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From Roots to Leaves: Tree Growth Phenology in Forest Ecosystems

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Abstract

Purpose of Review This review synthesizes recent advancements and identifies knowledge gaps in the tree growth phenology of both belowground and aboveground organs in extra-tropical forest ecosystems. Phenology, the study of periodic plant life cycle events, is crucial for understanding tree fitness, competition for resources, and the impacts of climate change on ecosystems. By examining the phenological processes of various tree organs, the review aims to provide a comprehensive understanding of how these processes are interconnected and how they influence overall tree growth and ecosystem dynamics. The review aims to provide a comprehensive overview of current knowledge, highlight recent technological advancements, and identify critical areas where further research is needed.

Recent Findings The review highlights significant progress in monitoring leaf and canopy phenology, thanks to advancements in remote sensing and automated observation systems. These technologies have enhanced our ability to track seasonal changes in leaf development and canopy dynamics more accurately and over larger areas. There has also been a substantial increase in research on wood formation in stems, expanding beyond northern hemisphere conifers to include a broader range of functional groups. However, despite these efforts, identifying the precise drivers of wood formation remains challenging, necessitating further integration of molecular and eco-physiological insights. A critical area of focus is root phenology, encompassing both primary and secondary growth. Despite the fundamental role of roots in tree physiology and ecosystem dynamics, our understanding of root phenology remains limited, primarily due to the inherent difficulties in monitoring root growth. The review emphasizes the need for more detailed studies on root growth processes and the development of new methodologies and technologies to improve root phenology assessments.

Summary The review highlights the importance of incorporating eco-physiological insights into phenological assessments. Leaf and canopy phenology would benefit from more studies focusing on autumnal events. Indeed, compared to the onset of the growing season, much less is known about its end, despite its critical importance for understanding processes such as carbon uptake and nutrient cycle. Advancing knowledge of wood growth phenology will require greater focus on angiosperms, as research on xylogenesis has historically been centered on gymnosperms. This will likely necessitate the development of new, tailored methodologies to address the characteristics of angiosperm wood formation. Similarly, further exploration of phloem phenology is essential to better understand the links between phenological processes across different organs. Finally, compared to other organs, root growth remains less well understood, underscoring the need for deepening the investigation on root phenology in the coming years.

Keywords Xylem phenology · Canopy phenology · Root phenology · Tree growth · Wood formation

Introduction

Phenology refers to the study of the timing of recurring life-cycle events and their biotic and abiotic drivers. The term "phenology" derives from the Greek word φαίνω (phainō), meaning "to show" and "to bring to light", and referring to visible changes in biological development [1]. Nevertheless, modern phenological research not only involves the

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description of observable events in connection with climatic fluctuations but also investigates the physiological mechanisms, interconnections and cascading effects of these events from the plant to ecosystem level [2, 3]. While records of phenological events date back thousands of years, phenology only gained recognition as a scientific discipline between the 19th and early 20th century. (Figure 1).

In the last decades, in response to growing concerns about global climate change and its potential impacts, international phenology networks have facilitated collaborative efforts for collecting and sharing large-scale data based on standard methods [2–4]. This monitoring is crucial for advancing our understanding of ecological processes and effectively managing resources in the face of climate change and habitat alterations [5]. Consequently, there has been a significant surge in phenological research in recent decades, accompanied by new methodologies and technologies to support these endeavors (Fig. 1). As a result, interdisciplinary frameworks for phenological research have gained prominence in the past two decades, harnessing technological advancements to monitor phenology and its impact on ecosystem functioning across different spatial and temporal scales.

The annual growth cycle of trees in extra-tropical climates is characterized by a long period of suspended growth and metabolic activity, the so-called winter dormancy, and active period of primary (i.e., growth from shoot and root apical meristems) and secondary (i.e., radial growth from cambium cells) growth. Predicting the timing of leaf and wood phenology in relation to climatic parameters has attracted attention from researchers due to its significance for tree fitness in terms of competition for resources (e.g., light, water, nutrients), frost avoidance, successful reproduction, and for its link with the global carbon cycle. Various studies have demonstrated that leaf emergence [6] and the general greening of the northern hemisphere [7] have all shifted in response to regional warming trends [8, 9]. These significant climate change induced phenological shifts can profoundly impact community structures and ecosystem functions [10, 11], with direct feedback effects on the climate system by modifying water and energy exchanges between terrestrial ecosystems and the atmosphere [12, 13]. Therefore, understanding phenology, its underlying drivers, and its impacts on ecosystems is essential for quantifying and modeling the interactions between ecosystems and the climate system.

While numerous studies have contributed significantly to our understanding of tree phenology, a closer examination reveals an often-underestimated aspect, the need to integrate physiological considerations into the assessment of phenological events [14]. As sessile organisms, trees show remarkable physiological adaptations that govern their life cycle events. These adaptations not only respond to external environmental signals but are also deeply embedded in the molecular and biochemical processes within the plant [15, 16].

This review offers a summary of phenological assessments of tree growth processes in both below and aboveground organs in extra-tropical forest ecosystems, to emphasize recent developments and identify knowledge gaps in the scientific literature. The focus of the review is on understanding the mechanisms and the drivers shaping phenological dynamics in trees. By synthesizing existing knowledge and highlighting key ecological drivers and physiological mechanisms, we aim to present a thorough overview, underscoring the importance of integrating new eco-physiological insights into the evaluation of tree phenology. This integration is vital for advancing our understanding of tree biology and guiding practical applications, such as sustainable forest management and conservation strategies, especially in response to the challenges posed by a swiftly changing climate.

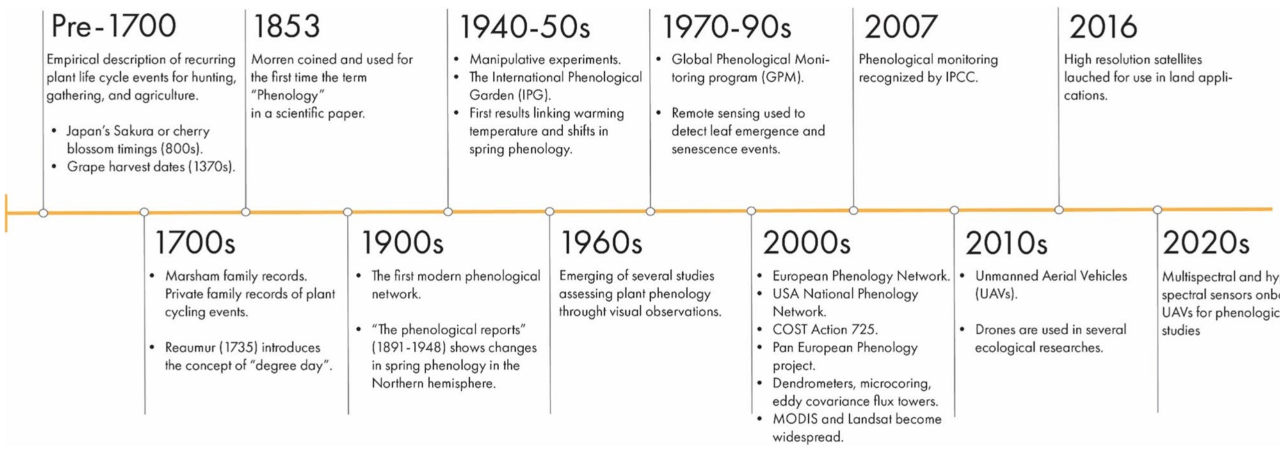

Fig. 1 Timeline history of the development of plant phenological observation, experiments and modelling (Table S1 provides a detailed list of references for these events)

