the flowering phenology of *Sternbergia vernalis* by 11.8 days and 27.8 days, respectively (Hassan et al. 2021). European beech budburst showed an advancement of 8.8 days per degree of winter and spring warming in an elevational transplanting experiment, whereas one-degree cooling resulted in a delay of 11 days (Signarbieux et al. 2017). These inconsistent results imply that warmer winters should advance the phenology of species with low chilling requirements but not in species with high chilling demands.

Global change has led to uneven warming changes across different seasons and scales (Roach et al. 2023). For instance, in central Europe, climate warming is not happening uniformly throughout the year, with warming in December–January (+0.4 °C per decade) being more pronounced than that in March–April (+0.35 °C per decade) (Renner and Zohner 2018). In northern North America, the warming trend in winter from 1952 to 2011 was most pronounced, with temperatures increasing by more than 0.4 °C per decade. Conversely, spring temperatures showed a cooling trend, decreasing by 0.1 °C per decade (J.M.Wang et al. 2021). In east Asia, the rate of winter (February–March) warming was 1.1–1.5 °C per decade, while spring (April–May) temperature increased by only 0.1–0.4 °C per decade from 1982 to 2000 (Jeong et al. 2009). Moreover, warming rates are typically higher at high elevations, high latitudes and in continental regions compared with low elevation, low latitude and oceanic areas (Bjerke et al. 2011, Z.Wang et al. 2021). However, how spring leaf phenology responds to uneven winter–spring warming remains poorly understood.

Global environmental change and climate warming would influence plant carbon availability through influencing carbon gain capacity (e.g. photosynthesis, herbivory outbreak), utilization and their balance (Li et al. 2002, 2013, Yang et al. 2021, 2022), which in turn could potentially influence spring leaf phenology (Lapointe 1998, Kwit et al. 2010, Heberling et al. 2019, Lee and Ibáñez 2021). During winter, carbon for plant survival and spring growth initiation is stored in different organs in the form of non-structural carbohydrates (NSCs)—mainly soluble sugars and starch (Li et al. 2002). Soluble sugars serve as readily available energy sources for immediate use in growth and metabolism, while starch acts as a carbon reserve for later use during stress recovery and subsequent growth (Li et al. 2002). The relationship between NSC availability and leaf bud growth might differ between conifers and deciduous species due to their difference in leaf habit. Unlike deciduous trees which lose their leaves in winter, conifers retain their foliage year-round, allowing for continuous photosynthesis and carbon absorption also during winter when the environment condition is suitable. Therefore, coniferous trees can utilize NSC stored both in needles and wood tissues (e.g. stem wood and roots) to initiate bud break in spring. On the other hand, however, deciduous trees rely on the winter NSC storage in wood tissues to support bud development during leaf emergence (Blumstein et al. 2024).

Regardless of whether the trees are evergreen or deciduous, severe defoliation in the previous year may lead to NSC depletion and result in similarly low levels of NSC storage during winter, potentially affecting spring leaf phenology in a similar manner. Deslauriers et al. (2019) found that previous-year removal of 80–95% leaves reduced tissue NSC levels, however, advanced budburst by 6–7 days in both black spruce and balsam fir and by 3.5 days in white spruce. Some temperate deciduous species, such as European beech (*Fagus sylvatica*), have shown the ability to survive complete defoliation by mobilizing several-year-old carbon reserves, followed by rapid recovery of NSC levels after leaf regrowth (D'Andrea et al. 2019). A strong coordination between NSC levels and phenological events acts as a potential molecular clock that signals the timing of leaf development in red oak (*Quercus rubra*) (Blumstein et al. 2024). A reduction in NSC levels could delay phenological events, such as leaf out, by disrupting this signaling mechanism and slowing the progression of developmental stages. To better understand the interactive effects of uneven winter–spring warming and NSC availability on winter chilling and spring forcing, and thus on spring leaf phenology between deciduous and coniferous trees, we conducted an experiment with saplings of a deciduous tree species (*Quercus petraea (Matt.) LieBlume*) and a coniferous species (*Pinus sylvestris L.*) subjected to winter or spring warming, or both winter and spring warming, in combination with defoliation (0% vs 100% leaves defoliated). We aimed to test three hypotheses.

(i) Winter warming advances budburst in sessile oak but not in Scots pine because oak has a lower chilling requirement than Scots pine, whereas warming in spring or in winter and spring advances budburst dates of both species (H1).

(ii) The impact of previous-year defoliation on spring phenology does not differ between the deciduous *Quercus petraea* and the evergreen *Pinus sylvestris*, because even the defoliated evergreen species do not have leaves and thus have no advantage in winter photosynthesis and carbon supply for spring leaf phenology (H2).

(iii) However, defoliated trees, compared with intact ones within each species, will advance spring leaf phenology, demonstrating a mechanism to compensate for the previous-year leaf loss and NSC depletion (H3).

Materials and methods

Experimental setup

The experiment was carried out between April 2019 and October 2020 at the Swiss Federal Institute for Forest, Snow and Landscape Research WSL (47° 21′48″ N, 8° 27′23″ E, 545 m a.s.l.), located in Birmensdorf, Switzerland. Saplings of *Quercus petraea* (sessile oak, 2 years old) and *Pinus sylvestris* (Scots pine, 4 years old) with a height of ~30 cm and a base diameter of ~0.6 cm were purchased from a local nursery. Healthy seedlings were planted in 2-L pots filled with soil mixed of sand and potting soil (1:2) in April 2019. From April 2019 to 22 November 2019, all the plants were grown under ambient conditions and well-watered with automatic sprinklers. During the entire experiment period (i.e. April 2019–October 2020), all plants were sufficiently watered using a fixed sprinkler irrigation system.

The defoliation treatment was conducted to modulate plant carbon availability. On 8 August 2019, for each species, we completely defoliated 32 randomly selected individuals (treatment called hereafter Defoliated) and kept intact 32 other individuals which served as controls (treatment called hereafter Control). For Defoliated plants, all leaves (with petioles for oak) or needles were manually removed. This defoliation treatment caused direct carbon loss due to the removal of foliage biomass and thus carbon, and indirect carbon loss due to loss of photosynthetically active foliage. In a few oak saplings, new leaves were growing before autumn and were swiftly removed to limit nutrient use for leaf growth and to stop these leaves from photosynthesizing and acquiring new carbon.

