








REVIEW

Phenology–Trait Relationships Across Different Scales and Organisational Levels

Internal physiological drivers of leaf development in trees: Understanding the relationship between non-structural carbohydrates and leaf phenology

Yunpeng Luo¹  | Constantin Zohner²  | Thomas W. Crowther²  | Jianlan Feng^{3,4} |
Günter Hoch⁵  | Peng Li⁶ | Andrew D. Richardson^{7,8}  | Yann Vitasse^{1,9}  |
Arthur Gessler^{1,10} 

¹Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland; ²Institute of Integrative Biology, ETH Zurich (Swiss Federal Institute of Technology), Zurich, Switzerland; ³Wales College, Lanzhou University, Lanzhou, China; ⁴Swansea College of Art, University of Wales Trinity Saint David, Swansea, UK; ⁵Department of Environmental Science-Botany, University of Basel, Basel, Switzerland; ⁶School of Geographic Sciences, Hunan Normal University, Changsha, China; ⁷Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, Arizona, USA; ⁸School of Informatics, Computing, and Cyber Systems, Northern Arizona University, Flagstaff, Arizona, USA; ⁹Oeschger Centre for Climate Change Research, University of Bern, Bern, Switzerland and ¹⁰Institute of Terrestrial Ecosystems, ETH Zurich (Swiss Federal Institute of Technology), Zurich, Switzerland

Correspondence

Yunpeng Luo

Email: yunpeng.luo@wsl.ch

Peng Li

Email: lipeng_gz@126.com**Funding information**

Swiss National Science Foundation (SNSF),

Grant/Award Number: 320030-232013;

Swiss National Science Foundation

(SNSF) Sinergia, Grant/Award Number:

CRSII5_216562; National Science

Foundation, Grant/Award Number: DEB

1832210

Handling Editor: Robert Rauschkolb**Abstract**

1. Plant phenology is crucial for understanding plant growth and climate feedback. It affects canopy structure, surface albedo, and carbon and water fluxes. While the influence of environmental factors on phenology is well-documented, the role of plant intrinsic factors, particularly internal physiological processes and their interaction with external conditions, has received less attention.
2. Non-structural carbohydrates (NSC), which include sugars and starch essential for growth, metabolism and osmotic regulation, serve as indicators of carbon availability in plants. NSC levels reflect the carbon balance between photosynthesis (source activity) and the demands of growth and respiration (sink activity), making them key physiological traits that potentially influence phenology during critical periods such as spring leaf-out and autumn leaf senescence. However, the connections between NSC concentrations in various organs and phenological events are poorly understood.
3. This review synthesizes current research on the relationship between leaf phenology and NSC dynamics. We qualitatively delineate seasonal NSC variations in deciduous and evergreen trees and propose testable hypotheses about how NSC may interact with phenological stages such as bud break and leaf senescence. We also discuss how seasonal variations in NSC levels, align with existing conceptual models of carbon allocation.
4. Accurate characterization and simulation of NSC dynamics are crucial and should be incorporated into carbon allocation models. By comparing and reviewing

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2024 The Author(s). *Functional Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

the development of carbon allocation models, we highlight the shortcomings in current methodologies and recommend directions to address these gaps in future research.

5. Understanding the relationship between NSC, source–sink relationships, and leaf phenology poses challenges due to the difficulty of characterizing NSC dynamics with high temporal resolution. We advocate for a multi-scale approach that combines various methods, which include deepening our mechanistic understanding through manipulative experiments, integrating carbon sink and source data from multiple observational networks with carbon allocation models to better characterize the NSC dynamics, and quantifying the spatial pattern and temporal trends of the NSC-phenology relationship using remote sensing and modelling. This will enhance our comprehension of how NSC dynamics impact leaf phenology across different scales and environments.

KEYWORDS

carbon allocation, carbon allocation modelling, carbon sink-source activity, leaf phenology, non-structural carbon (NSC), starch and sugar, tree

1 | INTRODUCTION

Over the last decades, forests have absorbed approximately 1.9 Gt C year⁻¹, representing around 60% of the total terrestrial carbon sink (Friedlingstein et al., 2023). Understanding tree growth and forest dynamics is paramount for accurately projecting global carbon cycling under future climate scenarios (Friedlingstein et al., 2023). Plant phenology is an important indicator of plant responses to climate change (Menzel et al., 2020; Schwartz, 2013), plays a pivotal role in tree carbon uptake and growth, and exerts strong feedback on climate by influencing canopy structure, surface albedo, and carbon and water fluxes (Richardson, Keenan, et al., 2013). This recognition has led to a surge in phenological research over the past decades (Tang et al., 2016).

A mechanistic understanding of the drivers of phenology is essential for predicting the start and end of trees' growing seasons, allowing for more accurate predictions of forests' carbon uptake capacity. While the influence of meteorological cues, like temperature and precipitation, on phenology has been extensively studied (Fu et al., 2015; Piao et al., 2019; Zohner et al., 2023), less attention has been paid to the internal physiological processes of trees, such as the mobilization of carbon or nutrients (Luo et al., 2020; Ma et al., 2022). These internal processes respond to meteorological cues but can also be affected by additional environmental factors such as soil conditions (Arend et al., 2015). Moreover, they integrate and balance source and sink processes with phenological timing, allowing remobilization of carbon reserves and adjustment of growth and photosynthesis. Indeed, recent studies have suggested a direct link between plant physiological activity and phenological patterns, including processes related to source activity, namely photosynthesis, and sink activity, such as growth and respiration (Deslauriers

et al., 2019; Zohner et al., 2023). Despite these insights, the exact causal relationship between leaf phenology and carbon sink-source dynamics, particularly the relationship with sink activities, remains unclear and underexplored.

Free sugars and starch in plants, referred to as non-structural carbohydrates (NSC), are often presumed to mirror the carbon balance between a plant's carbon supply and usage (Hoch, 2015). These compounds exhibit seasonal fluctuation and fulfil three primary roles: serving as carbon storage (mainly starch) and supply for energy-demanding processes, building blocks for new biomass, and assisting in osmoregulation (sugars) and cold acclimation (Deslauriers et al., 2021; Hartmann & Trumbore, 2016; Martínez-Vilalta et al., 2016). Elevated NSC levels indicate excessive accumulation of photosynthates during the growing season and can inhibit further leaf development and photosynthesis (Paul & Foyer, 2001). This can have cascading effects, including carbohydrate redistribution, programmed cell death, and consequently, leaf senescence (Kumar et al., 2019). Moreover, sapwood NSC accumulation in autumn and depletion in winter may be important in influencing leaf dormancy (D'Andrea et al., 2021) and controlling bud development and leaf emergence in the following spring (Amico Roxas et al., 2021). The regulation of plant growth by NSC is dependent on the accumulation of carbohydrates in leaves or adjacent twigs and the overall physiology of the plant, underscoring the complex interaction between carbon sink and source dynamics across different plant organs such as leaves, stems and roots (Hagedorn et al., 2016).

Leaf NSC concentrations can serve as a valuable indicator of plant overall physiological activities Gersony et al. (2020), and it remains to be examined how intra- and inter-annual variation of NSC in leaves and other plant organs influence the timing of spring leaf-out and autumn leaf senescence. Due to the varying leaf emergence

among species, the linkage between leaf phenology and NSC likely differs among leaf types, especially between deciduous and evergreen trees (Hoch et al., 2003).

Although NSC are recognized as a key physiology trait among the Essential Biodiversity Variables (EBVs), introduced by the Group on Earth Observations Biodiversity Observation Network (GEO BON) (Kissling et al., 2018), they have received relatively little attention in plant phenological studies compared to other plant traits. This is likely due to the labour-intensive nature of NSC measurements. However, recent advancements have increased the availability of NSC data, which is stored in resources such as the TRY plant trait database (Kattge et al., 2020). This offers an opportunity to explore the links between NSC and tree phenology more deeply.

In this paper, we review the current knowledge of variations in leaf phenology and NSC across different tree compartments alongside the current state of NSC modelling in various organs (Sections 2–4). Following this overview, we propose methodologies to deepen our understanding of the relationship between phenology and NSC, and to extend research beyond the conventional focus on individual plants (Sections 5 and 6). By integrating diverse approaches and scales, we aim to advance our comprehension of this vital relationship, emphasizing the importance of NSC as a critical indicator of physiological dynamics in ecological and phenological studies.

2 | UNDERSTANDING THE RELATIONSHIP BETWEEN LEAF PHENOLOGY AND NSC IN LEAVES AND ADJACENT BRANCHES

Previous studies have shown that leaf-out and leaf development processes are paralleled with the variation in NSC concentrations, particularly in leaves and adjacent branches (Blumstein et al., 2024; Klein et al., 2016). NSC accumulate initially in developing leaves and are transported to other organs once leaves mature after leaf-out (Hartmann & Trumbore, 2016). However, an important question remains: Do NSC play a role in triggering critical phenological stages such as leaf-out and leaf senescence? To address this, we need to (1) understand and depict the seasonality of NSC and (2) causally link the observed NSC dynamics with leaf phenological stages by confirming or falsifying testable hypotheses.