Leaves and Canopy Phenology

The timing of phenological events associated with leaf emergence, development, senescence, shedding, and the elongation of shoots driven by primary meristem is collectively referred as canopy phenology (Figure 2). In detail, while leaf phenology examines the seasonal life-cycle events of individual leaves such as budburst, leaf expansion, maturation, senescence, and abscission, canopy phenology examines the collective timing and progression of these events across the entire tree canopy or the forest canopy in studies focusing on ecosystem scale. These events constitute a key aspect of the annual growth cycle of all trees in seasonal climates. Even in evergreen species, canopy phenology regulates the amount of leaf area displayed, and hence has important consequences for interception and absorption of shortwave radiation and the fluxes of atmospheric C and water vapor associated with photosynthesis and transpiration.

Rigorous protocols have been developed to track canopy phenology from visual observations. These generally focus on identifying the progression towards specific, biologically-relevant, "phenophases". However, predicting the onset of primary growth still remains challenging, as the underlying physiological processes and their interactions with environmental cues take place during winter dormancy, when no visible changes can be detected. The physiological changes that take place during winter dormancy are therefore the key to better project plant phenology in the future and its repercussions on the carbon and water cycles.

At the end of the growing season, reduced photoperiod and exposure to low temperatures are correlated with growth cessation in all shoot meristems (Fig. 2). Trees in extra-tropical climates, preparing for winter dormancy, shield their shoot apical meristems within winter buds, a process known as budset or bud formation. Occurring typically in mid-summer, budset marks the end of shoot expansion and is therefore considered a proxy for growth cessation [17] (Fig. 2). Dormancy-Associated Mads-box (DAM) genes are assumed to play a major role in regulating primary growth cessation of the shoot and budset in summer. This strategic process to 'escape' unfavorable winter conditions for growth and photosynthesis [17, 18], to protect meristematic tissues from frost and to increase cold hardiness is regulated in a complex way by developmental, molecular and environmental factors.

Considering that autumnal phenology, and specifically bud set, is often used as a proxy for the end of growth, it is important to note that autumnal phenological events have received significantly less attention compared to those in spring [19]. This is particularly evident in the case of leaf senescence. While it is known that internal factors, such as leaf age and sugar concentrations, influence the timing of senescence, the effects of environmental factors remain

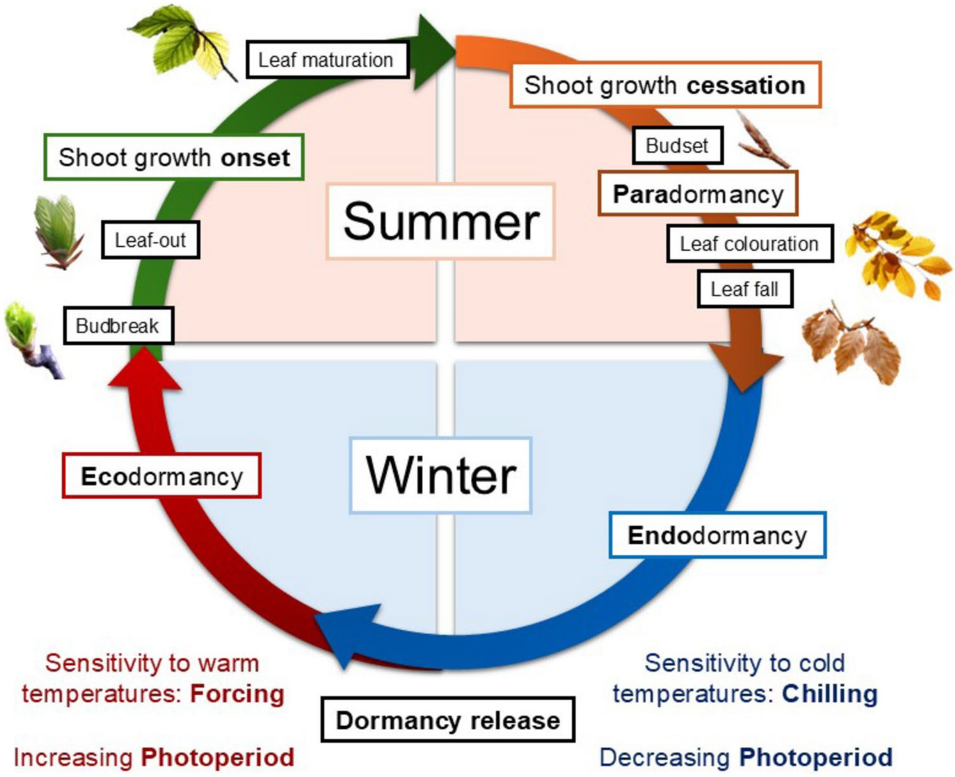

Fig. 2 Seasonal progression of canopy phenology in cold-limited trees, detailing key stages such as budset, para-dormancy, endodormancy and ecodormancy, and including the physiological processes during winter dormancy, including hormone regulation and the influence of chilling and forcing temperatures on budbreak and shoot elongation

poorly understood. There is, however, growing evidence of a link between spring and autumn phenology. For instance, in black spruce, an earlier onset of budburst was associated with an earlier timing of bud set, as observed in a provenance trial experiment [17, 20]. Similarly, Zohner et al. [21] reported that earlier spring phenology was accompanied by earlier leaf senescence, which also exhibited a slower progression. These observations highlight the interconnected nature of seasonal phenological events and underscore the need for further research into the drivers of autumnal phenology.

The new buds first undergo a phase of paradormancy (Figure 2), which consists of the inhibition of hormone-regulated growth and competition between distant organs. As unfavorable conditions progress, buds enter endodormancy, meristem growth is suspended, and buds must be exposed to chilling temperatures before being able to respond to warmer temperatures (i.e., forcing). Exposure to chilling temperatures (i.e., temperature ranging between −5 °C and +10 °C) [22] activate DAM genes which in turn control the level of two phytohormones involved in the maintenance and release of dormancy, respectively abscisic acid (ABA) and gibberellins (GA) [23]. A negative exponential relationship between the duration of chilling temperatures and the amount of forcing temperatures accumulated up to budburst is commonly found either experimentally (e.g. Baumgarten et al. [22], Laube et al. [24]) or in natural conditions (e.g. Vitasse and Basler [25]) though in natural conditions this relationship exists without necessary causal link [26]. In other words, the temperature required for budburst decreases as the duration of previous chilling increases and reaches a minimum beyond a certain threshold of chilling exposure, i.e. when the dormancy is assumed to be fully released. However, the range of chilling temperature effectiveness and the relationship between forcing and chilling that regulate dormancy are still unclear and very species-specific, resulting in many different phenological models [27] and in very different predictions of phenological growth timings in the future, especially for forest trees [28].