The winter or/and spring warming treatment was conducted both inside (warming) and outside (ambient) a greenhouse at the WSL research institute (Figure S1 available as Supplementary Data at *Tree Physiology* Online). In this experiment, the winter warming treatment was applied form 22 November 2019 to 8 February 2020 (10 weeks) and the spring warming treatment from 8 February to 15 March 2020 (5 weeks), where seedlings were assumed to be sensitive to forcing conditions. On 22 November 2019, for each species, 16 Control and 16 Defoliated saplings were randomly selected for the winter warming (winter-W) treatment inside the greenhouse, and the remaining 16 individuals were exposed to ambient winter temperatures (winter-C) outside the greenhouse as controls (Figure 1). On 8 February 2020, half (8) of the 16 winter-W-treated Control and Defoliated saplings (i.e. inside the greenhouse) for each species were moved to spring ambient temperature (spring-C, outside the greenhouse), while the other half (8) were kept inside the greenhouse (spring-W). Similarly, half (8) of the 16 winter-C-treated Control and Defoliated saplings were randomly assigned to be exposed to spring warming (spring-W, inside the greenhouse), and the other half (8) remained in ambient spring temperature (spring-C, outside the greenhouse). These two temperature levels (ambient C vs warmed W) for both winter and spring generated four winter–spring temperature combinations: CC (winter-C + spring-C), CW (winter-C + spring-W), WC (winter-W + spring-C) and WW (winter-W + spring-W). The temperatures inside and outside the greenhouse were automatically recorded. To ensure consistent conditions during the experiment, we maintained a minimum temperature of 7.5 °C for the greenhouse only, effectively excluding most chilling conditions. The average temperature in greenhouse, marked as 'Winter +6 °C, Spring +5 °C', was consistently 5.0–6.2 °C higher than the external environment (Figure S1 available as Supplementary Data at *Tree Physiology* Online). On 15 March 2020, defined as the beginning of the growing season, the temperature treatments were completed and all saplings inside the greenhouse were moved outside the greenhouse in preparation for spring phenological observations.

Phenology monitoring and growth measurements

The monitoring of phenological phases began in March 2020, with observations conducted every 2 or 3 days. The phenological monitoring followed the Phenology Handbook published by the University of California (Haggerty and Mazer 2008) combined with common observation criteria (Wan and Liu 1979). This study predominantly focused on the spring leaf phenology, including bud swell (BS), bud burst (BB), first leaf unfolding (FLU), peak leaf unfolding (PLU) and all leaf unfolding of all leaves (ALU) (Figure S2 available as Supplementary Data at *Tree Physiology* Online). The date of bud swelling (BS) was defined as the day of year (DOY) when buds were swelling and changing color. Bud burst (BB) referred to the date when buds began to open. The DOY on which the first leaf unfolding was called the date of first leaf unfolding (FLU). In conifers, FLU denoted the date when young needles emerge from the bud sheath. The date of peak leaf unfolding (PLU) was defined as the DOY when half of the buds reached leaf unfolding stage. In Pine, PLU corresponded to the date when the length of needles reached half the length of old needles. All leaf unfolding (ALU) for oak correspond to the day when 100% of the leaves reached leaf unfolding stage, whereas for pine, it was defined by the needles reaching a constant length (Figure S2 available as Supplementary Data at *Tree Physiology* Online).

Two morphological growth indicators were measured, i.e. leaf length (LL) and specific leaf area (SLA). The leaf length (LL) of oak leaves, in millimeters (mm), were determined by measuring from the leaf base to the tip, excluding the petiole. Measurements were taken from the third to fifth leaves from the apical bud, and the average was recorded as the sapling's leaf length. For pine needles, the length of the longest needle in each of the first five fascicles from the apical fascicle was measured, and the average of these measurements was recorded as the needle length of the sapling. To evaluate leaf growth rate, measurements were performed every 3 to 4 days from leaf appearance until three consecutive measurements showed no change. The number of days to reach half of the total leaf length (Day50%) and the number of days to reach the maximum leaf length (Day100%) were fitted using local polynomial regressions up to second degree. At the end of the 2020 growing season, five intact leaves were collected from each oak sapling, and 20 intact current-year needles

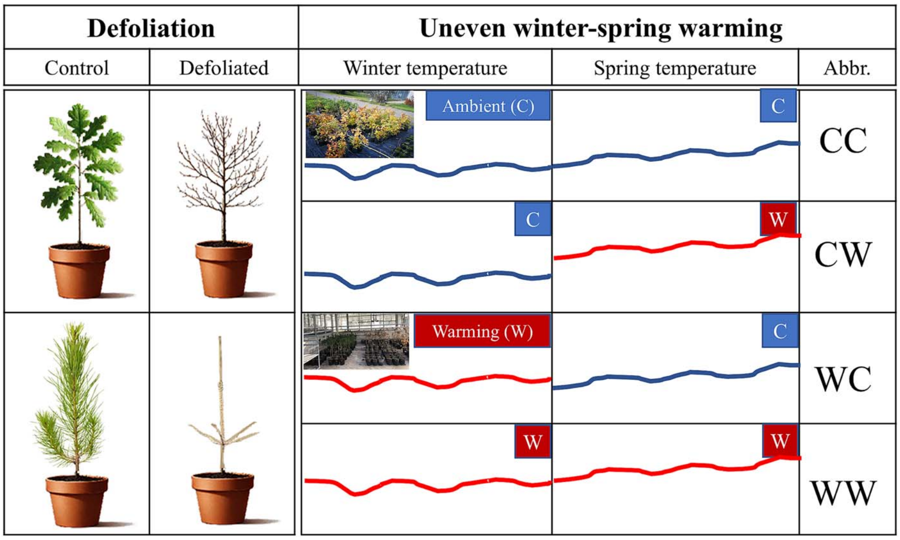

Figure 1. Schematic illustration of the treatment combinations for *Quercus petraea* and *Pinus sylvestris* saplings at the Swiss Federal Institute for Forest, Snow and Landscape Research WSL (47° 21′48″ N, 8° 27′23″ E, 545 m a.s.l.).

were collected from each pine sapling. The leaf area of these leaf samples was scanned using a scanner (EPSON Perfection V800 Photo; EPSON, Amsterdam, the Netherlands) and the samples were then dried and weighed, to calculate the specific leaf area (SLA, in cm^2 g^{-1}).

