

Viewpoint

From division to ‘divergence’: to understand wood growth across timescales, we need to (learn to) manipulate it

Summary

Wood formation is the Rosetta stone of tree physiology: a traceable, integrated record of physiological and morphological status. It also produces a large and persistent annual sink for terrestrial carbon, motivating predictive understanding. Xylogenesis studies have greatly expanded our knowledge of the intra-annual controls on wood formation, while dendroecology has quantified the environmental drivers of multi-annual variability. But these fields operate on different timescales, making it challenging to predict how short (e.g. turgor) and long timescale processes (e.g. disturbance) interactively influence wood formation. Toward this challenge, wood growth responses to natural climate events provide useful but incomplete explanations of tree growth variability. By contrast, direct manipulations of the tree vascular system have yielded unexpected insights, particularly outside of model species like boreal conifers, but they remain underutilized. To improve prediction of global wood formation, we argue for a new generation of experimental manipulations of wood growth across seasons, species, and ecosystems. Such manipulations should expand inference to diverse forests and capture inter- and intra-specific differences in wood growth. We summarize the endogenous and exogenous factors influencing wood formation to guide future experimental design and hypotheses. We highlight key opportunities for manipulative studies integrating measurements from xylogenesis, dendroanatomy, dendroecology, and ecophysiology.

Introduction

Trees lie at the heart of the terrestrial carbon cycle (Friedlingstein *et al.*, 2014) – but their size, longevity, and modularity challenges accurate prediction of tree growth across timescales. The trees of most interest for the carbon cycle are often large (Sillett *et al.*, 2015), where important processes happen high in the canopy or invisible underground. Long lifespans also mean key processes transpire over time periods exceeding funding cycles, careers, and patience. Tree growth is then driven by a poorly constrained combination of events over some (also poorly constrained) time into the past. Trees’

decentralized anatomical organization also exhibits extreme functional redundancy (Schenk *et al.*, 2008), with replicate branches and in extreme cases millions of leaves contributing to individual tree productivity as high as 0.77 Mg yr^{-1} (Sillett *et al.*, 2015). Then, because of this morphological complexity, tree height, rooting architecture, and canopy structure represent a physical–structural history (Jump *et al.*, 2017) of the climatic conditions and disturbances experienced over an individual’s lifespan.

Measurements of radial growth (like tree rings) integrate whole-tree physiological and metabolic status at the central node of the organism (bole) from hourly to multi-decadal timescales. At short timescales, xylem development, driven by the cambium, takes place within a highly complex regulatory environment in concert with the canopy (Fig. 1a). The interplay between structural, regulatory and environmental conditions then accumulates over many years to produce the record of tree growth observable in long tree-ring time series (Fig. 1b), that can be preserved for millennia. But reconciling direct observations of mechanistic processes over diurnal (Smith & Stitt, 2007) to seasonal timescales (Aloni, 2021) with emergent growth trends over decades (Bigler *et al.*, 2007) to centuries (D’Arrigo *et al.*, 2008) to millennia (Piovesan & Biondi, 2021) is an ongoing challenge (Fig. 2). As such, calls for increased understanding of wood formation and increased integration of disciplines and methodological approaches have certainly been made before (Groover, 2023).

Here, we argue that to further enhance our understanding of wood growth, we must target innovative manipulations toward individual wood formation processes across timescales. Our understanding of the regulatory and environmental controls over tree growth, and their interactions, is improving (Dow *et al.*, 2022), and has been the focus of numerous reviews (Eckert *et al.*, 2019). But, the roles of hormonal regulation, earlywood–latewood transitions and sink–source dynamics remain difficult to represent in models (Friend *et al.*, 2019), as does how such dynamics interact (Fig. 2). A renewed experimental focus on wood growth could enable our understanding of diverse global change phenomena, because novel combinations of manipulative conditions may produce novel outcomes. But where and when should we manipulate? The answer depends on which component process of wood formation (not just radial growth) we would like to manipulate (Fig. 2). Because wood formation is the summation of multiple component processes (division, enlargement, wall thickening, and lignification), manipulations should focus on specific processes at specified phenological stages, as the same manipulation at different times (spring and summer) may produce different outcomes (smaller ring and lighter ring) or even result in compensatory effects (Dow *et al.*, 2022).