After exposure to chilling conditions, buds gradually move from endodormancy to ecodormancy, during which they are able to resume growth in response to warm conditions (i.e., forcing) and increasing photoperiod (Figure 2). These seasonal changes yield significant biochemical feedbacks on plant carbon metabolism and the non-structural carbohydrates (NSC) dynamics [14]. At this stage, the concentration of gibberellins gradually increases while that of abscisic acid decreases, cell membrane fluidity increases and an influx of calcium enters the meristematic cells, eventually triggering cell elongation and division triggering budbreak. The resumption of primary shoot growth in spring is therefore a complex event to model which relies on a deep understanding of the physiological processes that occur during dormancy. Then, depending on the species, primary growth will either stop after a few weeks (deterministic growth), occur continuously throughout the growing season (indeterministic growth), or occur during several periods of intermittent growth (polycyclic growth). Polycyclic growth allows certain species to increase their resistance and flexibility to stress, such as drought, since they can re-flush once the stress is released and conditions again become favorable.

Advancements in Leaf and Canopy Phenological Monitoring

Leaf and canopy phenological observations have traditionally relied upon monitoring the occurrence dates of key events, such as budbreak, leaf unfolding, leaf coloration and leaf fall, which are scored visually from the ground. These phenological stages, the phenophases, are discrete points within the continuous sequences of phenological development. Visual scoring remains widely used for leaf phenology, especially in studies that require high detail or the ability to discriminate more specific phenological stages (see for example Silvestro et al. [17, 20]). However, this method comes with two major disadvantages: (i) it is inherently observer-biased, directly impacting the accuracy of recorded phenological dates, and (ii) it is constrained logistically and economically by the need for multiple site visits. The subjective nature of visual scoring not only introduces inaccuracies in recorded phenological dates but also restricts the sample size of monitored individuals, typically representing only a subset of the population that cannot always capture the phenological variability within and among individuals and populations. Nowadays, with the spreading of citizen science methodologies and the use of online platforms, it is possible to collect large datasets that cover larger spatial and climatic areas, thereby enhancing the ability to capture phenological variability across wider regions [29].

The advent of remote sensing platforms, including satellites [30], unmanned airborne vehicles [31], and near-surface digital cameras, commonly referred to as "phenocams" [32], have provided unparallel advantages for phenological monitoring. Remote sensing approaches typically yield high-frequency time series of vegetation indices calculated from the measurement of two or more spectral bands (e.g. Normalized Difference Vegetation Index, or NDVI, calculated from red and near-infrared reflectance [33]). Unlike the discrete phenophase approach of ground observations, these indices yield a continuous, ordinal representation of the overall trajectory of canopy phenology at community and population level [34].

Remote sensing can effectively characterize foliage development and senescence in broadleaf deciduous forests. Transition dates such as the start and end of the season, approximately corresponding to budbreak and leaf drop, can be extracted using curve fitting or spline-based methods [35]. The seasonality of leaf area index and other biophysical parameters has also been estimated from standard vegetation indices using model-based retrievals [36]. In evergreen forests, seasonal changes in leaf area index are generally smaller, and standard vegetation indices like NDVI may not adequately represent underlying seasonality. However, recent work has shown promising results with indices derived strictly from visible-wavelength data, such as the chlorophyll content index (CCI) [37].

At the forefront of technological advancement stands the PhenoCam Network (https://phenocam.nau.edu), which provides automated monitoring of canopy phenology across nearly 900 ecosystems worldwide [38]. Phenocam imagery boasts high resolution, typically at 1.3 megapixels or larger, facilitating detailed phenological tracking at both the canopy and, even if more rarely, individual tree crown levels [39, 40]. It is also straightforward to distinguish between different plant functional types, e.g., deciduous and evergreen trees in the field of view of a single camera (Figure 3), but the