Sampling and measurement of NSC

Prior to the start of winter temperature treatments on 22 November 2019, four twig and four root samples (each 5 cm in length; $n = 4$) were collected from the 32 Defoliated and 32 Control saplings of each species to determine initial NSC levels (Figure 2). Twigs samples were selected from the main stem of the sapling, and the root samples were selected from the fine roots. That is, twigs or roots collected from 4–6 plants were pooled into one mixed twig sample or one mixed root sample, respectively. Prior to the start of the spring temperature treatments on 7 February 2020, four twig samples and four root samples ($n = 4$) were collected from the 16 Control and 16 Defoliated saplings of each species at each of winter-C and winter-W treatment, respectively (i.e. twigs or roots collected from four saplings were pooled for one mixed twig sample or one mixed root sample, respectively). At the end of the spring temperature treatments on 15 March 2020 (defined as pre-spring), twigs or roots from two saplings were combined to form a single sample. These samples were collected from eight Control and eight Defoliated saplings under each of the four winter–spring temperature combinations (i.e. CC, CW, WC, WW), respectively. As a result, there are four twig samples and four root samples ($n = 4$) for each species (Figure 2; Figure S3 available as Supplementary Data at *Tree Physiology* Online).

The twig and washed root samples were immediately placed in a drying oven at 65 °C after sampling. They were then grind using ball mixer milling (MM400, Retsch, Germany). The NSC concentrations (including glucose, fructose, sucrose, and starch) in twig and root samples were analyzed using the method developed by Wong (1990) and further modified by Hoch et al. (2002). We weighed 10–12 mg sample powder into a 2 mL centrifuge tube and record the weight of the powder. Subsequently, we filled the centrifuge tube with 2 mL of distilled water and boiled for half an hour. Then, we extracted a 200 μL aliquot and mixed with Invertase (Sigma-Aldrich, Buchs, Switzerland) to degrade sucrose into glucose and fructose. After centrifugation, 500 μL was withdrawn from the sample aliquot and react it with amyloglucosidase (Sigma-Aldrich, Buchs, Switzerland) for 15 h at 49 °C to break down starch into glucose. This process is used for measuring the total NSC concentration. The concentration of NSC was determined using 340 nm photometry (HR 7000, Hamilton, Rone, NE, USA) in a 96-well microplate photometer (Sigma-Aldrich, Buchs, Switzerland). The NSC concentrations are expressed on a dry mass (d.m.) basis.

Statistical analysis

The ‘lme4’ and ‘nlme’ R-package (v.4.0.4) were used for linear mixed effects analysis, to detect the effects of treatments (species, defoliation and uneven winter–spring warming) on phenology, leaf growth rates and tissue NSC concentration using replicates as random effects. The two species, two defoliation levels, and four temperature combinations were treated as fixed factors. Due to significant species effects and species-treatment (defoliation or temperature) interactions on the parameters investigated (Table S1 available as Supplementary Data at *Tree Physiology* Online), the effects of defoliation, temperature treatment, and their interaction on parameters were then separately analyzed within each species (Table S2 available as Supplementary Data at *Tree Physiology* Online). A two-way analysis of variance (ANOVA) and T test (Tukey’s HSD) were applied on the effects of defoliation and temperature treatments on leaf phenological changes, leaf growth rates, leaf length, SLA and the NSC of oak and pine saplings (Table S4 available as Supplementary Data at *Tree Physiology* Online). Furthermore, one-way ANOVA for intra group comparisons and Fisher’s Least Significant Difference (LSD) were conducted to analyze the effects of treatments within each species.

Results

Non-structural carbohydrates concentrations in twigs and roots

Complete leaf defoliation (Defoliated) conducted on 8 Aug. 2019 resulted in significantly lower NSC levels stored in