Observations of NSC dynamics in trees at high temporal resolution (daily or weekly) are rarely available (Landhäusser, 2011); thus, the description of NSC seasonality is still unclear. By reviewing existing literature, we outline the seasonal patterns of NSC in leaves and adjacent branches, which are assumed to be directly linked to leaf development (Figure 1). Additionally, using data from a study integrating phenology and NSC measurements (Zahnd et al., 2024), we provide an example for quantifying the variation in NSC levels in both deciduous and evergreen trees (Table 1). We propose the

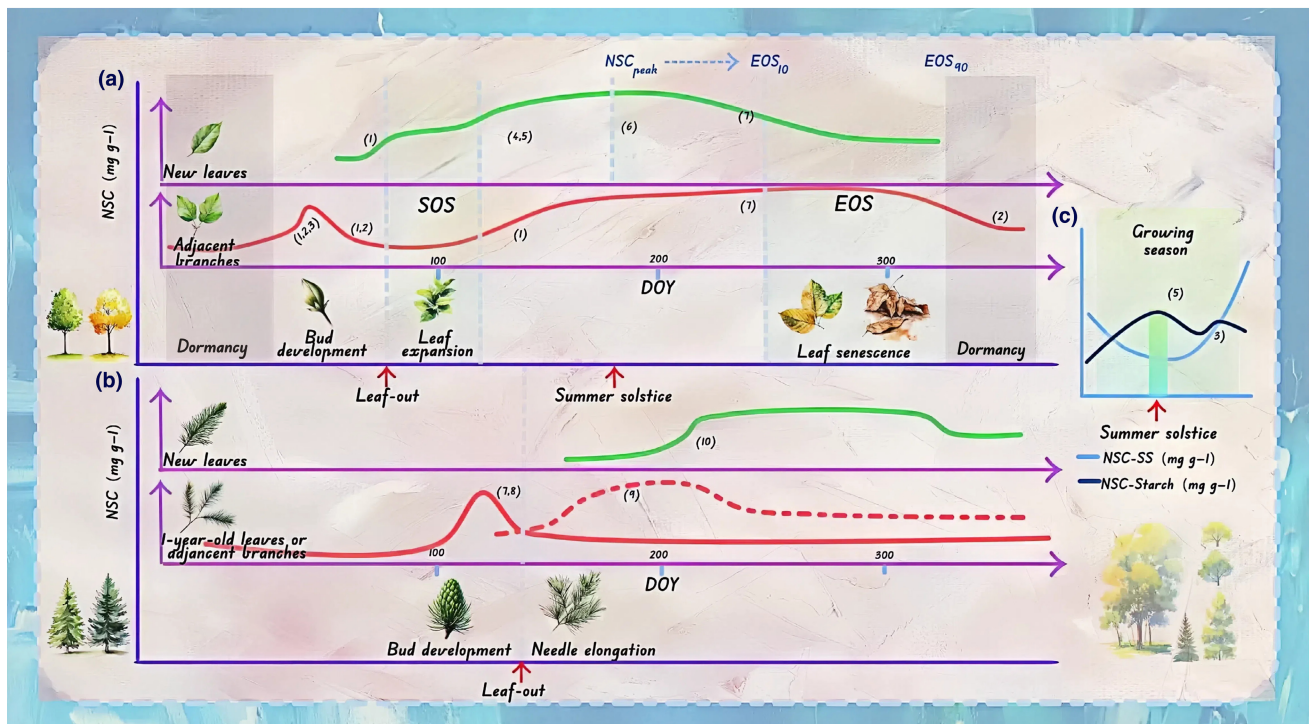


FIGURE 1 Non-structural carbohydrates (NSC) dynamics and its linkage to leaf/needle phenology in (a) deciduous and (b) evergreen trees. The conceptual variation of leaves' soluble sugar (SS) and starch in deciduous trees, as the two main components of NSC, are also displayed in (c). In deciduous trees (panel a), NSC in branches and leaves exhibit distinct seasonal dynamics. The literature on temporal dynamics is based on (1) Klein et al. (2016), (2) Sperling et al. (2017), (3) Tixier et al. (2019), (4) Bazot et al. (2013), (5) Rademacher et al. (2022), (6) Shi et al. (2023), (7) Hoch et al. (2003), (8) Furze et al. (2019), (9) Gruber et al. (2011), (10) Fischer and Höll (1991). EOS_{10} and EOS_{90} indicate the dates when the greenness dropped by 10% and 90% of the seasonal maximum, respectively. EOS_{10} stands for leaf senescence onset and EOS_{90} indicates the end of senescence.

TABLE 1 Variation of total NSC, starch, and sugar along different phenological stages in deciduous and evergreen trees^a.

		Dormancy	Bud development	Leaf-out	Leaf expansion	Leaf expansion—peak	Senescence	
Deciduous trees	DOY	0–91 ± 20	91 ± 20–100 ± 18	110 ± 13–124 ± 13	123 ± 11–134 ± 11	134 ± 11–274 ± 7	274 ± 7–317 ± 12	
	NSC trend		↘	↘	↗	↗		
	Total NSC (%)	Adjacent branches	10.30 ± 3.30	7.72 ± 2.43	4.48 ± 1.33	7.71	10.90 ± 2.73	\
	Starch (%)	Adjacent branches	7.66 ± 2.68	6.42 ± 2.37	3.06 ± 0.44	4.24	8.66 ± 2.39	\
	Sugar (%)	Adjacent branches	2.65 ± 1.25	1.30 ± 0.55	1.42 ± 0.89	3.48	2.20 ± 9.82	\
		Before bud-swell			Bud development	Leaf-out		
Evergreen trees	DOY	0–101 ± 7			101 ± 7–106 ± 8	120 ± 7–152 ± 8		
	NSC trend				↗	↘		
	Total NSC (%)	Adjacent branches			2.97 ± 0.84	3.54 ± 0.23	2.94 ± 0.57	
	Starch (%)	1-year-old leaves			3.71 ± 3.96	10.50 ± 2.85	5.85 ± 1.55	
		Adjacent branches			0.73 ± 0.62	1.99 ± 0.40	1.37 ± 0.62	
	Sugar (%)	1-year-old leaves			5.87 ± 1.28	5.69 ± 0.28	5.07 ± 0.52	
adjacent branches			2.24 ± 1.01	1.55 ± 0.37	1.58 ± 0.57			

^aThe data used for Table 1 were derived from Zahnd et al. (2024). In total, 6 deciduous and 3 evergreen needle tree species were used. Please refer to the details of tree species in Zahnd et al. (2024). Arrows in the line 'NSC trend' indicate increasing or decreasing trends during a given phenophase in adjacent branches compared to the previous one (so no arrow was added for the first phenophase).

potential mechanistic linkages between NSC in branches, buds, and leaves, and the key phenological phases such as bud break and leaf senescence (Figure 2). These relationships between leaf phenology and NSC dynamics among different tree organs warrant further investigation through carefully designed future experiments.

In deciduous trees (Figure 1a), previous research has suggested that NSC levels in branches can increase before leaf-out in some tree species due to carbon mobilization from distant branches and stems (Tixier et al., 2019). Before bud break, the proportion of starch increases in the twig adjacent to the buds, due to the conversion of free sugars to starch (Hoch et al., 2003). As the buds begin to swell, the NSC in adjacent branches decrease and are mobilized to supply the carbon demand during bud development (Klein et al., 2016; Sperling et al., 2017). This leads to a significant increase in carbon within the buds and enables cell activity in the meristems (division and elongation) during bud break and leaf emergence (Klein et al., 2016). With the expansion and maturation of new leaves, NSC levels in branches are replenished, and leaves become carbon autonomous as they produce photo-assimilates (Klein et al., 2016), often within a few days in fast-growing species like aspen (Landhäuser, 2011). NSC progressively accumulate in branches until early summer, after which branch NSC content remains relatively stable during the summer (Hoch et al., 2003). During autumn and winter, the accumulated starch in branches is gradually converted to sugars to support essential metabolic processes such as cell respiration (Sperling et al., 2017) and prevent damage from freezing temperatures by increasing cell osmotic potential (Tixier et al., 2019). In contrast, NSC levels in leaves show a steady rise until a few days or weeks after the summer solstice (Baumgarten et al., 2023; Bazot et al., 2013; Rademacher

et al., 2022). Thereafter, they gradually decrease until leaf senescence (Hoch et al., 2003).

Evergreen trees retain their leaves throughout the year but still exhibit changes in leaf greenness and phenology (Luo et al., 2022; Seyednasrollah et al., 2021). Similar to deciduous trees, NSC, specifically starch, in one-year-old leaves and adjacent branches of evergreen conifers or broadleaved trees increase before the emergence of new needles (Figure 1b) (Gao et al., 2022; Hoch et al., 2003; Löiez & Piper, 2022). This rise in NSC can be attributed to photosynthetic activity from existing leaves (Hoch et al., 2003) and the mobilization of NSC from other sink organs as seen in deciduous trees (Tixier et al., 2017). After the emergence of new needles, NSC concentrations in adjacent one-year-old needles and branches decrease and continue to drop gradually until the end of the year (Furze et al., 2019; Gruber et al., 2011; Hoch et al., 2003). However, there is still no consensus on the exact timing when NSC levels begin to decline in one-year-old needles, which might be due to the significant interspecific variations in the timing of needle emergence in evergreen species (Gruber et al., 2011; Hoch et al., 2003). NSC levels in newly formed leaves are thought to increase during the leaf elongation period and early summer, remain high from summer through autumn (Fischer & Höll, 1991), and decrease slightly during the inactive winter season. However, NSC dynamics in new leaves of evergreen trees have not been extensively studied, necessitating investigation in future research.

Soluble sugars and starch, as the two main components of NSC (Dietze et al., 2014; Hartmann & Trumbore, 2016), exhibit distinct seasonal dynamics in leaves of deciduous trees (Figure 1c) (D'Andrea et al., 2021; Rademacher et al., 2022). Soluble sugars