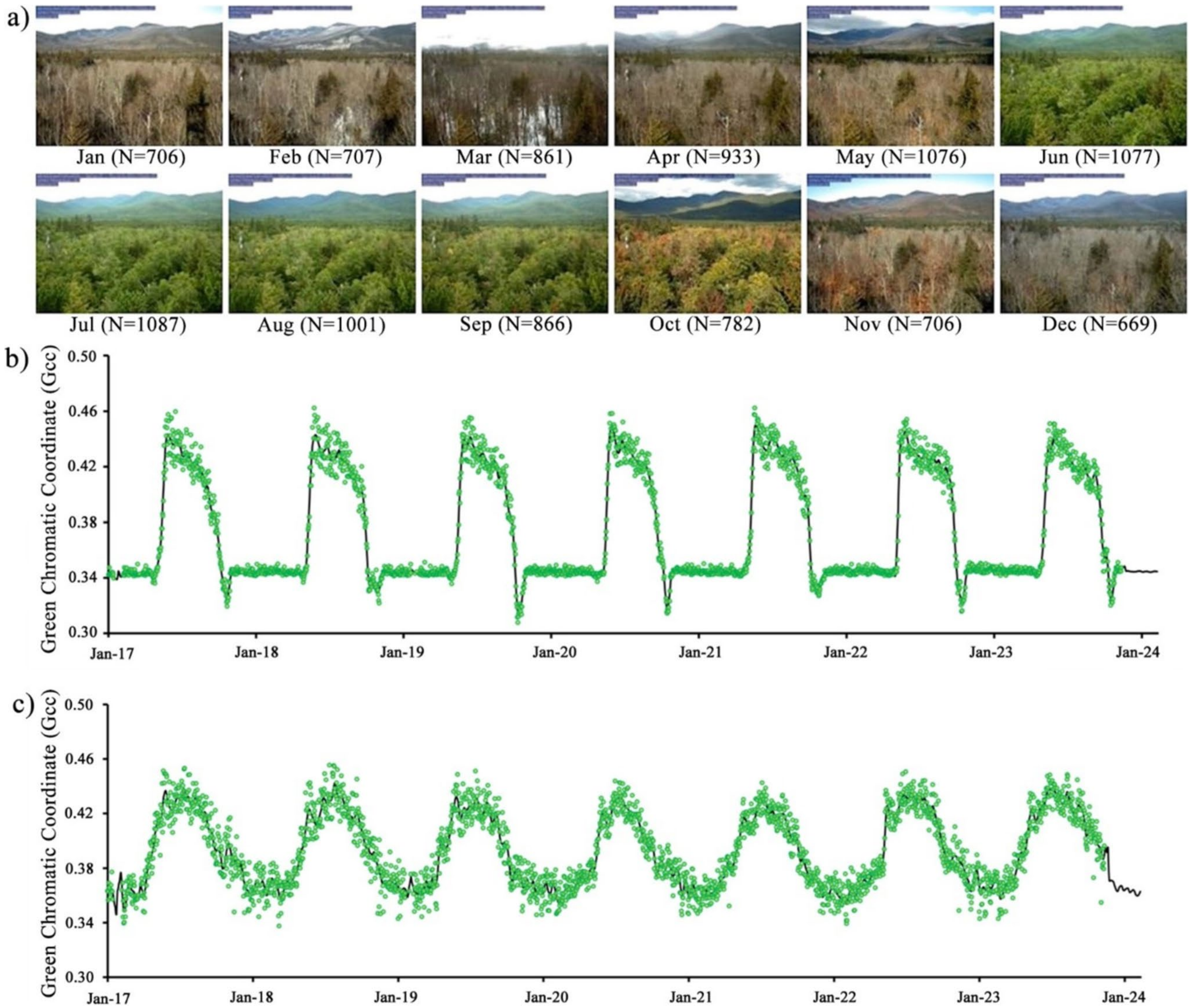

Fig. 3 Top: PhenoCam imagery from around the year at NEON's (National Ecological Observatory Network) Bartlett Experimental Forest site, located in a northern hardwood forest in the northeastern United States. The canopy is dominated by the deciduous species maple (*Acer*), beech (*Fagus*) and birch (*Betula*), with some conifer species (pine [*Pinus*] and hemlock [*Tsuga*]) mixed in and visible in the winter pictures. Middle: Time series of green chromatic coordinate, Gcc, for deciduous trees in the camera field of view, displaying the clear seasonal rhythm of spring green-up and autumn senescence. Bottom: Time series of Gcc for evergreen trees in the camera field of view; for evergreen trees, seasonality in Gcc is driven by biochemical changes in existing foliage rather than the production of new foliage and senescence of old foliage. Symbols are 1-day product derived from the mean Gcc value recorded each day; solid line is a smoothed time series derived from spline fit. See: https://phenocam.nau.edu/webcam/sites/NEON.D01.BART.DP1.00033/

identification of individual species can still be challenging. Phenocam also has additional advantages, including its cost-effectiveness, and the advancements in wireless and satellite communications currently allow real-time telemetry, even in remote areas [29].

PhenoCam images offer the flexibility of both visual inspection for detecting phenological transitions, such as budbreak and leaf drop, and quantitative analysis (Figure 3), also detecting any anomalies due to biotic (e.g. insect outbreak) or abiotic (e.g. damaging spring frost) factors [41]. These images, captured by digital cameras with RGB sensors, provide information about these three spectral bands for deriving vegetation indices such as the green chromatic coordinate (Gcc) [42], a reliable indicator of the seasonality in canopy structure and function. While Gcc's trajectory differs from leaf area index in deciduous forests due to its sensitivity to leaf color changes, studies have shown alignment with ground observations [43]. Additionally, recent advances in deep learning and neural network approaches further contribute to extracting canopy phenology information from Phenocam imagery [44], promising significant progress in this research area in the coming years.

Wood Phenology in the Stem

The phenology of wood growth, also known as wood formation or xylogenesis, refers to the timing of physiological phases occurring throughout the seasonal growth of wood in terms of both volume and mass. Formation of the xylem, or growth ring, begins with cambial reactivation and cell production by cambial initials [45]. Subsequent stages involve the differentiation of xylem cells, encompassing discrete events, defined as (i) cell enlargement, (ii) secondary wall formation and lignification, and ultimately (iii) programmed cell death [46] (Figure 4). The different timings between these phases constrain the overall length of the wood-growing season (Figure 4). Intra-annual monitoring of cambial activity and radial growth in trees allows for the assessment of short-term environmental influences on wood and phloem formation. The acquired data, characterized by high temporal resolution, enables a comprehensive evaluation of the environment's impact on tree development [47]. In detail, monitoring wood formation provides information on phenological events, such as the onset and cessation of cambial activity and the timings of cell differentiation [48], the transition from early- to late-wood [49], and the date of maximal growth [50, 51]. It also offers insights into the dynamics of xylem growth, including the cell production rate throughout the growing season and the kinetics of cell differentiation, such as the duration or rate of cell enlargement and wall deposition [52].

Studying xylem and phloem growth is essential for understanding tree productivity, wood quality and C sequestration [51, 53, 54]. However, while research on xylem formation in trees has grown rapidly over the past decades, phloem formation remains significantly less explored, with only few studies investigating phloemogenesis (e.g. [55]or for a review [46]). For wood phenology, extensive sample size

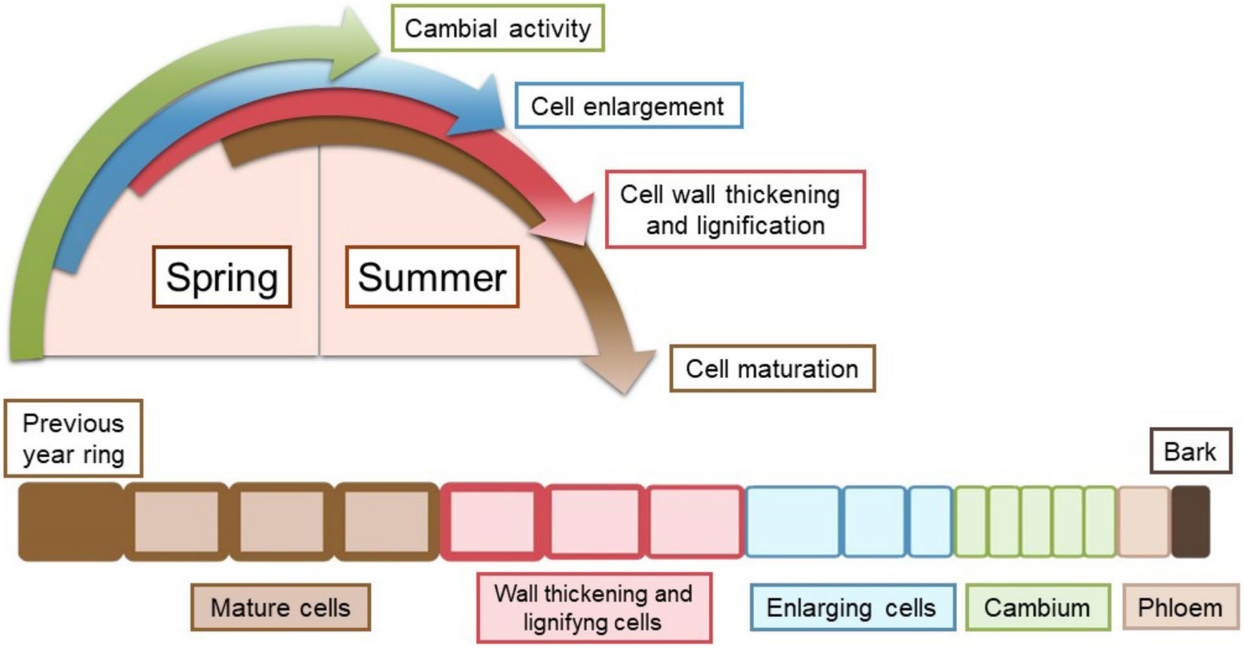

Fig. 4 Phenological phases of wood formation including cambial activity and differentiation stages such as cell enlargement, secondary wall formation and lignification and programmed cell death leading to complete cell maturation

collection has allowed the study of phenological variability within populations [48]. Long-term observations of wood formation in diverse environments reveal how trees respond to changing conditions, assessing the adaptation strategies of different species [56],understanding climate change implications [57], and evaluating the temporal and functional relationships among sink and source activities [51].