In cases where wood formation has been targeted by experimental treatments like drought, compression, girdling,

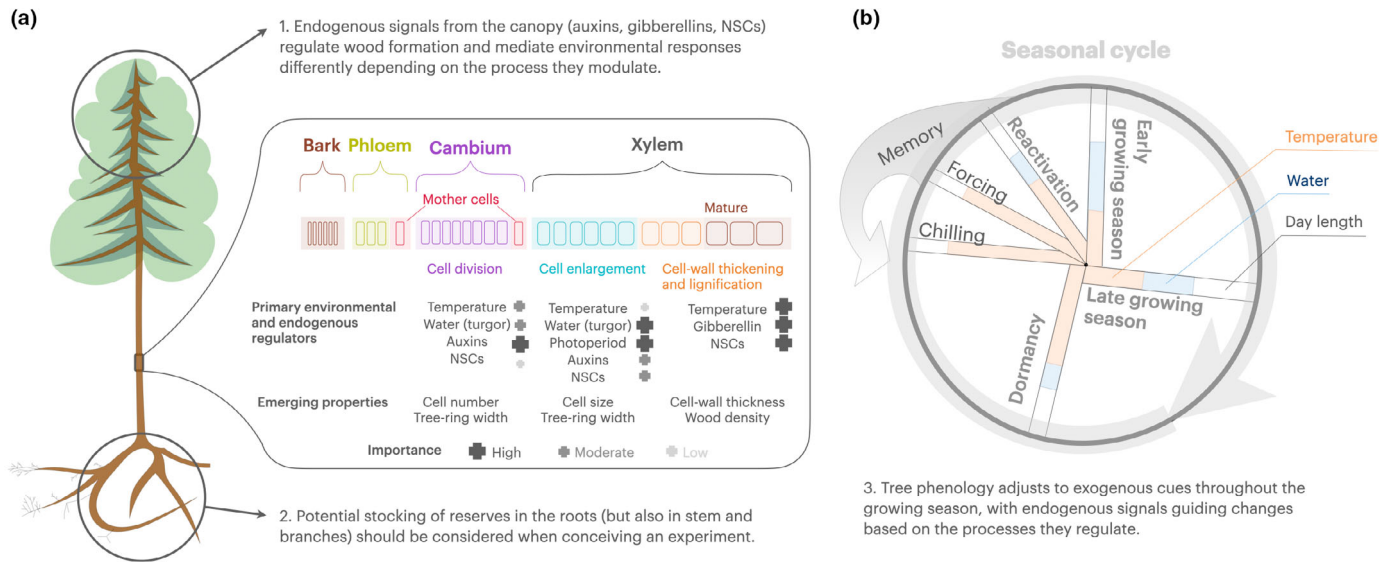


Fig. 1 Simplified conceptual framework of some key aspects of our review of wood growth, illustrating the integration across (a) tissues (e.g. canopy, roots, and the cambium) and (b) time (e.g. memory, early- and late season). (a) Illustration of a set of hypotheses for the role of various endogenous factors (auxin, gibberellin, and nonstructural carbohydrates (NSCs)) and exogenous factors (temperature and water/turgor) and their relative importance (high, moderate, and low) for progressive stages of wood formation from division to enlargement to cell-wall thickening and lignification. Emergent from these interactions and hormonal cross-talk are properties, such as tree-ring widths measured by dendroecologists. (b) Over time, the cyclical combination of exogenous drivers, endogenous constraints, and developmental trajectories perturbs physiology to impact growth (i.e. through reserve dynamics, physical, or structural changes), sometimes referred to as memory. The progression of chilling, forcing, reactivation, growing season, and dormancy is illustrated along with the hypothesized roles of temperature (orange), water (blue), and day length (white) on wood growth phenology.