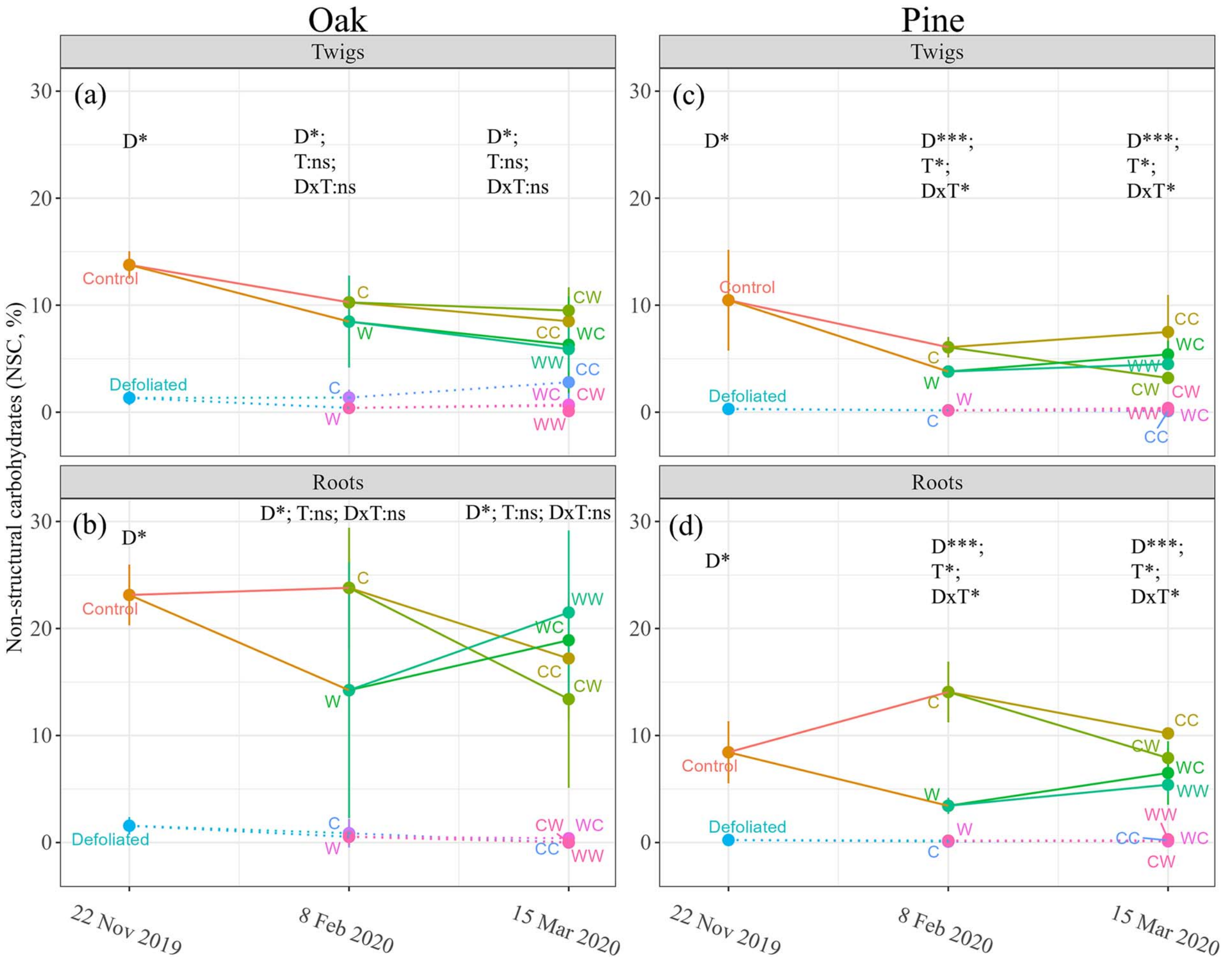

Figure 2. Non-structural carbohydrates concentrations in twigs and roots of oak (*Quercus petraea*) and pine (*Pinus sylvestris*) saplings in relation to defoliation (conducted on 8 August 2019) across a winter–spring temperature treatment from 22 November 2019 to 8 February 2020 (winter treatment period), and from 8 February to 15 March 2020 (spring treatment period).

twigs and roots than in non-defoliated saplings (Control) for the two species at the end of the 2019 growing season (Figure 2; Tables S1 and Tables S2 available as Supplementary Data at *Tree Physiology* Online). The decline in NSC following complete defoliation was primarily driven by reductions in starch rather than in soluble sugars, especially in the roots of both oak and pine (Figure S4 and S5 available as Supplementary Data at *Tree Physiology* Online). For pine saplings (Figure 2c and d), we found a significant effect of winter–spring temperature and interactions with the defoliation treatment on NSC concentrations in the storage tissue before bud break (Table S2 available as Supplementary Data at *Tree Physiology* Online). In details, Control pine saplings (i.e. not Defoliated) in the CC group had higher tissue NSC levels than those grown for at least one season in the greenhouse (WC, CW, WW) (Figure 2c and d), primarily due to increased starch accumulation in the roots. No significant effect of the temperature treatment was found for oak on storage tissue NSC (Figure 2a and b).

Leaf phenology

Overall leaf phenology differed significantly between the two species (Table S1 available as Supplementary Data at *Tree Physiology* Online). Defoliation (D) interacted with temperature (T) to significantly affect four out of the five leaf-phenological stages (Table S1 available as Supplementary Data at *Tree Physiology* Online). Significant interactions of S (species) × D or S × T demonstrated that the leaf phenology of the two species responded significantly differently to defoliation and temperature treatments (Tables S1 and S3 available as Supplementary Data at *Tree Physiology* Online), except for non-significant interaction of S × D on BS and BB. For oak, spring phenology was more strongly affected by winter–spring temperature rather than by defoliation but the defoliation significantly advanced its phenology in the winter spring warming (Figure 3a1–a5; Table S3 available as Supplementary Data at *Tree Physiology* Online). The winter and spring warming (WW) treatment led to stronger advance in spring phenology compared with the winter warming treatment (WC) and the control (CC), especially in the defoliation treatment (Figure 3a1–a5). Generally, the spring leaf phenology of oak saplings followed an early-to-late order of WW < CW < WC < CC, and this temperature effect on spring leaf phenology was amplified by defoliation (Figure 3a1–a5). For example, defoliated (Defoliated) saplings in the previous summer showed a more pronounced advance in budburst in response to full warming and a greater delay in response to control group compared with control (Control) saplings (Figure 3a1–a5), showing significant interactions between defoliation and temperature treatments (Table S3