It is important to note that most studies have focused on conifers rather than angiosperms. This is partly due to the simpler wood structure of conifers, which is composed of approximately 90% tracheids, compared to the more complex structure of angiosperm wood, which includes vessels, fibers, and, in some species, tracheids. In conifers, the counting of cells with distinct morphological features representing specific phenophases has been widely applied. In contrast, studies on broadleaved trees have generally relied on measuring the radial distance between developmental zones. In this context, most of the knowledge summarized in the following paragraphs is based on studies of conifers. However, there is a substantial rise in interest within the scientific community in advancing our understanding of wood formation in broadleaved trees. This growing focus is likely to result in more comprehensive overviews of wood phenology in the coming years, as well as the development of new methodologies tailored to studying xylogenesis in broadleaved species.

Cambial activity

Cambial activity marks the initial phase of wood formation, characterized by reactivation of the cambium, a layer of meristematic cells (i.e., cambial initials) that produces new xylem and phloem cells. The transition from dormancy to active cambial growth in spring is driven by increasing temperatures and day length, which stimulate hormonal changes [58]. In spring when temperatures rise above critical thresholds of 4–5 °C cambial activity can resume [57]. Manipulative experiences, such as heating and cooling experiments, have further confirmed the importance of temperature in determining the timings of cambial activity and subsequent xylem differentiation [59]. However, the influence of temperature on cambium activity depends also on photoperiod, an independent factor constant over time [60]. Indeed, if temperature were the sole determinant, xylem cell production should follow seasonal thermal patterns, increasing in spring, peaking around July, when temperature reaches the maximum, and declining in late summer and autumn. Contrary to this expectation, Rossi et al. [50] found that the maximum rate of xylem cell production in various North American and European species culminated at the summer solstice, when day length, not temperature, reaches its peak. After the solstice, cell production gradually diminishes and eventually ceases [51]. This suggests that trees have evolved to synchronize their phenology and growth rates with day length, also providing an advantage in avoiding thermally unfavorable growth periods at the beginning and ending of the season.

Water availability plays a crucial role in defining the phenology and dynamics of wood formation [61]. In Mediterranean ecosystems, plants exhibit two peaks of secondary growth activity within the same growing season, the first in spring and the second in autumn [62]. This bimodal growth pattern is associated with changes in the growing conditions. In early summer, water stress can lead to a temporary suspension of wood formation, possibly also associated with the formation of tracheids with small lumen areas. The reactivation of growth in autumn is a response to precipitation, allowing for the resumption of xylem cell differentiation and, in a few cases, cambial activity [63].

The auxin indoleacetic acid (IAA) is considered the primary hormonal signal among those involved in the regulation of cambial activity and subsequent cell differentiation [64]. Auxin concentrations peak in the cambial zone, as observed in *Pinus sylvestris* [65]. The highest concentration of auxin is found at the point where cambial cells divide, stimulating radial growth. This process is further regulated by cytokinin [66] and ethylene [64], suggesting that these hormones crosstalk to coordinate their regulation of various developmental processes [67]. Additionally, cell division is sustained by the availability of carbohydrates, which need to be mobilized at the beginning of the growing season. Among others, sucrose represents the most abundant NSC compound in the cambium of *Picea mariana* [68]. Sucrose concentrations progressively decrease from the phloem to the mature xylem due to its utilization in the subsequent developmental phases [69]. This decline in sucrose levels reflects its role as a critical energy source and structural component, supporting, in particular, cell wall thickening and lignification process during xylem differentiation [69].

Cessation of cell divisions in the cambium appears less affected by temperature, as in the Northern Hemisphere this phenological phase typically occurs in August, when the temperatures are still favorable for growth. Abscisic acid (ABA) accumulation has been observed to trigger cambial activity cessation, likely due to a negative interaction with auxin [65].

Cell Differentiation

Xylem differentiation can be described as a sequence of interconnected phenological events, including cell enlargement, cell wall thickening and lignification, and maturation [70]. During this process, the cambial derivatives (i.e., the cells produced by cambial division) undergo significant morphological and physiological changes, gradually acquiring their definitive characteristics. Research on xylem phenology is often conducted due to its critical relationship with overall cell production and consequently on C sequestration. For instance, studies on conifers have observed that individuals with an earlier onset of xylem differentiation tend to have a later cessation, which corresponds to greater cell production [48, 70, 71]. Thus, the onset and ending of cell formation could be indirectly connected, suggesting also that any change in the timing of one phenological phase can potentially affect the occurrence of subsequent phases [70].

The eco-physiological processes and molecular mechanisms underlying xylem differentiation are currently not well understood. As for cambial activity, several hormones crosstalk, regulating the occurrence and succession of xylem differentiation phenophases. However, among all, there is a general agreement that the overexpression of gibberellin is the main driver of the onset of xylem differentiation [64, 66, 67].

The first phenological phase during xylem differentiation is cell enlargement, in which the newly formed xylem cells increase in size (Fig. 4). Cell enlargement is primarily a turgor-driven process [72] in which expansion of the thin primary cell walls is observed. At this developmental stage gibberellins show their maximum concentration accompanied by moderate levels of auxins [64]. Despite their moderate levels, auxins play a crucial role in cell expansion by altering the rigidity of the cell wall, promoting growth [73]. Auxins acidify the extracellular matrix, which loosens the bonds between cellulose microfibrils and other wall components, allowing cell enlargement through water uptake. At the same time, hexose concentrations (i.e., glucose and fructose) peak in the differentiating zone [69], contributing to the buildup of the required turgor pressure [68]. In detail, hexoses, along with other cyclitols, negatively increase the osmotic potential, which aids in generating turgor pressure, leading to cell enlargement.

After cell enlargement, the cells undergo secondary wall thickening and lignification (Fig. 4). During this phenological phase, it is observed that actual biomass production occurs after a substantial time lag compared to the stem-girth increase triggered by cell enlargement [53]. In general, this phenological phase involves the deposition of additional layers of cellulose, hemicellulose and lignin, which strengthen the cell walls and enhance their structural integrity. From a biomechanical perspective, cell enlargement progressively slows during the deposition of subsequent layers of the cell wall due to the inhibition of wall relaxation processes and the decreasing accessibility of polysaccharides and pectins to the outer wall layers near the middle lamella [62]. Therefore, as new wall layers are progressively deposited, the potential for cell wall relaxation and further increment in cell size is gradually inhibited. Experimental manipulation has shown that auxin treatment reduces cell wall thickness, whereas gibberellins have a promotive effect on secondary cell wall deposition [74]. Accordingly, during this phenological phase low levels of auxin and moderate levels of gibberellin can be observed accompanied by a gradual accumulation of ethylene and brassinosteroids that in turn will promote the programmed cell death [64].

During the process of cell wall deposition, a large quantity of sucrose is required for cell wall biosynthesis, making this phenological phase the greatest carbon sink during the wood formation process. Several genes and proteins are expressed and produced during this phase, in particular sucrose synthase, which breaks down sucrose into UDP-glucose and fructose [67]. The former is then incorporated into cellulose synthase for the biosynthesis of cellulose [67]. Trees with reduced sucrose synthase activity show decreased cell wall components and wood density [75] because of a reduction in the incorporation of sucrose-derived carbon into the developing cell wall [76].