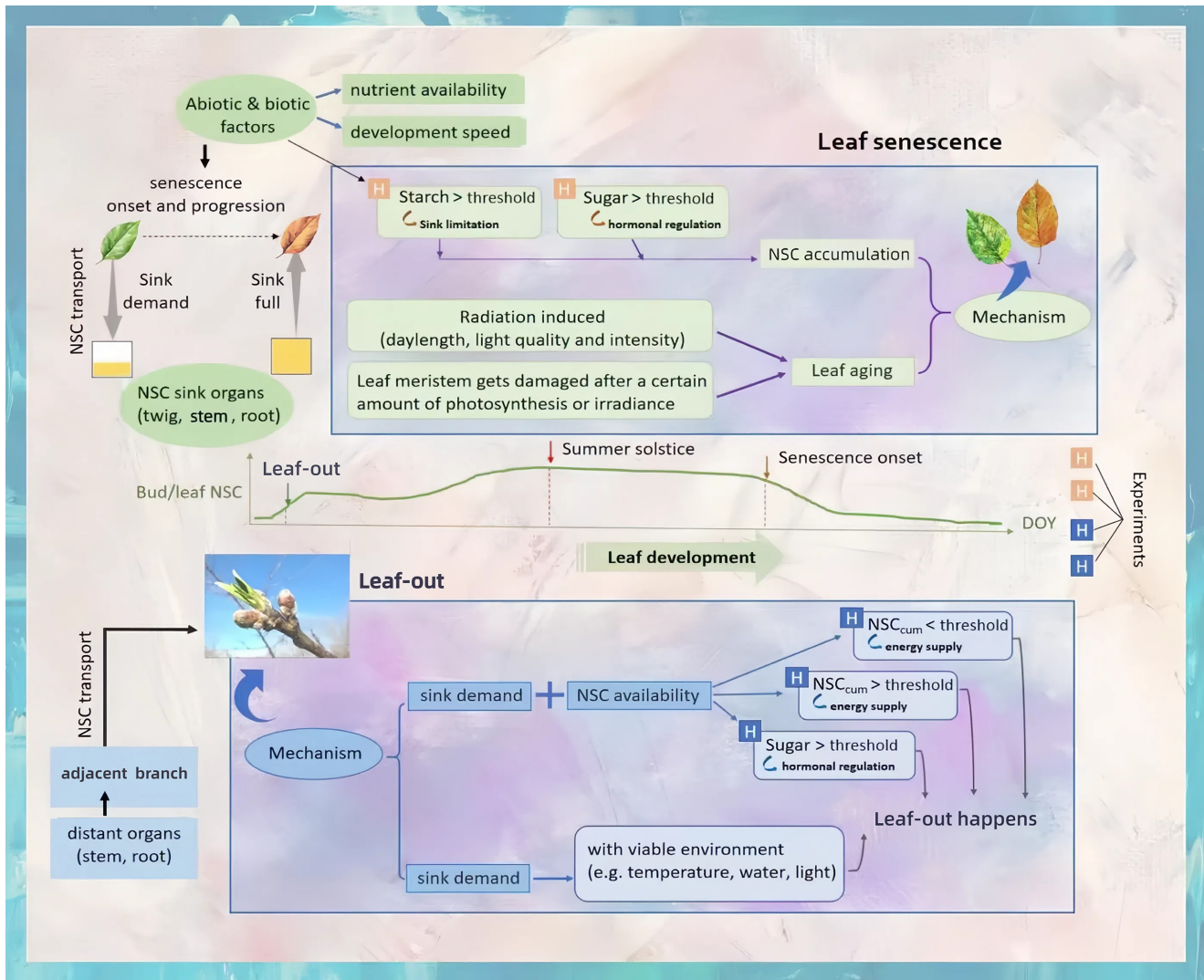


FIGURE 2 Proposed possible mechanisms driving critical phenological stages bud break and leaf senescence include the involvement of non-structural carbohydrates (NSC). NSC are mobilized from branches, stems, and roots to meet the energy demands of bud break, which may be induced when NSC levels in leaf buds surpass or are below a certain threshold. During leaf senescence, aging caused by radiation, photosynthetic activity, and NSC accumulation may trigger the onset and progression of senescence. This process might be influenced by both abiotic and biotic factors, such as nutrient availability and the developmental speed of trees. ‘H’ stands for the proposed hypotheses.

in leaf buds decrease before bud break and maintain low concentrations in emerged leaves until the summer solstice. Then, they gradually accumulate NSC until the end of the growing season. In contrast, starch concentrations increase in spring, reaching a peak in early summer. This is followed by a decline to a low point in mid-summer, before rising to high concentrations at the end of summer and then gradually decreasing until the end of the growing season. Starch is typically considered as a carbon storage molecule, while soluble sugars perform immediate functions such as osmoregulation and energy supply. They are kept above a certain threshold for plant health and functionality (Dietze et al., 2014; Martínez-Vilalta et al., 2016). Maurel et al. (2004) highlighted the significant role of hexoses (glucose and fructose) over sorbitol or sucrose in supporting budburst, suggesting that sugars differ in their importance in regulating plant developmental processes. Despite these insights,

the specific roles and interactions between different types of NSC in influencing critical phenological stages remain unclear.

As the occurrence of phenological stages concurs with the variations in NSC in leaves and branches, it remains unclear whether these relationships are correlational or causal. It is uncertain whether the co-occurring variation of NSC and the progression of phenological stages are primarily (and directly) controlled by environmental factors or whether NSC plays the main role in inducing phenological stages. Moreover, the causal relationship between NSC and phenology can be bidirectional. For instance, NSC may help to induce bud break, while NSC dynamics in the growing season are likely to be strongly influenced by the timing of full leaf emergence. By summarizing the known processes and proposing potential mechanisms that induce the phenological stages, particularly those related to NSC (Figure 2), we advocate for revealing

a clear causal relationship between NSC and phenology through designed experiments.

One of the driving forces of bud break can be attributed to sink demand (Gessler & Zweifel, 2024). The carbon demand of sink tissues of trees starts to increase with a suitable environment in spring. It is mainly influenced by variations in environmental factors such as temperature, water, and light availability. At the same time, buds respond to warming, leading to budburst once a certain number of growing degree days has been reached (Fu et al., 2015). We hypothesize three potential processes in which NSC availability may regulate and modify leaf phenology (Figure 2):

1. NSC in a tree become depleted before leaf-out due to the increasing demand from sink and storage tissues across the plant driven by respiration and other metabolic processes that intensify with warmer temperatures (Sperling et al., 2015). Before the storage threshold drops below a critical threshold, bud break might be initiated to replenish carbon stores via photosynthates from the newly developed leaves. The observation that trees maintain a large safety margin in their NSC reserves relative to the carbon demand for new leaf production (Hoch et al., 2003) does not contradict this hypothesis. This storage safety margin, sufficient to replace canopy leaves up to four times, is essential to ensure recovery from events like late frost or insect defoliation, which can destroy the emerging foliage. A second flush would have to be supported by the NSC storage (Baumgarten et al., 2023). In addition, it is known that not all stored carbon can be remobilized again (Sala et al., 2012).
2. Beyond the demand in sink and storage tissues, bud break may occur when cumulative NSC levels in leaf buds, sourced both from the buds themselves and other plant organs, surpasses a certain threshold.
3. Furthermore, bud break is triggered when sugar concentration, increasing with starch decomposition, exceeds a threshold, stimulating the production of plant hormones such as auxin (Chen et al., 2022).

How NSC concentration influences the timing of leaf senescence (especially relevant with deciduous trees) remains incompletely understood. The phenomenon observed by Zohner et al. (2023) raises questions about the mechanisms underlying the varied temperature effects. By reflecting on whole-tree carbon relations, we hypothesized that variations in NSC within leaves may be a key to understanding leaf senescence.

We hypothesize that leaf aging and NSC accumulation, interacting with environmental factors such as nutrient availability, might interactively regulate the initiation of leaf senescence (Figure 2). Changes in radiation (daylength, radiation intensity, and light spectral components) combined with a constrained leaf life span (leaf photosystems get damaged after a certain amount of photosynthetic activity (Zavafer & Mancilla, 2021)) have previously been suggested to induce leaf aging. However, a recent study suggested that radiation intensity and leaf lifespan do not

significantly affect the onset and progression of leaf senescence (Zohner et al., 2023). Instead, this study supports the idea that the rate at which plants complete their seasonal developmental stages—and consequently, the point at which the demand from sinks markedly decreases—plays a crucial role in determining the timing of senescence. It is possible that NSC accumulation mediates these processes (Figure 2):

1. There may be a threshold of starch concentration in the leaves beyond which leaf senescence is induced. After leaf-out, with leaf expansion and development, sucrose is transported to sink organs to meet the carbon demand for growth and storage. Excessive photosynthates produced by leaves increase leaf NSC concentration levels while satisfying the carbon demand of sink organs such as branches, stems, roots, and fruits reduces them (Dietze et al., 2014). This carbon demand typically declines after the summer solstice, as indicated by a marked decrease in stem growth rate (Etzold et al., 2022). Starch may then accumulate to a level that induces negative feedback such as decreasing expression of photosynthetic genes that, in turn, signals the cessation of leaf development and the initiation of leaf senescence (Paul & Foyer, 2001). This process may be affected by both abiotic and intrinsic biotic factors. Environmental factors such as temperature and water availability drive the trees' intra-annual development speed and determine their developmental stages. For instance, sufficient rainfall and warm temperatures in spring may promote the development of trees' leaves and photosynthesis and result in the starch threshold being reached earlier in the leaves in summer, which nudges the trees to initiate the senescence process earlier. In contrast, spring drought may lead to inadequate synthesized NSC to fulfil the carbon supply for tree growth and reach the starch threshold later, which leads to a delay of leaf senescence in the later stage. Nutrient deficiency, which limits the production of new biomass, combined with reduced sink demand during advanced developmental stages, may further elevate NSC concentrations, potentially triggering the onset and progression of leaf senescence.
2. A threshold of sugar concentration in mature leaves may also initiate negative feedback, inhibiting photosynthetic capacity (Tian et al., 2024) and impacting the production of hormones such as abscisic acid (Chen et al., 2022), thereby accelerating leaf senescence. As the demand for storage decreases towards autumn, when sufficient starch has been accumulated for over-winter storage (Furze et al., 2019; Zahnd et al., 2024), phloem unloading in storage tissues such as stems and roots is reduced leading to a decreased concentration (and consequently pressure) gradient between the collecting phloem in the leaves and the release phloem in the storage tissues (Gessler & Zweifel, 2024). This inhibits leaf phloem loading and thus increases leaf sugar concentrations.

To further confirm the causal relationship between phenology and NSC levels, we need to integrate information on C supply and demand with leaf phenology data, improve the temporal sampling

of NSC, especially around critical transition times such as summer solstice, and plan targeted experiments.

Experiments are needed to falsify or validate testable hypotheses related to the proposed questions above. Such hypotheses might be H1: Starch and sugar accumulation induced by sink demand changes affect autumn senescence. This accumulation is not necessarily dependent on direct environmental effects on the leaf-level metabolism but can also result from environmentally induced changes in the sink demand. H2: Reduced sink demand decreases phloem loading, and as a consequence, NSC accumulates in the leaves, potentially also affecting the plant hormones, and induce the leaf senescence. This mechanism would only act after the summer solstice and is thus circadian clock dependent.

To test these hypotheses, experiments that alter the concentrations of NSC independently of environmental cues are needed. As a control, (1) it needs to be assessed how altering the key environmental drivers for plant growth such as light, temperature, and water availability, impacts NSC and phenology. In addition, (2) NSC needs to be manipulated without changing environmental cues, for example manipulating the NSC distribution pattern through girdling (Hoch, 2005; Rademacher et al., 2021), phloem chilling (Rademacher et al., 2022), injecting of sugar (Zhang et al., 2023), atmospheric CO₂ manipulation (Huang et al., 2019; Schädel et al., 2010), shading (Weber et al., 2019), or repetitive defoliation (Schmid et al., 2017). Manipulating stem and soil temperature and keeping leaf temperature constant might additionally allow to manipulate sink but not source activity. Finally, (3) NSC concentrations could be altered by mimicking the living conditions under disturbances and extreme events such as the droughts, heatwave, frost and pest attack. A synoptic analysis of (1)–(3) could then distinguish between external impacts on phenology that potentially affect NSC control and NSC being a regulator of phenology. Assessing (1)–(3) at different simulated daylengths will additionally elucidate the influence of the circadian clock.