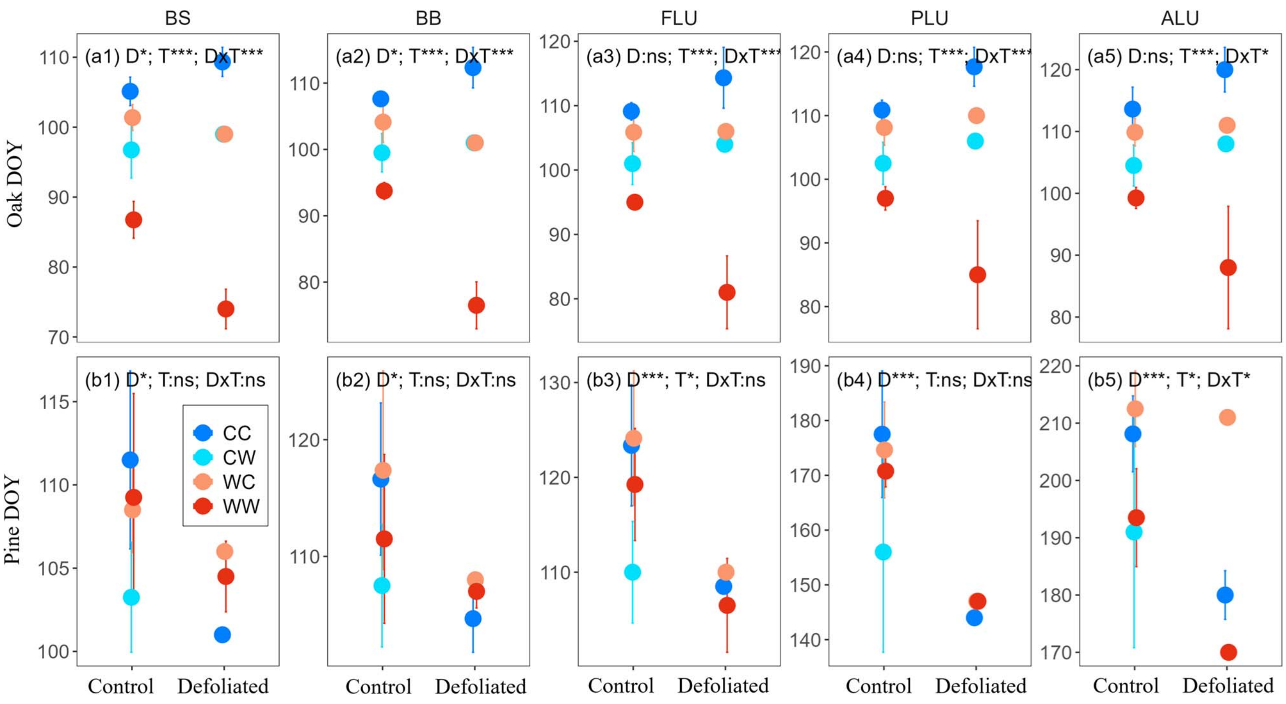

Figure 3. Dates of spring phenophases (DOY ± 1 SD of oak (*Quercus petraea*) and pine (*Pinus sylvestris*) saplings in relation to previous season defoliation and winter–spring temperature treatments (CC, CW, WC, WW).

available as Supplementary Data at *Tree Physiology* Online). In the non-defoliated sapling, bud swelling in the full warming treatment occurred 18.3 days earlier than in the control group (Figure S6; Table S4 available as Supplementary Data at *Tree Physiology* Online), while in the defoliated saplings (Defoliated) it occurred 35.3 days earlier in the WW treatment than in the control group (Figure S6 and Table S4 available as Supplementary Data at *Tree Physiology* Online).

The role of defoliation in spring leaf phenology was found to be more significant for pine, whereas temperature effects were only observed during first leaf unfolding (FLU) and all leaf unfolding stages (ALU) (Figure 3b1–b5; Table S3 available as Supplementary Data at *Tree Physiology* Online). The defoliated pine saplings significantly advanced their spring leaf phenology compared with non-defoliated saplings, irrespective of the warming treatment (Figure 3b1–b5). BS, BB, FLU, PLU and ALU in CC group were 10.5, 11.9, 15.2, 33.2 and 28.1 days earlier in the defoliated group than in the non-defoliated group, respectively (Figure S6; Table S4 available as Supplementary Data at *Tree Physiology* Online). Under full warming, the five phenological stages in the defoliated saplings occurred 4.8, 4.5, 12.8, 23.8 and 23.5 days earlier compared with the non-defoliated control saplings, respectively (Figure S6 and Table S4 available as Supplementary Data at *Tree Physiology* Online). The phenology of plants in spring warming treatment tended to be earlier than those exposed to the winter warming treatment (Figure 3b1–b5).

Leaf growth

Interestingly, defoliation but not winter–spring temperature significantly decreased the maximum length of leaves reached during early summer for both oak and pine saplings, especially for oak (Figure 4a1 and b1; Figure S7 and Table S4). SLA was not affected by defoliation or winter and spring warming treatments for any species (Figure 4a2 and b2; Table S2). Finally, neither defoliation from previous summer nor winter and spring warming treatments affected the number of days to reach 50% leaf maturation and 100% leaf maturation (Figure 4a3, a4, b3 and b4; Table S2 available as Supplementary Data at *Tree Physiology* Online), except for oak where spring warming was found to advance the time to reach 50% of the maximum leaf length (i.e. CW and WW, Figure 4a3; Table S4 available as Supplementary Data at *Tree Physiology* Online).

Relationships between leaf growth and storage tissue NSC

A positive correlation was found between maximum leaf length and pre-spring NSC concentration in the twigs (Figure 5a1 and b1) and roots (Figure 5a2 and b2) of both oak and pine saplings. However, for both species, SLA, the number of days to reach 50% leaf maturation and 100% leaf maturation were not associated with NSC levels in pre-spring twigs and roots (Figures S9 and S10 available as Supplementary Data at *Tree Physiology* Online). Leaf growth rate was not different between control and defoliated in oak (Figure 5a3), whereas in pine the growth rate of defoliated seedlings was faster than the control (Figure 5b3).

Discussion

Interactive effects of carbohydrates and winter–spring temperature on leaf phenology

The two studied species exhibited distinct responses to the warming and defoliation treatments. In pine, winter warming delayed the later stages of phenology (FLU and ALU), whereas in oak, both winter and spring warming advanced phenology across all stages. Additionally, summer defoliation led to reduced pre-spring NSC concentrations in twigs and roots in