The final phase in wood formation is complete maturation of the xylem cells (Fig. 4). During this phase, the cells complete their development and reach their final form. This includes the completion of secondary wall thickening and lignification, followed by the programmed cell death (i.e., apoptosis) of the xylem cells [70].

Considering environmental factors, it is important to note that there is limited understanding of how various environmental conditions can impact xylem phenology. While temperature and water availability are known to significantly influence the timing and progression of xylem differentiation, other factors such as soil characteristics and its nutrients availability are often overlooked in wood formation studies. Gričar et al. [77] identified significant differences in radial growth dynamics in *Quercus pubescens* growing in two nearby plots with distinct bedrock and soil characteristics. By removing the snow cover, Jyske et al. [78] demonstrated the substantial influence of a freezing soil on cambial activity and the formation of annual rings. On the other hand, manipulative experiments were unable to confirm the effect of nitrogen concentration on xylem phenology at short- and mid-term [79]. In general, these environmental variables could potentially affect hormonal balances, sugar availability and overall cellular processes involved in xylem formation. Future studies will need to focus on conducting more detailed analyses of microsite conditions at the individual tree scale, such as variations in soil moisture and temperature, nutrient availability, and factors related to microclimate and microtopography. These micro-scale changes in environmental conditions could significantly influence wood phenology and may help explain the variability observed among trees within the same population in addition to genetic factors.

Root Phenology

The current understanding of belowground phenological processes remains strongly constrained [80]. The first major challenge is to classify roots into precise categories to define which belowground entities should be considered to answer specific questions [81]. Root diameter-based classification, which distinguishes between fine and coarse roots, is the most used in ecological studies [82]. Fine roots, encompassing those with a diameter ≤ 2 mm, often lack lignified structures, although other diameter thresholds may include portions of woody roots [83]. In contrast, coarse roots exceeding 2 mm in diameter typically exhibit lignification and clear secondary development.

A critical aspect of this classification lies in the challenge of not only morphologically classifying roots but also acknowledging their distinct functional roles. Fine roots, as short-lived organs, fulfill two distinct functional roles, absorption and transport [82]. In contrast, coarse roots, characterized by an extended lifespan, alongside their transport role, serve an additional dual function, providing mechanical support and acting as repositories for C reserves [84].

Fine Root Phenology

Despite their marginal contribution to total biomass of a tree, fine roots significantly affect the biogeochemical processes, particularly soil C cycling. They represent 33–67% of annual net primary production at ecosystem scale, although they hardly exceed 5% of tree biomass [83, 85]. Fine root phenology typically considers onset, peak growth and lifespan [86].

In contrast to the onset of shoot growth, much less is known about the onset and cessation of primary growth of fine roots [87], even though they are the most dynamic part of the root system and play an essential role in supplying water and nutrients to emerging leaves in spring. A review of studies on root phenology showed that, generally, roots do not exhibit winter dormancy like buds, and growth can occur at temperatures as low as 5 °C in temperate environments [86]. The primary driver of growth reactivation is soil temperature, although other factors like soil water and nitrogen availability can also play a role [88]. Internal signals play a crucial role in this phenological phase, including the influence of hormones (i.e., auxins and cytokinins) and C availability. However, reliance upon C resources appears to be species-specific, with some species utilizing current photosynthates while others depend on previously stored C resources. Indeed, in manipulative experiments in which plants were exposed to elevated atmospheric CO_2 concentrations, stored C was not used to produce new fine roots [89, 90]. Conversely, in *Pinus strobus* and *Quercus rubra*, root growth in spring is known to be sustained by the carbohydrates accumulated in woody tissues during the previous autumns [91].

The variation in the utilization of C reserves for fine root production among different species or ecosystems requires deeper and wider investigations [90]. A common garden involving mature trees belonging to 11 temperate species revealed that evergreens did not exhibit earlier root growth than deciduous species [92]. The same study demonstrated synchronized peaks of root production across species, while a meta-analysis indicated that in conifers generally reached their maximum of fine root growth later than broadleaves [87]. Presently, also the number and timings of the peaks diverge between studies, with authors detecting either one or two major root growth peaks [92]. The single root growth peak typically occurs after leaf and shoot development [80, 93].

When two growth peaks occur during the growing season, the former peak produces a limited root growth. The second and more prominent peak occurs in late summer or in autumn, generally under abundant rains and the consequent increase in soil moisture [94]. During late autumn or early winter, the combination of decreasing soil temperature and declining photosynthate availability results in a growth cessation. However, as previously stated, roots are not typically dormant and may reactivate during warming events in winter, when the soil reaches a sufficient temperature. This factor is crucial as it directly influences soil respiration and the C cycle of forest ecosystems [85].

Only a small proportion of fine roots undergo secondary growth to become secondary roots. For this reason, a key aspect in phenological monitoring of fine roots concerns their lifespan and turnover. Changes in climatic and edaphic factors, such as water availability, temperature and soil nutrients, affect fine root longevity and mortality [95]. Generally, the lifespan of fine roots extends when a limiting factor for plant growth is boosted, allowing plants to allocate additional resources to maintain root performance. Conversely, fine root longevity drops when a factor or resource miss the plant needs or tolerance [95].

Mortality of fine roots, and the consequent root turnover, directly impacts ecosystem biogeochemical cycles. The necromass of fine roots swiftly releases substantial amounts of C and nutrients into the soil. Variation in C reserves leads to differing lifespans and turnover rates of fine roots across growing seasons, with the fine roots produced in spring typically exhibiting a short lifespan. This pattern may be linked to the trade-off between costs and benefits in terms of C derived from the processes of resource acquisition [96].

Coarse Root Phenology

Studies on belowground phenology typically focus on fine roots due to their perceived higher activity than coarse roots [97]. Despite the variations in anatomy, functionality and physiology [84], the mechanisms of xylogenesis exhibit similarities between stem and roots [97, 98]. Consequently, some insights gained from one organ can be applied to the other. However, given the limited number of studies on root phenology, complete transfer of knowledge from stem phenology remains premature [98].

The importance of temperature in the reactivation of root growth has mainly been assessed in cold environments [84, 99]. A soil temperature < 6 °C inhibits root activity [100]. Indeed, in a manipulative experiment on black spruce in the field, soil warming affected roots phenology compared to control trees [99]. Under non-limiting temperature conditions, a wide phenological variability is usually observed among individuals in the reactivation of root growth [101]. The dynamics of the end of cambial activity also remains uncertain, with conflicting results indicating different patterns. Some studies suggest earlier cessations of cambial activity at the top of the tree, while other authors propose that the initiation of dormancy spreads acropetally from the collar. Finally, some findings observed synchronous occurrence of this phenological phase between above and belowground organs [97, 101].

The current knowledge on root xylogenesis is also very limited, with boreal forests being the primary focus of the few available studies. Under comparable climatic conditions, species-specific differences were observed at the onset but not at the ending of cell differentiation in *Picea mariana* and *Abies balsamea* [97, 99, 101]. However, differences in xylem phenology were highlighted between stems and roots, with the total duration of xylogenesis being shorter in roots [97]. The rate of xylem production culminated early in the stem and one month later in the roots, likely due to the lag in increase of temperature between air and soil. Both organs exhibited a single peak growth pattern [97]. However, annual changes in root radius showed bimodal patterns in two sympatric Mediterranean oaks, marked by growth interruptions during summer droughts [102].