Along with key questions regarding the reciprocal relationship between NSC and phenological stages, many open questions remain to be answered to gain a holistic picture of plant growth:

1. The carbon budget and the conversion coefficients: it is crucial to understand the carbon mass balance and the conversion coefficients of carbon between source and sink organs to better estimate the carbon demand of trees. For example, how much NSC is needed from foliage to build each unit of branch and stem carbon, and how much photosynthates are required to regain the carbon needed to produce a leaf?
2. Carbon mobilization trajectories: our knowledge of carbon allocation and the exact interaction mechanisms between different organs remains limited (Merganičová et al., 2019). Isotope labeling experiments and whole-tree budgets of the fate of assimilates (e.g. Joseph et al., 2020) might shed light on this aspect.
3. Role of the internal circadian clock: the importance of the summer solstice in the temperature response of autumn phenology indicates central contributions of photoperiodic cues and, thus of the

circadian clock, either acting directly on leaf processes (e.g. via hormonal control) or indirectly via its effect on growth and storage (de Lucas et al., 2008; Dodd et al., 2005). Thus, investigating how the internal circadian clock of plants regulates the relationship between NSC and phenology is essential.

3 | NSC DYNAMICS AS A RESULT OF CARBON SINK AND SOURCE ACTIVITY AND CARBON FLOWS IN DIFFERENT ORGANS

While sink and source activities and carbon allocation determine the trees' NSC levels, the exact mechanisms that drive NSC dynamics are not fully understood. Different tree species have their own endogenous growth rhythm and internal clock to govern the time window of critical development stages (e.g. bud break and stem growth) and ensure their survival and competitive advantages (Delpierre et al., 2016; Dodd et al., 2005; Way & Montgomery, 2015). In addition, NSC allocation could be influenced by tree's water use strategies (isohydric or anisohydric) and different water transport systems (ring-porous versus diffuse-porous) in trees (Dietze et al., 2014; Huang et al., 2024). The recently postulated adjustment of source activity and sink demand through stomatal optimization of tree growth might play a role in modifying the effects of NSC allocation depending on water and carbon availability (Gessler & Zweifel, 2024).

Along with exploring carbon allocation patterns, conceptual models have also been proposed to describe the mechanisms of carbon and NSC flows. A conceptual model suggests that temperature assists the process of carbohydrate redistribution processes. NSC distribution patterns differ among seasons, potentially due to varying temperature patterns between tree crowns and roots (Sperling et al., 2017; Tixier et al., 2019; Zwieniecki et al., 2015). During spring, the soil is typically colder than the air. Xylem redistributes the stored NSC by transporting sugars upwards to the canopy to support leaf-out and vegetative growth before the leaves mature and become productive (Sperling et al., 2017). In contrast, when the soil is generally warmer than the air in autumn, a compartmentalization of carbon allocation between the canopy and the roots is shown. The colder canopies restrain the export of assimilated carbohydrates towards the warmer roots, resulting in an accumulation of NSC in the upper stem. Meanwhile, the warmer lower part, including the stem and roots, continues transporting NSC towards the deeper roots (Sperling et al., 2015). This proposed conceptual model generally explains the seasonal allocation pattern of NSC to different tree organs. However, it contradicts field observations and experiments that demonstrate that higher soil temperatures advance leaf-out (Baldocchi et al., 2005; Malyshev et al., 2023), and there are no significant NSC differences among vertical profiles of the stem (Richardson et al., 2015). Future studies are necessary to refine these conceptual models and validate them through designed experiments and field observations.

4 | IMPROVING THE REPRESENTATION OF NSC DYNAMICS IN CARBON ALLOCATION MODELS

Capturing the dynamics of NSC in different compartments is critical in establishing the relationship between leaf phenology and NSC (or vice-versa). The currently unsatisfactory representation of NSC dynamics in models limits the potential to link leaf phenology and NSC at spatial scales. As key components of forest carbon dynamics, simulating NSC variations in different organs should be integrated into the framework of carbon allocation modelling. However, current carbon allocation models are often oversimplified and lack organ-specific NSC simulations (Merganičová et al., 2019). Reviewing the current state of carbon allocation modelling, we highlight the knowledge gaps in NSC (and general carbon allocation) modelling and summarize potential approaches to fill these gaps.

Most models still fully or partially apply a 'fixed ratio', which sets fixed fractions of the assimilated carbon to be allocated to each tree organ (Franklin et al., 2012). These fixed coefficients, can be mainly attributed to the lack of a convincing dynamic and prognostic scheme for carbon allocation. (De Kauwe et al., 2014; Poorter et al., 2012). Apart from the fixed carbon allocation ratios, current carbon allocation models have other shortcomings, such as (1) a deficiency in accounting for the direct sensitivity of carbon allocation to environmental conditions (Merganičová et al., 2019); (2) ignorance of the impacts of disturbances on carbon allocation such as the influences from drought, wind damage, insects, ice storms, and pathogens (Seidl et al., 2011, 2017); (3) failure to represent certain carbon pools in reproductive and storage organs that are used for defence and repair (Merganičová et al., 2019) and particularly carbon pools for mycorrhiza (Vargas, 2009) and root exudates; (4) coarse temporal resolution so that the models are not efficient to compute seasonal changes in carbon allocation (Merganičová et al., 2019); (5) a lack of high-quality observational data to calibrate and validate carbon allocation in different carbon pools (Hartmann & Trumbore, 2016).

Closing these gaps in carbon allocation has considerable potential to improve forecasts of NSC concentrations and their seasonality, especially concerning warmer and more extreme climate scenarios (Robinson et al., 2021). To pursue reliable modelled NSC estimates under climate change, we need to consider (1) identifying the allocation processes we particularly need to understand and formulating the specific scientific questions (e.g. how root: shoot ratio varies in response to nutrient availability) and testable hypotheses; (2) prioritizing the development of the models that represent carbon allocation variations under changing environmental conditions; (3) incorporating relevant factors and processes that are assumed to be more crucial under future conditions, for instance, different disturbances, trees' defence and repair strategies; (4) integrating the underrepresented carbon pools in the carbon allocation models such as fruits and seeds, root exudates and trees' symbionts like mycorrhiza (Merganičová et al., 2019). To better understand shifts in carbon allocation and NSC dynamics in ecosystems in a changing environment, comprehensive measurements at specific 'super experiment

sites' such as FACE sites and basic carbon pool measurements from multi-site networks (Franklin et al., 2012) should be leveraged. Such approaches can provide valuable data to quantify carbon flow patterns in different tree and ecosystem compartments both temporally and spatially.

5 | UNDERSTANDING THE RELATIONSHIP BETWEEN NSC CONCENTRATION AND LEAF PHENOLOGY OVER LARGE SCALES

We have seen that linking NSC concentrations and leaf phenology is not straightforward, and it becomes particularly challenging at larger scales. Leaf phenology data at large spatial scales are the less problematic part. They are, for example, available from (1) ground phenological observations from the Pan European Phenology Project (PEP725), the USA National Phenology Network (USANPN), and other citizen science projects (Brown et al., 2016); (2) vegetation indexes acquired from near-surface remote sensing networks and satellites, expanding the observations of phenology beyond the individual plants. Specifically, establishing regional or continental near-surface observation of plants through digital cameras (PhenoCam) facilitates phenology monitoring at canopy and landscape scales (Nasahara & Nagai, 2015; Richardson, 2023). Satellite spectral sensors such as MODIS, Landsat, and Sentinel-2 provide opportunities to compute different vegetation indexes at various temporal and spatial resolutions. Phenological stages such as green-up and senescence can be extracted through different phenological extraction algorithms (Filippa et al., 2016; Luo et al., 2018). However, a recent study demonstrates that extracted phenological stages might differ substantially with various phenological derivation methods and data sources, including ground observations and remote sensing data. Thus, it has been suggested that using an ensemble of available phenological data may be best for assessing phenology trends, especially in autumn (Kloos et al., 2024).

In contrast, NSC concentrations are currently not easy to measure because of the difficulties of sampling plant material from trees (e.g. canopy access, root sampling, and identification), the time-consuming sample preparation, and laboratory analyses. This challenges NSC measurements at large spatial scales and creates a bottleneck in investigating the relationship between NSC and leaf phenology. Theoretically, process-based models can simulate spatial variations in NSC (e.g. Ninomiya et al. (2023)), potentially linking these variations to phenological changes. However, accurate simulation of NSC temporal and spatial variation hinges on two key factors: (1) a proper understanding of the mechanisms that govern carbon allocation among different pools in trees (see Section 4), and (2) abundant and high-quality NSC data suitable for model calibration and validation (Merganičová et al., 2019). As demonstrated in the model section, these prerequisites are often not met. With new tools and approaches such as cavity-enhanced Raman spectroscopy, a shift from measuring only NSC concentration to a more

process-oriented approach that pinpoints NSC flows between different pools and how they vary over time is strongly advocated (Hartmann & Trumbore, 2016).

With the development of remote sensing techniques, alternative approaches might arise to quantify the spatial variation of NSC in leaves (Liu et al., 2024; Wang et al., 2020). For instance, airplane-based imaging spectroscopy captures signals reflecting biochemical compounds even though not all traits are well modelled concurrently (Wang et al., 2020). This might open the possibility of characterizing the foliar NSC spatial variations at canopies using spectral information (Wang et al., 2020) or combining spectra with environmental factors (Asner et al., 2017). However, airborne imaging spectroscopy is expensive and often has limited temporal (usually one to few times per year) or spatial coverage (Asner et al., 2017). To overcome these shortcomings, recent endeavours have been made, such as combining the spectra, time series of vegetation indexes obtained from high-resolution satellite (e.g. Sentinel-2) images, and machine learning methods to retrieve high-resolution and accurate mapping of foliar traits, including NSC in 14 National Ecological Observatory Network (NEON) sites (Liu et al., 2024). The global Sentinel-2 archives and the scalability of this method imply a promising avenue for future high temporal and spatial mapping of leaf NSC.