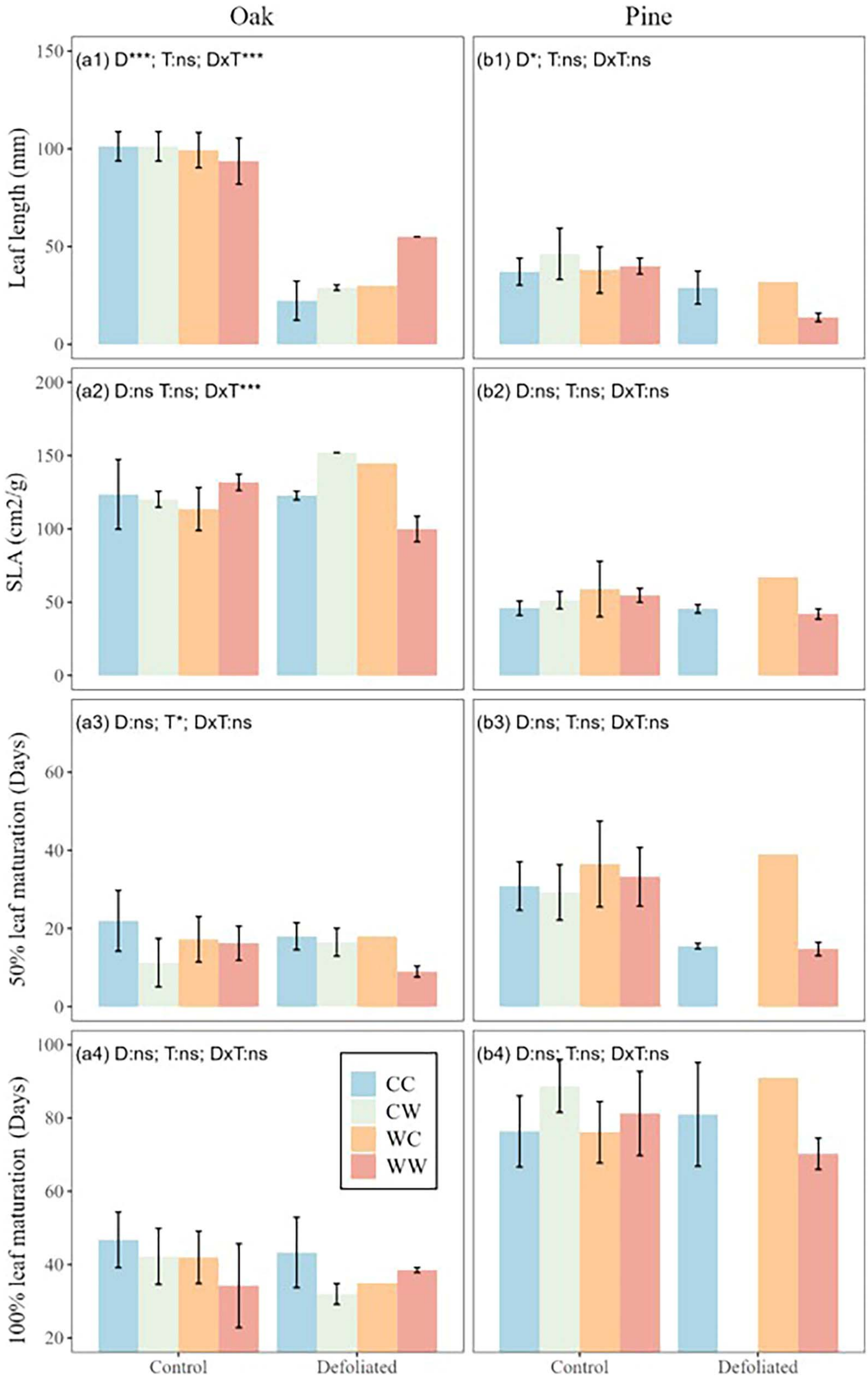

Figure 4. Maximum leaf length (mm), specific leaf area (SLA, cm^2 g^{-1}), and days of leaf reached 50% maturation and 100% maturation for oak (*Quercus petraea*) and pine (*Pinus sylvestris*) saplings treated with winter–spring temperature and defoliation.

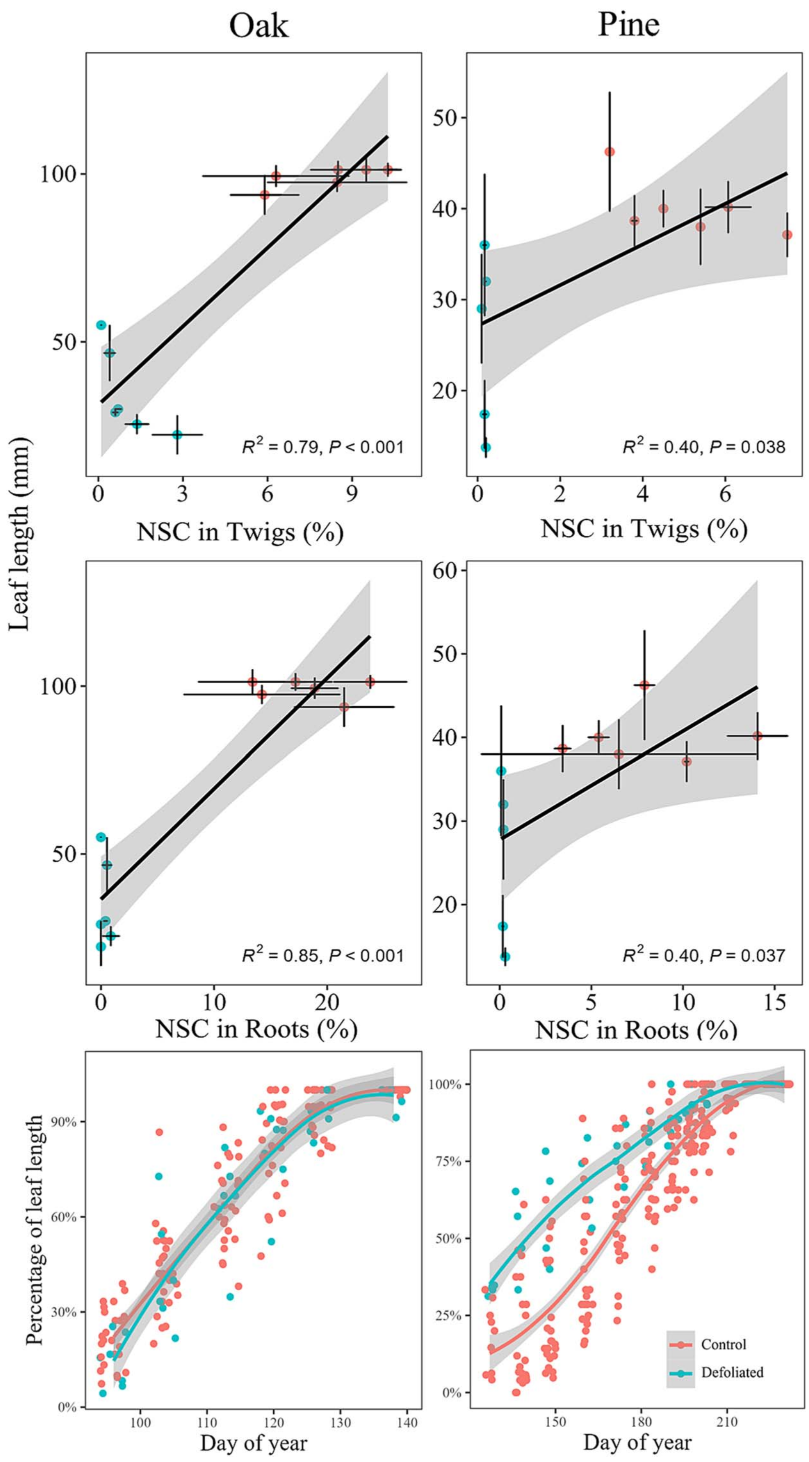

Figure 5. Maximum leaf length in relation to NSC concentrations in twigs and roots collected on 7 February and 15 March 2020, and the percentage of maximum leaf length for oak (*Quercus petraea*) and pine (*Pinus sylvestris*) saplings.