Given the important role of roots in ecological processes at the ecosystem scale, unraveling the mechanisms and factors controlling their phenology is crucial for accurately tracking the impacts of climate change on forests. Despite this significance, there are substantial gaps in our understanding of the eco-physiological mechanisms regulating root activity and phenology, combined with a rarely explored variation within and among species and ecosystems.

Interconnected Phenology

The interaction between primary and secondary growth in trees is intricate and yet crucial for predicting forest ecosystem dynamics and assessing the impacts of climate change on tree growth and productivity. The synchronism between primary and secondary growth within and among organs is influenced by both environmental conditions and internal controls, and yet is species-specific [87]. Climatic factors, primarily thermic thresholds and water availability, affect both primary and secondary growth, but in different ways and at different times. The seasonal fluctuations in abiotic constraints can also introduce compensatory dynamics, significantly influencing the timings of different or subsequent phenological processes [51]. However, a comprehensive understanding of the phenological and functional relationships between primary and secondary growth remains limited for several reasons. These include substantial variation in responses to abiotic factors across species, the difficulty in disentangling how internal regulation modulates responses to external factors, and the fact that to date very few studies have focused on both primary and secondary growth.

The phenology of needles and leaves follows a typical seasonal rhythm, independent from xylogenesis [103]. Several studies in the literature aimed to examine the temporal relationships between canopy phenology and wood formation, often with contradictory results. In boreal conifers, synchrony and correlations between the onset of bud development and xylem differentiation has been observed [104]. This study also found that while degree-days accumulation better predicted bud development resumption, thermal thresholds were more suitable for assessing cambium phenology. These findings are further supported by a provenance trial, where early-flushing provenances of *Picea mariana* also demonstrated earlier xylem formation [105]. However, recent studies found contrasting results in other ecosystems. In a temperate arid and semi-arid region of China and central Europe was found that bud development and radial growth were asynchronous [106, 107]. In broadleaves the temporal relationships between canopy phenology and wood formation have been explored particularly considering different functional groups with distinct wood structures. This interest arises from the well-established observation that ring-porous species often exhibit both an earlier cambial reactivation and xylem cell differentiation compared to diffuse-porous species [108, 109]. The earlier growth in ring-porous species is attributed to the winter embolism of their large xylem vessels, requiring restoration of the water transport pathway before new leaves can unfold and begin transpiring [108, 109]. In this complex framework, however, as for conifers, studies assessing the temporal relationships between canopy phenology and wood formation in ring-porous and diffuse-porous species yield contradictory results.

In ring-porous species, D'Orangeville et al. [110] found that budbreak and the early stages of xylem phenology occurred concurrently with canopy development, reaching completion around the same time as the peak in wood growth. The study also observed that wood formation continued for a longer duration than canopy development. Conversely, some studies suggested that the onset of xylem formation typically precedes leaf unfolding in ring-porous species in Europe [111, 112]. In diffuse-porous species, as observed in the study by D'Orangeville et al. [110], budbreak and canopy development were completed before 25% of annual diameter growth was achieved. However, other studies on diffuse-porous species indicated a close synchronization between the onset of xylem formation and leaf phenology, with leaf unfolding and the onset of xylem development usually occurring simultaneously [108]. Some results even suggested that secondary growth might initiate before leaf unfolding [111]. However, it is important to note methodological differences among these studies. Variations in observation frequency, along with the use of different techniques, such as dendrometers or microcoring and visual scoring of bud development or phenocams, can significantly affect the detection of growth initiation and cessation [113], thereby influencing interpretations of synchrony.

Marchand et al. [114] investigated the relationships between leaf and wood phenology in several deciduous trees across diverse sites with temperate climates. They observed a direct relationship between budbreak and timing of the previous year's ending of wood formation. Specifically, earlier budbreak correlated with an earlier ending of wood formation in the preceding year. The study attributed this pattern to the larger reserve storage resulting from the accumulation of photoassimilates produced by the leaves before senescence. Using $^{13}CO_2$ pulse-labeling, it has been observed that stored carbohydrates from previous seasons contribute to earlywood formation in the following year [115]. In this study, earlywood shows carbon signatures from the prior season, while latewood reflects photosynthesis from the current season. This finding highlights a possible carry-over effect, illustrating how growing conditions from the previous year influence the phenology and radial growth in the subsequent year. However, the carry-over effect in secondary growth remains a subject of debate, with contrasting results in the current scientific literature [116]. Further studies integrating both leaf and wood phenology are likely necessary to clarify this phenomenon.

In Central Europe, the cessation of growth ring formation in beech typically precedes leaf senescence by several weeks [45] despite considerable variability in timing among individuals and across years [117]. Dox et al. [118] examined autumn phenology in several deciduous species across different climatic regimes, focusing on the ending of wood formation and leaf senescence. In that study, leaf senescence coincided with the ending of xylem formation. The authors suggested sink limitation as a potential regulator for the timing of leaf senescence. Overall, as both primary and secondary growth are driven by a complex interplay of physiological processes and hormonal signals, integrating the analysis of non-structural carbohydrate dynamics and expanding research on hormone synthesis represent promising avenues for understanding the temporal and functional relationships among growth processes across different organs. Additionally, advancing our understanding of the interconnections between leaf and xylem phenology will likely depend on gaining deeper insights into the dynamics of phloem formation [119].

Incorporating the roots into the analysis introduces additional uncertainties. Some considerations can be made about the bimodal growth pattern shown by fine roots in some environments. This pattern may reflect a hierarchy in C allocation and the trade-offs among different C pools [120]. At the beginning of the growing season, the emerging leaves represent a main C sink and, consequently, root growth is markedly constrained. In the bimodal peak, indeed, the most prominent peak is usually observed in late summer or autumn. The cessation of root growth seems to occur mainly during leaf senescence, and could result from a combination of short photoperiods and cool temperatures, as well as a decrease in water and nutrient demand from the aboveground part of the plant as a response of phytohormones [87].

Contradictory information also exists on the temporal sequence of cambial activity onset and ending comparing different tree organs. Some studies suggest cambial reactivation occurring first near buds with basipetal propagation, making the cambium of roots the last meristem to reactivate [91]. Conversely, other studies suggested that the hormones like cytokinin and strigolactones, primarily produced in roots, also trigger cambial activity in the stem [121]. Finally, the cambial activity in both organs were also found to be synchronous under natural conditions [97]. Similar considerations can be extended to the cessation of cambial activity [97, 101]. Overall, since both primary and secondary growth are regulated by a complex interplay of physiological processes and hormonal signals, expanding research on hormone synthesis represents a promising research field for understanding the temporal and functional relationships among growth processes in different organs.

Modeling Phenology, Why?

Phenological models are versatile tools with diverse applications, extending beyond mere prediction of phenological phases or events to encompass a deeper understanding of their consequences in time and space. For example, phenological models can be coupled to terrestrial biosphere models, contributing to improve the estimations of C assimilation [122]. Additionally, they serve as valuable proxies for predicting the occurrence of disturbances, including forest fires [123] and frost hazards [124]. Integrating phenology into models of species' distributions or niches aids in refining these models and identifying or predicting phenological mismatches [125].