Besides, remote sensing also helps to spatially quantify carbon sink-source activities and biomass in different tree components (Eitel et al., 2023; Li et al., 2018). Sun-induced fluorescence provides a proxy for photosynthesis and thus photosynthetic (source) activity (Li et al., 2018; Magney et al., 2019). At the same time, spectral indices from PlanetScope satellites have been shown to correlate with tree stem growth phenology and, therefore, sink activity (Eitel et al., 2023). Moreover, by leveraging terrestrial laser scanning in the forest inventories (Liang et al., 2016) and airborne radar and lidar data across the landscape to a large scale (Tian et al., 2023), we potentially will be able to separate the stem, the branches, and leaves and estimate their biomass (and biomass change) applying 3D tree modelling methods (Liang et al., 2016) soon. We can better estimate the NSC in various tree pools by combining the measured NSC concentration in different tree compartments and reliable NSC models.

Based on the above background, we suggest improving the following aspects to characterize better spatial NSC variations and further link them to leaf phenology:

1. More strategic planning to improve the spatial representation of NSC measurements: our sampling resources should be prioritized to differentiate confounding factors and better understand the carbon allocation patterns. Various factors such as leaf habit (e.g. deciduous versus evergreen, broadleaf versus needle leaf), wood anatomy (e.g. ring-porous versus diffuse-porous), shade tolerance preference, water use strategy (e.g. isohydric versus anisohydric) can be considered (Furze et al., 2019; Huang et al., 2024) when designing the NSC sampling plan for various tree species. Additionally, it has been shown that NSC concentrations often decline from sapwood to heartwood (Hoch et al., 2003), so intra-compartment/organ variations of
2. Improving the temporal NSC sampling in different tree organs: to better discern the relationship between leaf phenology and NSC, we particularly need to increase the sampling frequency of NSC (several days to weekly resolution) at representative experimental sites such as FACE and eddy covariance sites and focus on the variation of NSC during critical climatic and phenological stages such as budburst and leaf flushing, summer solstice, and leaf senescence. Analysis of masting years and extreme climatic conditions, such as drought and heat, will also provide crucial insights due to their substantial direct and lagged impact on tree NSC storage dynamics (D'Andrea et al., 2021).
3. Harmonizing different datasets and approaches to improve spatial representation in NSC models: apart from the traditional method of using allometric relationships to estimate the biomass and thus NSC storage in tree organs (Furze et al., 2019; Hoch et al., 2003; Merganičová et al., 2019), other techniques and data sources that reflect carbon sink and source activities, as well as variations in biomass, can be leveraged to refine the NSC models. For instance, spatially representative eddy covariance towers can provide data on canopy photosynthesis (source activity) in specific forest stands globally (Baldocchi et al., 2001). Concurrently, coupled with on-site NSC measurements, forest growth data, such as stem and root growth (sink activity), can be continuously measured through co-located infrastructures like dendrometers and microcores samplings. As mentioned above, remote sensing products can potentially improve the spatial characterization of NSC in different tree organs for large spatial scales. With a better understanding of carbon flow among different carbon pools, these datasets can be used as constraints in carbon allocation models, improving their reliability in spatial simulation.

6 | CONCLUDING REMARKS: INTEGRATING MULTIPLE APPROACHES TO GAIN A HOLISTIC UNDERSTANDING OF THE RELATIONSHIP BETWEEN NSC AND LEAF PHENOLOGY

How internal physiological factors regulate plant phenology, has received relatively little attention. We summarize recent advances in this area by echoing a growing number of studies (Blumstein et al., 2024; Klein et al., 2016; Tixier et al., 2019), stressing that NSC concentration can be a key internal physiological trait that influences leaf development and phenology. Here, we call for a holistic understanding of the relationship between leaf NSC and phenology at various spatial scales through different approaches (Figure 3):

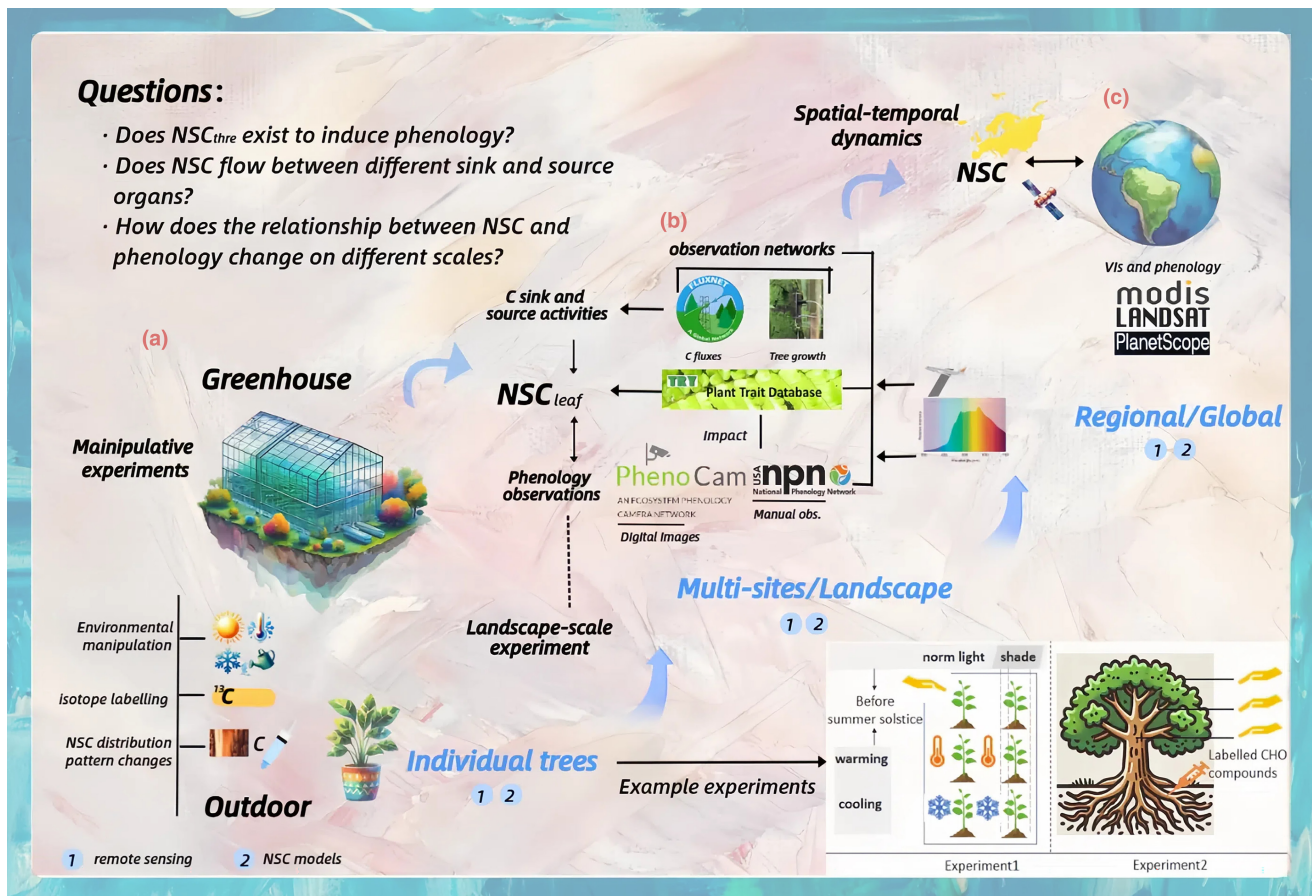


FIGURE 3 Integrating different approaches to understand the relationship between NSC and leaf phenology at various spatial scales involves examining (a) individual trees, (b) Multi-sites and the landscape, and (c) the regional or global scale. At the individual tree scale, two example experiments are proposed to test (1) if NSC thresholds induce senescence after the summer solstice and (2) how NSC are transported among different organs. Environmental drivers are planned to be manipulated (Experiment 1) and multi-isotopically labelled carbohydrates (e.g. ^{13}C and ^2H labelled sucrose) are proposed to be injected (Experiment 2) into tree roots before critical phenological stages, respectively. Data from different observation networks representing phenology and carbon (C) source and sink activities are used at the multiple sites and landscape scale. At regional and global scales, remote sensing data products can help understand the spatial-temporal dynamics of NSC and phenology. Across these scales, remote sensing and modelling are essential for comprehending the NSC-phenology relationship. NSC thresholds (NSC_{thre}) refer to the concentrations of leaf NSC (sugar or starch) that trigger phenological stages. CHO, carbohydrates such as sucrose; manual obs., manual phenology observation; NSC, non-structural carbohydrates; VIs, vegetation indexes.

- Deepening the mechanistic understanding of the relationship between leaf NSC and phenology through manipulative experiments. Manipulative experiments are advocated to be implemented under natural and controlled conditions. By manually altering NSC levels through different experiments and applying isotope labelling (Joseph et al., 2020; Sperling et al., 2015), we can better understand the changes in allocation patterns under chronic and abrupt environmental changes, the turnover rate of different carbon pools, and how newly assimilated and stored carbon is distributed in response to the environment (Joseph et al., 2020), which lays the foundation for improving the mechanistic NSC models.
- Integrating data from different observation networks and carbon allocation models to better link NSC and phenology. Integrating different measurements such as leaf phenology, carbon fluxes, stem growth, and different tree compartments'

NSC, primarily focusing on the sites that harbour all these measurements, we could better understand how carbon sink and source activities impact the NSC variations in different organs, thus providing a more holistic perspective at the whole-tree level. Such datasets further provide opportunities to constrain and better parameterize carbon allocation models with high temporal resolution data, therefore, better simulating the NSC dynamics in different organs (Richardson, Carbone, et al., 2013). This will improve our understanding of the complex interplay between leaf development and the activities of the rest of the plants (Zohner et al., 2023) and the relation between NSC and leaf phenological changes.

- Quantifying the patterns and trends of relationships between NSC and phenology using remote sensing and modelling. With the progress of remote sensing techniques and the integration of different measurements in observation networks (Wang

et al., 2020), the possibility of quantifying the spatial variation of leaf NSC is increasing. By integrating remote sensing products that represent carbon sink and source activities, we can better constrain process-based carbon allocation models and more accurately estimate the spatial variation of NSC in different carbon pools. In conjunction with already enriched large-scale phenology products in the past decades, we are likely to better identify the relationship between leaf phenology and NSC both spatially and temporally.