both species. Starch, as the main storage form, was preferentially mobilized to support metabolic demands following carbon loss due to defoliation. Interestingly, despite reduced NSC levels, pine exhibited earlier needle emergence under defoliation, suggesting a compensatory response involving rapid photosynthetic activation by newly formed needles. In oak, however, defoliation did not produce consistent phenological shifts. However, both carbohydrates and temperature significantly influenced phenology across all stages in oak, indicating that the availability of NSC, coupled with temperature fluctuations, synergistically regulates growth and leaf development. Short-term heat stress alters NSC accumulation and remobilization, significantly impacting growth during critical phenological stages (Mahmood et al. 2024). Experimental warming caused a significant increase in the proportion of NSC allocated to the roots of evergreen conifers, while broadleaved deciduous trees showed a notable decrease in root NSC allocation under the same conditions (Liu et al.

2020, Xiong et al. 2020). This suggests that warming temperatures, in certain contexts, accelerate the mobilization of NSC in deciduous trees. As a result, warming conditions amplified the delayed phenological responses in oaks, likely due to reduced NSC availability. These findings indicate that temperature plays a crucial role in modulating carbohydrate metabolism, respiration and utilization, thereby influencing phenology under complex conditions, as observed in oak. During periods with limited photosynthesis (e.g. winter or early spring), respiration is sustained by stored NSCs (Hartmann and Trumbore 2016). Changes in temperatures and other stressors like drought may disturb NSC allocation, affecting the timing and success of phenological events (Li et al. 2018). Thus, the interplay between NSC and temperature is key, with temperature-driven changes in NSC dynamics acting as a major mechanism that shapes plant phenology under varying environmental conditions.

Additionally, these interactions influenced leaf length and SLA in oak but not in pine. We found that maximum leaf length in the following year was shorter that were defoliated in the previous summer, with a positive correlation between pre-spring NSC and maturation leaf length. However, defoliation and pre-spring NSC did not alter the time needed to reach 50% or 100% of mature leaf length. Warmer conditions typically promote rapid growth, which can lead to higher SLA (thinner leaves) to optimize photosynthetic efficiency. However, after defoliation, plants might lower SLA (producing thicker leaves) to enhance resistance and ensure long-term survival. These regulatory mechanisms vary between species, as demonstrated by the differences between oak and pine in their SLA adjustments (Wright et al. 2001, Sala et al. 2012).

Winter–spring warming differently affects leaf phenology of a deciduous and an evergreen species

We observed that warming in winter or spring significantly advanced spring leaf phenology of oak saplings, and slightly delayed the late spring phenological phases of pine saplings. This indicates a distinct response to warming between these two species which could be explained by their differences in chilling requirement to release dormancy. Oak demonstrated a pronounced response to warming, with earliest first leaf unfolding (14.1 days earlier compared with the control) observed in the full warming treatment, followed by spring warming (8.1 days earlier) and winter warming (3.2 days earlier). As this species is known to have very low chilling requirements to break dormancy (Baumgarten et al. 2021), its buds become sensitive to forcing shortly after the beginning of dormancy in autumn and, accordingly, warming in winter leads to earlier budburst in spring. However, our results also show that spring warming exerts a more pronounced effect on advancing leaf phenology than winter warming, in line with findings from previous experiments demonstrating that buds become progressively more sensitive to warming as dormancy depth and cold hardiness decrease (Signarbieux et al. 2017, Kovaleski 2022). In contrast, for pine saplings, winter warming delayed leaf unfolding by 0.7–4.4 days compared with the control, suggesting that chilling requirement were less satisfied in this treatment which, in turn, required greater forcing to leaf out. In lines with or findings, in conifers such as white pine (*Pinus strobus*) and red pine (*Pinus resinosa*), insufficient chilling was found to lead to a higher forcing requirement for budburst, thereby delaying the onset of spring phenological events (Man et al. 2021). These responses became more pronounced towards the later stages of leaf unfolding which might indicate an interaction with photoperiod. Studies by Laube et al. (2014) and Zohner et al. (2016) showed that spring phenology of *Pinus sylvestris* is affected by photoperiod which may also explain the stronger response to spring warming compared with winter warming. The likely involvement of photoperiod, chilling and forcing requirements in triggering pine leaf out highlights the complexity of these interactions and the need for a detailed understanding of how seasonal temperature variations affect plant phenology.

Different responses of leaf phenology and growth to carbon resource availability between a deciduous and an evergreen species