Phenological models fill the gap in observations with limited spatial or temporal coverage, effectively scaling data from sources like transect data, citizen science networks (e.g., PlantWatch), or phenocams. Since the discovery of climate-change-driven phenological shifts, there has been a growing interest in collecting time-series, which in turn enabled the possibility of modeling phenological patterns or shifts. Phenological models play a dual role, extrapolating beyond the sample space, especially concerning global warming, and interpolating within the existing sample space [126]. This evolving approach in phenological modeling underscores the importance of these models in comprehending and responding to the complex dynamics underlying phenological observations.

Modeling Phenology, How?

Typically, one or multiple phases of the visual development of organs, mostly leaves or fruits, are modeled using a selection of environmental variables. The primary objective of phenological modeling often involves the effects of variations in environmental factors, with a particular focus on weather or climate, and their variability [127]. For nearly two centuries, temperature has played a prominent role as a driver of phenological models. While our understanding of the processes underlying phenological observations has progressed, some of the most skilled models remain relatively simple, while more complex models often lack the predictive power expected to warrant their complexity [128, 129].

Numerous environmental drivers beyond temperature have been proposed for phenological modeling, including precipitation, atmospheric humidity and daylength, e.g. [24, 130]. On the one hand, processed-based models increasingly try to incorporate, albeit implicitly, representations of various internal and external signals. These models generally draw on the conceptual framework of paradormancy, endodormancy and ecodormancy. On the other hand, models are increasingly trained on large data sets, using techniques such as machine learning. Such models often do not have any enforced representation or structure [126] and may overfit observational data [131].

The hierarchical nature of phenological data (e.g., linear trends of seasonally occurring processes) and its representation (or lack thereof) in models has been evoked to explain the persistent difficulty in modeling phenological processes and events [132]. Trusting model predictions without a comprehensive understanding of the underlying biology poses challenges, as biologically incorrect models can generate reasonable within-sample predictions but may deviate out of the sample. Even models parameterized with large data sets are not immune to this and still run the risk of misrepresenting the underlying processes, hence providing false predictions [133]. While newer statistical approaches can integrate multiple or large data sources and have shown promise in tasks like gap-filling existing phenological time series [126], they should be used within their limits.

To ensure model skill, benchmarking and model comparison become crucial exercises, with frameworks such as PHENOR facilitating intercomparisons [129], but they will eventually require additional and independent data sets. Remote sensing by satellite has become a valuable tool for model development and evaluation, providing synoptic scale and continuous data [134]. Near-surface remote sensing provided by Phenocams or ground observations are other important data sources, but scaling among these sources is still challenging [135].

The ultimate test of any model remains its evaluation against experimental data [133], which has been shown to refine model selection [136]. More generally, model evaluation remains essential, as projections of different phenological models can diverge [137], and model structure remains a primary source of uncertainty in future projections [138]. Regardless of the underlying model structure, adaptation and resulting variations in species traits are often not represented in phenology models. However, emerging empirical approaches to integrate adaptation are gaining attention [139]. Depending on the scale of interest, differences in traits resulting from adaptation or adaptive processes themselves might be a marginal detail or an integral part of the response, e.g. [124].

Modeling Phenology, What?

Phenological models for flowering and leaf development have a long and rich history. However, the phenology of other organs, such as the cambium, phloem, or fine roots, are rarely modeled. The phenology of wood formation has seen increased interest over the past decade, yet models specifically addressing cambial phenology are scarce, with only a few notable exceptions. Among these is the "band model" of cambium development [140], which advances upon the previously established Vaganov-Shashkin (VS) model [141]. The band model reduces the number of input parameters required, allowing for greater simplicity and flexibility in application. Additionally, it accommodates variability among individual trees, improving its adaptability across diverse tree species and environmental conditions.

The XyDyS2 model further enriches our understanding of cambial dynamics by incorporating biochemical signal crosstalk, offering a more physiologically nuanced framework for simulating wood formation and tree-ring structures [142]. The rarity of wood phenology models is probably due to a lack of understanding of the underlying processes and their drivers. Efforts to model the phenology of roots are even more seldom [2]. However, modeling the phenology of various organs beyond leaves is crucial, as they may exhibit asynchrony with leaf phenology, as observed in the case of roots [87]. Additionally, the phenology of different organs may be governed by distinct drivers and sensitivities [2]. Even within leaf development, models have predominantly focused on green-up, neglecting the equally important processes of leaf senescence in autumn [136].

While models serve as valuable heuristics for advancing our understanding of phenological processes and events, their utilization is not without challenges. The complexity arises from various factors, including diverse data sources, numerical methods, and experimental designs, all of which are expected to contribute to future advancements in understanding and model development. Nevertheless, given the existing constraints and uncertainties inherent in phenological modeling, benchmarking and model evaluation are indispensable, mainly when applied to different species, organs, or periods. This emphasis on rigorous evaluation becomes vital to ensure the reliability and applicability of phenological models in diverse ecological contexts, especially when predicting outside of the actual training space (e.g., climate change).

Conclusions

This review presents a synthesis of phenological assessments of the growth processes in both above and belowground organs, offering insights into their current understanding. The synthesis of existing knowledge offers several noteworthy conclusions. Overall, the imbalance in our current understanding among diverse growth processes within trees is clearly discernible. With a longer history, the monitoring of leaf and canopy development now benefits significantly from technological advancements, strengthening our capabilities in phenological tracking. While our knowledge of wood formation in stems has seen substantial increased interest in recent decades, also expanding beyond its assessment in northern hemisphere conifers, the precise identification of its drivers remains a major challenge that will likely require the integration of new insights at the molecular scale. A critical area that stands out in this unbalanced comprehension is root phenology, which encompasses both primary and secondary growth. Despite its fundamental role in tree physiology and ecosystem dynamics, our understanding of root phenology remains relatively superficial. This calls for a substantial effort to further investigate root growth processes. The disparity in understanding growth processes is not indicative of a lack of interest in these phenomena. Instead, it is primarily driven by the inherent difficulties associated with monitoring the phenology of growth in stems and roots, i.e., organs that lack easily discernible visual signals.

The imbalance in our understanding of phenological processes among organs is clearly reflected in the contradictory results within the existing literature regarding phenological and functional interconnections among phenological processes. However, addressing this gap is critical for understanding drivers of phenological processes and resource allocation strategies at the tree, species, or functional groups level. Moreover, this gap-filling would directly provide a more precise definition of key phenological periods that profoundly influence the overall C cycle on ecosystem scale. The limitations in our understanding of these growth processes are mirrored in modeling efforts and outcomes. While there have been recent advancements in representing cambial activity and wood growth, these models still rely heavily on conifer data, highlighting the need for further research on other functional groups to improve model applicability and accuracy across diverse species. This limitation emphasizes the potential advantages of developing our comprehension of the ecophysiological drivers governing phenology and their phenological and functional relationships.

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Data Availability No datasets were generated or analysed during the current study.

Declarations

Competing Interest The authors declare no competing interests.

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