AUTHOR CONTRIBUTIONS

Yunpeng Luo, Constantin Zohner, and Arthur Gessler conceived the original idea. Yunpeng Luo organized the review and drafted the first draft. Jianlan Feng and Yunpeng Luo made the figures. Thomas W. Crowther, Günter Hoch, Peng Li, Andrew D. Richardson, Yann Vitasse contributed critical and substantial improvements to the drafts and all authors gave final approval for publication.

ACKNOWLEDGEMENTS

The authors acknowledge the financial support from the Swiss National Science Foundation SNF (Project 320030-232013 and Sinergia-funded project 'Upscale' CRSII5_216562). ADR acknowledges support from the National Science Foundation (DEB 1832210). We thank Ms. Chengjing Nie for her assistance on revising figures.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The raw phenology and NSC data are available at Figshare Repository: Phenology (<https://doi.org/10.6084/m9.figshare.21952826>), and NSC (<https://doi.org/10.6084/m9.figshare.23559837>) (Zahnd et al., 2024). The reanalyzed code can be found in Zenodo (<https://zenodo.org/records/13948679>).

ORCID

Yunpeng Luo  <https://orcid.org/0000-0001-6383-8300>

Constantin Zohner  <https://orcid.org/0000-0002-8302-4854>

Thomas W. Crowther  <https://orcid.org/0000-0001-5674-8913>

Günter Hoch  <https://orcid.org/0000-0003-0985-9746>

Andrew D. Richardson  <https://orcid.org/0000-0002-0148-6714>

Yann Vitasse  <https://orcid.org/0000-0002-7454-505X>

Arthur Gessler  <https://orcid.org/0000-0002-1910-9589>

REFERENCES

- Amico Roxas, A., Orozco, J., Guzmán-Delgado, P., & Zwieniecki, M. A. (2021). Spring phenology is affected by fall non-structural carbohydrate concentration and winter sugar redistribution in three Mediterranean nut tree species. *Tree Physiology*, 41(8), 1425–1438.
- Arend, M., Gessler, A., & Schaub, M. (2015). The influence of the soil on spring and autumn phenology in European beech. *Tree Physiology*, 36(1), 78–85.
- Asner, G. P., Martin, R. E., Knapp, D. E., Tupayachi, R., Anderson, C. B., Sinca, F., Vaughn, N. R., & Llacayo, W. (2017). Airborne laser-guided imaging spectroscopy to map forest trait diversity and guide conservation. *Science*, 355(6323), 385–389.
- Baldocchi, D., Falge, E., Gu, L., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, C., Davis, K., Evans, R., Fuentes, J., Goldstein, A., Katul, G., Law, B., Lee, X., Malhi, Y., Meyers, T., Munger, W., Oechel, W., ... Wofsy, S. (2001). FLUXNET: A new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. *Bulletin of the American Meteorological Society*, 82(11), 2415–2434.
- Baldocchi, D. D., Black, T. A., Curtis, P. S., Falge, E., Fuentes, J. D., Granier, A., Gu, L., Knohl, A., Pilegaard, K., Schmid, H. P., Valentini, R., Wilson, K., Wofsy, S., Xu, L., & Yamamoto, S. (2005). Predicting the onset of net carbon uptake by deciduous forests with soil temperature and climate data: A synthesis of FLUXNET data. *International Journal of Biometeorology*, 49(6), 377–387.
- Baumgarten, F., Gessler, A., & Vitasse, Y. (2023). No risk-no fun: Penalty and recovery from spring frost damage in deciduous temperate trees. *Functional Ecology*, 37(3), 648–663.
- Bazot, S., Barthes, L., Blanot, D., & Fresneau, C. (2013). Distribution of non-structural nitrogen and carbohydrate compounds in mature oak trees in a temperate forest at four key phenological stages. *Trees-Structure and Function*, 27(4), 1023–1034.
- Blumstein, M., Oseguera, M., Caso-McHugh, T., & Des Marais, D. L. (2024). Nonstructural carbohydrate dynamics' relationship to leaf development under varying environments. *New Phytologist*, 241(1), 102–113.
- Brown, T. B., Hultine, K. R., Steltzer, H., Denny, E. G., Denslow, M. W., Granados, J., Henderson, S., Moore, D., Nagai, S., SanClements, M., Sánchez-Azofeifa, A., Sonntag, O., Tazik, D., & Richardson, A. D. (2016). Using phenocams to monitor our changing Earth: Toward a global phenocam network. *Frontiers in Ecology and the Environment*, 14(2), 84–93.
- Chen, Q., Zhang, J., & Li, G. (2022). Dynamic epigenetic modifications in plant sugar signal transduction. *Trends in Plant Science*, 27(4), 379–390.
- D'Andrea, E., Scartazza, A., Battistelli, A., Collalti, A., Proietti, S., Rezaie, N., Matteucci, G., & Moscatello, S. (2021). Unravelling resilience mechanisms in forests: Role of non-structural carbohydrates in responding to extreme weather events. *Tree Physiology*, 41(10), 1808–1818.
- de Kauwe, M. G., Medlyn, B. E., Zaehle, S., Walker, A. P., Dietze, M. C., Wang, Y.-P., Luo, Y., Jain, A. K., el-Masri, B., Hickler, T., Wärlind, D., Weng, E., Parton, W. J., Thornton, P. E., Wang, S., Prentice, I. C., Asao, S., Smith, B., McCarthy, H. R., ... Norby, R. J. (2014). Where does the carbon go? A model-data intercomparison of vegetation carbon allocation and turnover processes at two temperate forest free-air CO₂ enrichment sites. *New Phytologist*, 203(3), 883–899.
- de Lucas, M., Davière, J.-M., Rodríguez-Falcón, M., Pontin, M., Iglesias-Pedraz, J. M., Lorrain, S., Fankhauser, C., Blázquez, M. A., Titarenko, E., & Prat, S. (2008). A molecular framework for light and gibberellin control of cell elongation. *Nature*, 451(7177), 480–484.
- Delpierre, N., Vitasse, Y., Chuine, I., Guillemot, J., Bazot, S., Rutishauser, T., & Rathgeber, C. B. K. (2016). Temperate and boreal forest tree phenology: From organ-scale processes to terrestrial ecosystem models. *Annals of Forest Science*, 73(1), 5–25.
- Deslauriers, A., Fournier, M. P., Carteni, F., & Mackay, J. (2019). Phenological shifts in conifer species stressed by spruce budworm defoliation. *Tree Physiology*, 39(4), 590–605.
- Deslauriers, A., Garcia, L., Charrier, G., Buttò, V., Pichette, A., & Paré, M. (2021). Cold acclimation and deacclimation in wild blueberry: Direct and indirect influence of environmental factors and non-structural carbohydrates. *Agricultural and Forest Meteorology*, 301–302, 108349.