Our study supports our hypothesis that tree defoliation impacts spring phenology more significantly in evergreen species (*Pinus sylvestris*) than in deciduous species (*Quercus petraea*). This finding may be explained by species-specific differences in NSC levels prior to the temperature treatments: intact oak > intact pine, and defoliated oak > defoliated pine (Figure 2; Figures S4 and S5 available as Supplementary Data at *Tree Physiology* Online). These differences suggest that lower carbohydrate reserves may increase sensitivity to spring phenological changes. This interpretation is further supported by the observed relationship between tissue NSC levels and spring leaf phenology. For sessile oak, our results indicated no significant correlation between NSC levels in root or twig tissues and the timing of leaf out (Figures S10 and S11 available as Supplementary Data at *Tree Physiology* Online). In contrast, the evergreen Scots pine exhibited a significant positive correlation between lower carbon supply and earlier needle emergence (Figures S10 and S11 available as Supplementary Data at *Tree Physiology* Online). This pattern is consistent with findings in black spruce (*Picea mariana*), balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*), where bud phenology advanced by 3.5–7.0 days following defoliation (Deslauriers et al. 2019). This difference between deciduous broadleaves and evergreen conifers may also reflect variations in both bud development strategies and carbon reserve levels. Deciduous species often have their leaves pre-formed in the buds and tend to maintain higher total NSC reserves during dormancy, allowing for rapid deployment in spring. In contrast, evergreen species rely more directly on current NSC availability for needle growth. Conifers typically develop new needles gradually, a process that relies strongly on stored NSCs. Interestingly, in defoliated pines where NSC levels were low, earlier needle emergence was still observed. This may reflect a compensatory mechanism, in which newly formed needles rapidly initiate photosynthesis to support their own growth despite limited internal reserves, resulting in smaller and less developed foliage (Liu et al. 2018, Palacio et al. 2018). However, it is also possible that manual defoliation introduced additional physiological stress, such as altered hormonal balance or increased metabolic demands, which may have contributed to the observed phenological responses. While defoliation is a widely used method to reduce carbon assimilation and investigate NSC-related responses (D'Andrea et al. 2019, J.M.Wang et al. 2021), stress-induced effects beyond carbon limitation may also play a role, particularly in the case of oak saplings that produced new leaves before autumn in the same year. Moreover, evergreens maintain their leaves year-round, allowing them to regenerate needles more quickly after defoliation. In contrast, temperate deciduous trees like oak remain leafless during dormancy and may delay leaf out in the following spring to avoid frost damage. They use their carbon reserves to delay leaf out until conditions are optimal, thereby minimizing the risk of frost damage (Zohner et al. 2019). Future studies could benefit from combining defoliation with complementary treatments (e.g. shading, hormonal assays) to better disentangle carbon-specific effects from general stress responses.

Leaf defoliation significantly reduced NSC concentrations in twigs and roots in both species, with Scot pine in particular reaching an impressive ~0% of NSC (Figure 2). Moreover, in CW group of pine, saplings all dead indicating that at least in part from carbon starvation due to defoliation. Interestingly, there was a significantly positive correlation between stored NSC concentration and maximum leaf length in oak and pine saplings. Buds were smaller in the defoliation treatments due to lower NSC reserves, particularly in oak saplings, leading to smaller leaves and slower leaf growth rate in the following growing season. However, smaller leaves in the following season after defoliation could also be a strategy to cope with herbivores (Coley and Barone 1996, Carmona et al. 2011). After being stressed by defoliation, trees may produce smaller leaves with a higher concentration in defense component durations such as tannins or polyphenols (Eisenring et al. 2024). Needle regeneration in NSC-depleted pine saplings likely occurred through synergistic mechanisms: (i) residual NSCs in woody tissues, (ii) lipid catabolism, which is known to play a vital role in conifer stress responses (Hoch and Körner 2003), and (iii) rapid photosynthetic activation from protected buds. However, regeneration was limited, with needle length in defoliated saplings reduced by ~30% compared with controls in the CC group and by ~70% in the WW group (Figure 4; Figures S7 and S9 available as Supplementary Data at *Tree Physiology* Online). Thus, our results indicate that pre-formation conditions of buds critically influence the availability of reserves for leaf production in the following spring (Jacquet et al. 2014, Wiley et al. 2017) as well as leaf size.

We did not observe significant effects of winter or spring warming before budburst on maximum leaf length, SLA, and the time required for leaves to reach 50% and 100% of their maximum leaf length. Leaf traits are crucial for plant functions under varying climatic conditions. The interval from bud swelling to leaf out in both oak and pine is influenced by temperature (Figure S8 available as Supplementary Data at *Tree Physiology* Online), which correlates with changes in leaf length. In oaks, defoliation from the previous summer led to smaller bud sizes, which in turn resulted in shorter leaf lengths. Although the duration of leaf growth remained consistent between defoliated and non-defoliated treatments, the growth rate was significantly slower under lower NSC levels in stored tissues. Consequently, while the time to reach leaf maturity was the same, the final leaf length at maturity was much smaller in defoliated treatments compared with non-defoliated ones. This indicates that depleted NSC availability prior to budburst slows down the growth rate, whereas higher NSC levels enable faster growth, resulting in larger leaves within the same growth period. This pattern may also reflect a shift in sink hierarchy during post-stress recovery, in which limited carbon resources are preferentially allocated to essential growth processes (e.g. bud development), while leaf expansion is constrained under low NSC conditions (Sala et al. 2012, Wang et al. 2021). For pine, initial phenological stages may be more dependent on photoperiod, but later stages of leaf out and growth are predominantly driven by temperature.

Conclusions

In this experimental study, we investigated the effects of uneven winter–spring warming and pre-spring NSC availability on the spring leaf phenology of both deciduous and evergreen tree species. Our findings reveal distinct responses between the two species: spring leaf phenology of the deciduous oak was significantly influenced by warming in winter and spring, whereas that of the evergreen pine displayed a noticeable response to defoliation. For oak trees, the duration from bud swelling to leaf out is primarily influenced by temperature. In contrast, for pines, both temperature and defoliation jointly affected the timing of leaf unfolding. Interestingly, winter warming delayed the late stages of pine phenology. In oak, defoliation and reduced pre-spring NSC availability had no effect on spring phenology, but led to smaller leaves and slower leaf growth to reach maturity. These results highlight the complexity of phenological and physiological responses to climate change and emphasize the importance of considering species-specific traits when predicting phenological responses. Our study underscores the diverse adaptive strategies between deciduous and evergreen species to environmental changes, providing valuable information to the field of climate change biology.

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Supplementary Data

Supplementary data for this article are available at *Tree Physiology* Online.

Author contributions

Y. Y. (Investigation, Methodology, Writing—original draft), Y. V. (Writing—review & editing), Constantin M. Z. (Writing—review & editing), L. W. (Investigation, Data curation), Y. Z. (Investigation, Data curation), A. W. (Investigation, Data curation), D. G. (Investigation, Data curation), S. Z. (Investigation, Data curation), H. D. (Investigation, Data curation), Z. W. (Funding acquisition), H. S. H. (Funding acquisition), Z. H. (Funding acquisition) and M.-H. L. (Conceptualization, Writing—review & editing, Supervision, Project administration, Funding acquisition). M.-H.L. holds the position of Editor for *Tree Physiology* and has not peer reviewed or made any editorial decisions for this paper.

Conflict of interest

The authors declare that there are no conflicts of interest.

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Data availability

Data available on request.

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