- Dietze, M. C., Sala, A., Carbone, M. S., Czimczik, C. I., Mantooth, J. A., Richardson, A. D., & Vargas, R. (2014). Nonstructural carbon in woody plants. *Annual Review of Plant Biology*, *65*, 667–687.
- Dodd, A. N., Salathia, N., Hall, A., Kévei, E., Tóth, R., Nagy, F., Hibberd, J. M., Millar, A. J., & Webb, A. A. R. (2005). Plant circadian clocks increase photosynthesis, growth, survival, and competitive advantage. *Science*, *309*(5734), 630–633.
- Eitel, J. U. H., Basler, D., Braun, S., Buchmann, N., D'Odorico, P., Etzold, S., Gessler, A., Griffin, K. L., Krejza, J., Luo, Y., Maguire, A. J., Rao, M. P., Vitasse, Y., Walthert, L., & Zweifel, R. (2023). Towards monitoring stem growth phenology from space with high resolution satellite data. *Agricultural and Forest Meteorology*, *339*, 109549.
- Etzold, S., Sterck, F., Bose, A. K., Braun, S., Buchmann, N., Eugster, W., Gessler, A., Kahmen, A., Peters, R. L., Vitasse, Y., Walthert, L., Ziemnińska, K., & Zweifel, R. (2022). Number of growth days and not length of the growth period determines radial stem growth of temperate trees. *Ecology Letters*, *25*(2), 427–439.
- Filippa, G., Cremonese, E., Migliavacca, M., Galvagno, M., Forkel, M., Wingate, L., Tomelleri, E., Di Cella, U. M., & Richardson, A. D. (2016). Phenopix: AR package for image-based vegetation phenology. *Agricultural and Forest Meteorology*, *220*, 141–150.
- Fischer, C., & Höll, W. (1991). Food reserves of scots pine (*Pinus sylvestris* L.). *Trees*, *5*(4), 187–195.
- Franklin, O., Johansson, J., Dewar, R. C., Dieckmann, U., McMurtrie, R. E., Brännström, Å., & Dyzbinski, R. (2012). Modeling carbon allocation in trees: A search for principles. *Tree Physiology*, *32*(6), 648–666.
- Friedlingstein, P., O'Sullivan, M., Jones, M. W., Andrew, R. M., Bakker, D. C. E., Hauck, J., Landschützer, P., Le Quéré, C., Luijckx, I. T., Peters, G. P., Peters, W., Pongratz, J., Schwingshackl, C., Sitch, S., Canadell, J. G., Ciais, P., Jackson, R. B., Alin, S. R., Anthoni, P., ... Zheng, B. (2023). Global carbon budget 2023. *Earth System Science Data*, *15*(12), 5301–5369.
- Fu, Y. H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., Ciais, P., Huang, M., Menzel, A., Peñuelas, J., Song, Y., Vitasse, Y., Zeng, Z., & Janssens, I. A. (2015). Declining global warming effects on the phenology of spring leaf unfolding. *Nature*, *526*(7571), 104–107.
- Furze, M. E., Huggett, B. A., Aubrecht, D. M., Stolz, C. D., Carbone, M. S., & Richardson, A. D. (2019). Whole-tree nonstructural carbohydrate storage and seasonal dynamics in five temperate species. *New Phytologist*, *221*(3), 1466–1477.
- Gao, L., Aubrey, D. P., Wang, X., & Sun, H. (2022). Seasonal non-structural carbohydrate dynamics differ between twig bark and xylem tissues. *Trees*, *36*(4), 1231–1245.
- Gersony, J. T., Hochberg, U., Rockwell, F. E., Park, M., Gauthier, P. P. G., & Holbrook, N. M. (2020). Leaf carbon export and nonstructural carbohydrates in relation to diurnal water dynamics in mature oak trees. *Plant Physiology*, *183*(4), 1612–1621.
- Gessler, A., & Zweifel, R. (2024). Beyond source and sink control—Toward an integrated approach to understand the carbon balance in plants. *New Phytologist*, *242*(3), 858–869.
- Gruber, A., Pirkebner, D., Oberhuber, W., & Wieser, G. (2011). Spatial and seasonal variations in mobile carbohydrates in *Pinus cembra* in the timberline ecotone of the central Austrian Alps. *European Journal of Forest Research*, *130*(2), 173–179.
- Hagedorn, F., Joseph, J., Peter, M., Luster, J., Pritsch, K., Geppert, U., Kerner, R., Molinier, V., Egli, S., Schaub, M., Liu, J. F., Li, M., Sever, K., Weiler, M., Siegwolf, R. T. W., Gessler, A., & Arend, M. (2016). Recovery of trees from drought depends on belowground sink control. *Nature Plants*, *2*(8), 16111.
- Hartmann, H., & Trumbore, S. (2016). Understanding the roles of non-structural carbohydrates in forest trees—From what we can measure to what we want to know. *New Phytologist*, *211*(2), 386–403.
- Hoch, G. (2005). Fruit-bearing branchlets are carbon autonomous in mature broad-leaved temperate forest trees. *Plant, Cell & Environment*, *28*(5), 651–659.
- Hoch, G. (2015). Carbon reserves as indicators for carbon limitation in trees. In U. Lüttge & W. Beyschlag (Eds.), *Progress in botany: Vol. 76* (pp. 321–346). Springer International Publishing.
- Hoch, G., Richter, A., & Körner, C. (2003). Non-structural carbon compounds in temperate forest trees. *Plant, Cell & Environment*, *26*(7), 1067–1081.
- Huang, J., Hammerbacher, A., Weinhold, A., Reichelt, M., Gleixner, G., Behrendt, T., van Dam, N. M., Sala, A., Gershenson, J., Trumbore, S., & Hartmann, H. (2019). Eyes on the future—Evidence for trade-offs between growth, storage and defense in Norway spruce. *New Phytologist*, *222*(1), 144–158.
- Huang, J., Ladd, S. N., Ingrisch, J., Kübert, A., Meredith, L. K., van Haren, J., Bamberger, I., Daber, L. E., Kühnhammer, K., Bailey, K., Hu, J., Fudyma, J., Shi, L., Dippold, M. A., Meeran, K., Miller, L., O'Brien, M. J., Yang, H., Herrera-Ramírez, D., ... Lehmann, M. M. (2024). The mobilization and transport of newly fixed carbon are driven by plant water use in an experimental rainforest under drought. *Journal of Experimental Botany*, *75*, 2545–2557.
- Joseph, J., Gao, D., Backes, B., Bloch, C., Brunner, I., Gleixner, G., Haeni, M., Hartmann, H., Hoch, G., Hug, C., Kahmen, A., Lehmann, M. M., Li, M. H., Luster, J., Peter, M., Poll, C., Rigling, A., Rissanen, K. A., Ruehr, N. K., ... Gessler, A. (2020). Rhizosphere activity in an old-growth forest reacts rapidly to changes in soil moisture and shapes whole-tree carbon allocation. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(40), 24885–24892.
- Kattge, J., Bönsch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., Abedi, M., Acosta, A. T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert, C. H., Alcántara, J. M., Alcázar, C. C., Aleixo, I., Ali, H., ... Wirth, C. (2020). TRY plant trait database—Enhanced coverage and open access. *Global Change Biology*, *26*(1), 119–188.
- Kissling, W. D., Walls, R., Bowser, A., Jones, M. O., Kattge, J., Agosti, D., Amengual, J., Basset, A., van Bodegom, P. M., Cornelissen, J. H. C., Denny, E. G., Deudero, S., Egloff, W., Elmendorf, S. C., Alonso García, E., Jones, K. D., Jones, O. R., Lavorel, S., Lear, D., ... Guralnick, R. P. (2018). Towards global data products of essential biodiversity variables on species traits. *Nature Ecology & Evolution*, *2*(10), 1531–1540.
- Klein, T., Vitasse, Y., & Hoch, G. (2016). Coordination between growth, phenology and carbon storage in three coexisting deciduous tree species in a temperate forest. *Tree Physiology*, *36*(7), 847–855.
- Kloos, S., Klosterhalfen, A., Knohl, A., & Menzel, A. (2024). Decoding autumn phenology: Unraveling the link between observation methods and detected environmental cues. *Global Change Biology*, *30*(3), e17231.
- Kumar, R., Bishop, E., Bridges, W. C., Tharayil, N., & Sekhon, R. S. (2019). Sugar partitioning and source–sink interaction are key determinants of leaf senescence in maize. *Plant, Cell & Environment*, *42*(9), 2597–2611.
- Landhäusser, S. M. (2011). Aspen shoots are carbon autonomous during bud break. *Trees*, *25*(3), 531–536.
- Li, X., Xiao, J., He, B., Altaf Arain, M., Beringer, J., Desai, A. R., Emmel, C., Hollinger, D. Y., Krasnova, A., Mammarella, I., Noe, S. M., Ortiz, P. S., Rey-Sanchez, A. C., Rocha, A. V., & Varlagin, A. (2018). Solar-induced chlorophyll fluorescence is strongly correlated with terrestrial photosynthesis for a wide variety of biomes: First global analysis based on OCO-2 and flux tower observations. *Global Change Biology*, *24*(9), 3990–4008.
- Liang, X., Kankare, V., Hyypä, J., Wang, Y., Kukko, A., Haggrén, H., Yu, X., Kaartinen, H., Jaakkola, A., Guan, F., Holopainen, M., & Vastaranta, M. (2016). Terrestrial laser scanning in forest inventories. *ISPRS Journal of Photogrammetry and Remote Sensing*, *115*, 63–77.
- Liu, S., Wang, Z., Lin, Z., Zhao, Y., Yan, Z., Zhang, K., Visser, M., Townsend, P. A., & Wu, J. (2024). Spectra-phenology integration for high-resolution, accurate, and scalable mapping of foliar functional traits

- using time-series Sentinel-2 data. *Remote Sensing of Environment*, 305, 114082.
- López, S., & Piper, F. (2022). Phenology explains different storage remobilization in two congeneric temperate tree species with contrasting leaf habit. *Tree Physiology*, 42(3), 501–512.
- Luo, Y., el-Madany, T., Ma, X., Nair, R., Jung, M., Weber, U., Filippa, G., Bucher, S. F., Moreno, G., Cremonese, E., Carrara, A., Gonzalez-Cascon, R., Cáceres Escudero, Y., Galvagno, M., Pacheco-Labrador, J., Martín, M. P., Perez-Priego, O., Reichstein, M., Richardson, A. D., ... Migliavacca, M. (2020). Nutrients and water availability constrain the seasonality of vegetation activity in a Mediterranean ecosystem. *Global Change Biology*, 26(8), 4379–4400.
- Luo, Y., el-Madany, T. S., Filippa, G., Ma, X., Ahrens, B., Carrara, A., Gonzalez-Cascon, R., Cremonese, E., Galvagno, M., Hammer, T. W., Pacheco-Labrador, J., Martín, M. P., Moreno, G., Perez-Priego, O., Reichstein, M., Richardson, A. D., Römermann, C., & Migliavacca, M. (2018). Using near-infrared-enabled digital repeat photography to track structural and physiological phenology in Mediterranean tree-grass ecosystems. *Remote Sensing*, 10, 1293.
- Luo, Y., Pacheco-Labrador, J., Richardson, A. D., Seyednasrollah, B., Perez-Priego, O., Gonzalez-Cascon, R., Martín, M. P., Moreno, G., Nair, R., Wutzler, T., Bucher, S. F., Carrara, A., Cremonese, E., el-Madany, T. S., Filippa, G., Galvagno, M., Hammer, T., Ma, X., Martini, D., ... Migliavacca, M. (2022). Evergreen broadleaf greenness and its relationship with leaf flushing, aging, and water fluxes. *Agricultural and Forest Meteorology*, 323, 109060.
- Ma, X., Zhu, X., Xie, Q., Jin, J., Zhou, Y., Luo, Y., Liu, Y., Tian, J., & Zhao, Y. (2022). Monitoring nature's calendar from space: Emerging topics in land surface phenology and associated opportunities for science applications. *Global Change Biology*, 28(24), 7186–7204.
- Magney, T. S., Bowling, D. R., Logan, B. A., Grossmann, K., Stutz, J., Blanken, P. D., Burns, S. P., Cheng, R., Garcia, M. A., Köhler, P., Lopez, S., Parazoo, N. C., Raczka, B., Schimel, D., & Frankenberg, C. (2019). Mechanistic evidence for tracking the seasonality of photosynthesis with solar-induced fluorescence. *Proceedings of the National Academy of Sciences of the United States of America*, 116(24), 11640–11645.
- Malyshev, A. V., Blume-Werry, G., Spiller, O., Smiljanić, M., Weigel, R., Kolb, A., Nze, B. Y., Märker, F., Sommer, F. C.-F. J., Kinley, K., Ziegler, J., Pasang, P., Mahara, R., Joshi, S., Heinsohn, V., & Kreyling, J. (2023). Warming nondormant tree roots advances aboveground spring phenology in temperate trees. *New Phytologist*, 240(6), 2276–2287.
- Martínez-Vilalta, J., Sala, A., Asensio, D., Galiano, L., Hoch, G., Palacio, S., Piper, F. I., & Lloret, F. (2016). Dynamics of non-structural carbohydrates in terrestrial plants: A global synthesis. *Ecological Monographs*, 86(4), 495–516.
- Maurel, K., Leite, G. B., Bonhomme, M., Guillot, A., Rageau, R., Pétel, G., & Sakr, S. (2004). Trophic control of bud break in peach (*Prunus persica*) trees: A possible role of hexoses. *Tree Physiology*, 24(5), 579–588.
- Menzel, A., Yuan, Y., Matiu, M., Sparks, T., Scheifinger, H., Gehrig, R., & Estrella, N. (2020). Climate change fingerprints in recent European plant phenology. *Global Change Biology*, 26(4), 2599–2612.
- Merganičová, K., Merganič, J., Lehtonen, A., Vacchiano, G., Sever, M. Z. O., Augustynczyk, A. L. D., Grote, R., Kyselová, I., Mäkelä, A., Yousefpour, R., Krejza, J., Collalti, A., & Reyer, C. P. O. (2019). Forest carbon allocation modelling under climate change. *Tree Physiology*, 39(12), 1937–1960.
- Nasahara, K. N., & Nagai, S. (2015). Review: Development of an in situ observation network for terrestrial ecological remote sensing: The Phenological Eyes Network (PEN). *Ecological Research*, 30(2), 211–223.
- Ninomiya, H., Kato, T., Végh, L., & Wu, L. (2023). Modeling of non-structural carbohydrate dynamics by the spatially explicit individual-based dynamic global vegetation model SEIB-DGVM (SEIB-DGVM-NSC version 1.0). *Geoscientific Model Development*, 16(14), 4155–4170.
- Paul, M. J., & Foyer, C. H. (2001). Sink regulation of photosynthesis. *Journal of Experimental Botany*, 52(360), 1383–1400.
- Piao, S., Liu, Q., Chen, A., Janssens, I. A., Fu, Y., Dai, J., Liu, L., Lian, X., Shen, M., & Zhu, X. (2019). Plant phenology and global climate change: Current progresses and challenges. *Global Change Biology*, 25, 1922–1940.
- Poorter, H., Niklas, K. J., Reich, P. B., Oleksyn, J., Poot, P., & Mommer, L. (2012). Biomass allocation to leaves, stems and roots: Meta-analyses of interspecific variation and environmental control. *New Phytologist*, 193(1), 30–50.
- Rademacher, T., Fonti, P., LeMoine, J. M., Fonti, M. V., Basler, D., Chen, Y., Friend, A. D., Seyednasrollah, B., Eckes-Shephard, A. H., & Richardson, A. D. (2021). Manipulating phloem transport affects wood formation but not local nonstructural carbon reserves in an evergreen conifer. *Plant, Cell & Environment*, 44(8), 2506–2521.
- Rademacher, T., Fonti, P., LeMoine, J. M., Fonti, M. V., Bowles, F., Chen, Y., Eckes-Shephard, A. H., Friend, A. D., & Richardson, A. D. (2022). Insights into source/sink controls on wood formation and photosynthesis from a stem chilling experiment in mature red maple. *New Phytologist*, 236(4), 1296–1309.
- Richardson, A. D. (2023). PhenoCam: An evolving, open-source tool to study the temporal and spatial variability of ecosystem-scale phenology. *Agricultural and Forest Meteorology*, 342, 109751.
- Richardson, A. D., Carbone, M. S., Huggett, B. A., Furze, M. E., Czimeczik, C. I., Walker, J. C., Xu, X., Schaberg, P. G., & Murakami, P. (2015). Distribution and mixing of old and new nonstructural carbon in two temperate trees. *New Phytologist*, 206(2), 590–597.
- Richardson, A. D., Carbone, M. S., Keenan, T. F., Czimeczik, C. I., Hollinger, D. Y., Murakami, P., Schaberg, P. G., & Xu, X. (2013). Seasonal dynamics and age of stemwood nonstructural carbohydrates in temperate forest trees. *New Phytologist*, 197(3), 850–861.
- Richardson, A. D., Keenan, T. F., Migliavacca, M., Ryu, Y., Sonnentag, O., & Toomey, M. (2013). Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology*, 169, 156–173.
- Robinson, A., Lehmann, J., Barriopedro, D., Rahmstorf, S., & Coumou, D. (2021). Increasing heat and rainfall extremes now far outside the historical climate. *npj Climate and Atmospheric Science*, 4(1), 45.
- Sala, A., Woodruff, D. R., & Meinzer, F. C. (2012). Carbon dynamics in trees: Feast or famine? *Tree Physiology*, 32(6), 764–775.
- Schädel, C., Richter, A., Blöchl, A., & Hoch, G. (2010). Hemicellulose concentration and composition in plant cell walls under extreme carbon source-sink imbalances. *Physiologia Plantarum*, 139(3), 241–255.
- Schmid, S., Palacio, S., & Hoch, G. (2017). Growth reduction after defoliation is independent of CO₂ supply in deciduous and evergreen young oaks. *New Phytologist*, 214(4), 1479–1490.
- Schwartz, M. D. (2013). Part II: Phenologies of selected bioclimatic zones. In M. D. Schwartz (Ed.), *Phenology: An integrative environmental science* (pp. 157–274). Springer.
- Seidl, R., Fernandes, P. M., Fonseca, T. F., Gillet, F., Jönsson, A. M., Merganičová, K., Netherer, S., Arpacı, A., Bontemps, J.-D., Bugmann, H., González-Olabarria, J. R., Lasch, P., Meredieu, C., Moreira, F., Schelhaas, M. J., & Mohren, F. (2011). Modelling natural disturbances in forest ecosystems: A review. *Ecological Modelling*, 222(4), 903–924.
- Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M. J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T. A., & Reyer, C. P. O. (2017). Forest disturbances under climate change. *Nature Climate Change*, 7(6), 395–402.
- Seyednasrollah, B., Bowling, D. R., Cheng, R., Logan, B. A., Magney, T. S., Frankenberg, C., Yang, J. C., Young, A. M., Hufkens, K., Arain, M. A., Black, T. A., Blanken, P. D., Bracho, R., Jassal, R., Hollinger, D. Y., Law, B. E., Nescic, Z., & Richardson, A. D. (2021). Seasonal variation

- in the canopy color of temperate evergreen conifer forests. *New Phytologist*, 229(5), 2586–2600.
- Shi, W., Li, J., Zhan, H., Yu, L., Wang, C., & Wang, S. (2023). Relation between water storage and photoassimilate accumulation of *Neosinocalamus affinis* with phenology. *Forests*, 14(3), 531.
- Sperling, O., Earles, J. M., Secchi, F., Godfrey, J., & Zwieniecki, M. A. (2015). Frost induces respiration and accelerates carbon depletion in trees. *PLoS One*, 10(12), e0144124.
- Sperling, O., Silva, L. C. R., Tixier, A., Th  roux-Rancourt, G., & Zwieniecki, M. A. (2017). Temperature gradients assist carbohydrate allocation within trees. *Scientific Reports*, 7(1), 3265.
- Tang, J., K  rner, C., Muraoka, H., Piao, S., Shen, M., Thackeray, S. J., & Yang, X. (2016). Emerging opportunities and challenges in phenology: A review. *Ecosphere*, 7(8), e01436.
- Tian, L., Wu, X., Tao, Y., Li, M., Qian, C., Liao, L., & Fu, W. (2023). Review of remote sensing-based methods for forest aboveground biomass estimation: Progress, challenges, and prospects. *Forests*, 14(6), 1086.
- Tian, M., Salmon, Y., Lintunen, A., Oren, R., & H  ltd  , T. (2024). Seasonal dynamics and punctuated carbon sink reduction suggest photosynthetic capacity of boreal silver birch is reduced by the accumulation of hexose. *New Phytologist*, 243(3), 894–908.
- Tixier, A., Gambetta, G. A., Godfrey, J., Orozco, J., & Zwieniecki, M. A. (2019). Non-structural carbohydrates in dormant woody perennials; the tale of winter survival and spring arrival. *Frontiers in Forests and Global Change*, 2, 1–8. <https://doi.org/10.3389/ffgc.2019.00018>
- Tixier, A., Sperling, O., Orozco, J., Lampinen, B., Amico Roxas, A., Saa, S., Earles, J. M., & Zwieniecki, M. A. (2017). Spring bud growth depends on sugar delivery by xylem and water recirculation by phloem M  nch flow in *Juglans regia*. *Planta*, 246(3), 495–508.
- Vargas, R. (2009). On the fate of old stored carbon after large-infrequent disturbances in plants. *Plant Signaling & Behavior*, 4(7), 617–619.
- Wang, Z., Chlus, A., Geygan, R., Ye, Z., Zheng, T., Singh, A., Couture, J. J., Cavender-Bares, J., Kruger, E. L., & Townsend, P. A. (2020). Foliar functional traits from imaging spectroscopy across biomes in eastern North America. *New Phytologist*, 228(2), 494–511.
- Way, D. A., & Montgomery, R. A. (2015). Photoperiod constraints on tree phenology, performance and migration in a warming world. *Plant, Cell & Environment*, 38(9), 1725–1736.
- Weber, R., Gessler, A., & Hoch, G. (2019). High carbon storage in carbon-limited trees. *New Phytologist*, 222(1), 171–182.
- Zahnd, C., Zehnder, M., Arend, M., Kahmen, A., & Hoch, G. (2024). Uniform carbon reserve dynamics along the vertical light gradient in mature tree crowns. *Tree Physiology*, 44(2), tpae005. <https://doi.org/10.1093/treephys/tpae005>
- Zavafer, A., & Mancilla, C. (2021). Concepts of photochemical damage of photosystem II and the role of excessive excitation. *Journal of Photochemistry and Photobiology C: Photochemistry Reviews*, 47, 100421.
- Zhang, Y.-L., Yang, Y., Saurer, M., Schaub, M., Gessler, A., Lehmann, M. M., Rigling, A., Walser, M., Stierli, B., Hajjar, N., Christen, D., & Li, M. H. (2023). Sugar infusion into trees: A novel method to study tree carbon relations and its regulations. *Frontiers in Plant Science*, 14, 1142595.
- Zohner, C. M., Mirzaghali, L., Renner, S. S., Mo, L., Rebindaine, D., Bucher, R., Palouš, D., Vitasse, Y., Fu, Y. H., Stocker, B. D., & Crowther, T. W. (2023). Effect of climate warming on the timing of autumn leaf senescence reverses after the summer solstice. *Science*, 381(6653), eadf5098.
- Zwieniecki, M. A., Tixier, A., & Sperling, O. (2015). Temperature-assisted redistribution of carbohydrates in trees. *American Journal of Botany*, 102(8), 1216–1218.

How to cite this article: Luo, Y., Zohner, C., Crowther, T. W., Feng, J., Hoch, G., Li, P., Richardson, A. D., Vitasse, Y., & Gessler, A. (2024). Internal physiological drivers of leaf development in trees: Understanding the relationship between non-structural carbohydrates and leaf phenology. *Functional Ecology*, 00, 1–14. <https://doi.org/10.1111/1365-2435.14694>