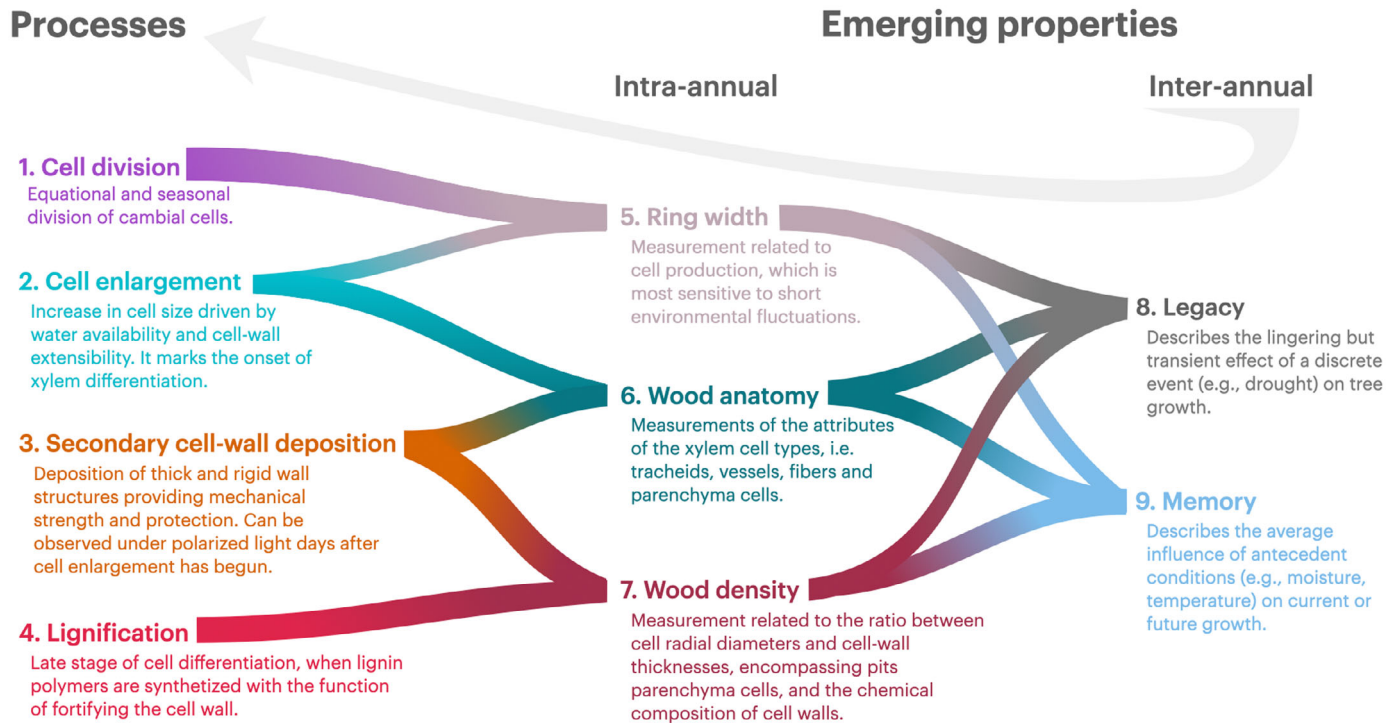


Fig. 2 Processes and intra- and inter-annual emerging properties defining wood development and wood features. The grey arrow points to the effect of past environmental conditions, which are modulated by the wood developmental processes.

heating, and chilling, results have sometimes been surprising. A stem-chilling experiment in two co-occurring species led to reduced cell division in red maple (Rademacher *et al.*, 2022), but a reduction in cell-wall deposition, triggering the formation of light rings in white pine (Fig. 3). Moreover, the late-season chilling of white pine induced the formation of false rings in some trees (Fig. 3). False rings have previously been related to extreme (warm) temperatures (Marchand & Filion, 2012) and are generally thought of as a cambial response to temporary drought (Battipaglia *et al.*, 2016) not reduced temperature. Trees that formed false rings during this experiment had also formed a false ring in 2016 (Fig. 3) during a known late-season drought event, suggesting that multiple triggers for false ring formation may exist. In another surprising outcome, blue rings (rings without lignification in the latewood; Fig. 3) were observed in a compression treatment, but not in a chilling treatment, although these features have previously been associated with ephemeral summer cooling due to volcanic eruptions (Piermattei *et al.*, 2020). These examples show how wood-formation manipulations can produce unexpected results, illustrating our incomplete understanding of wood formation and highlighting their critical value.

In the following, we briefly review the controls on wood formation, from endogenous signals to long-term climate, and highlight some questions to then outline the pressing need for a new generation of targeted manipulations of wood formation to enhance our predictive capacity of the global carbon cycle. In our review, we focus on key ‘moments’ and processes that might be

future targets for manipulations, as well as uncertainties around the controls on wood formation.

Reviewing the controls on wood formation

Phenology of wood formation

Extensive study of xylogenesis in conifers from high latitudes, where cell numbers are easily counted, has identified four clear developmental stages of wood formation: cambial cell division, xylem cell enlargement, secondary wall deposition, and lignification (Fig. 2). In angiosperms, the process is more complex due to cell-type-dependent differentiation mechanisms that contribute to their intricate wood structure (Noyer *et al.*, 2023). In some tropical angiosperms, this complexity is further evident with phloem and xylem forming simultaneously, and no dormancy due to weaker seasonality (Schmitz *et al.*, 2008; David *et al.*, 2014). Regardless, wood formation processes identified in conifers, even if not universal, represent a fundamental model against which to contrast wood formation behaviors across diverse ecological and phylogenetic contexts.

The four fundamental and co-occurring wood formation processes are each responsive to environmental cues, such as variations in temperature, day length, and water availability at different moments of the growing season (Buttò *et al.*, 2021). Certain wood formation processes respond similarly to environmental drivers, while others can respond differently – much of this

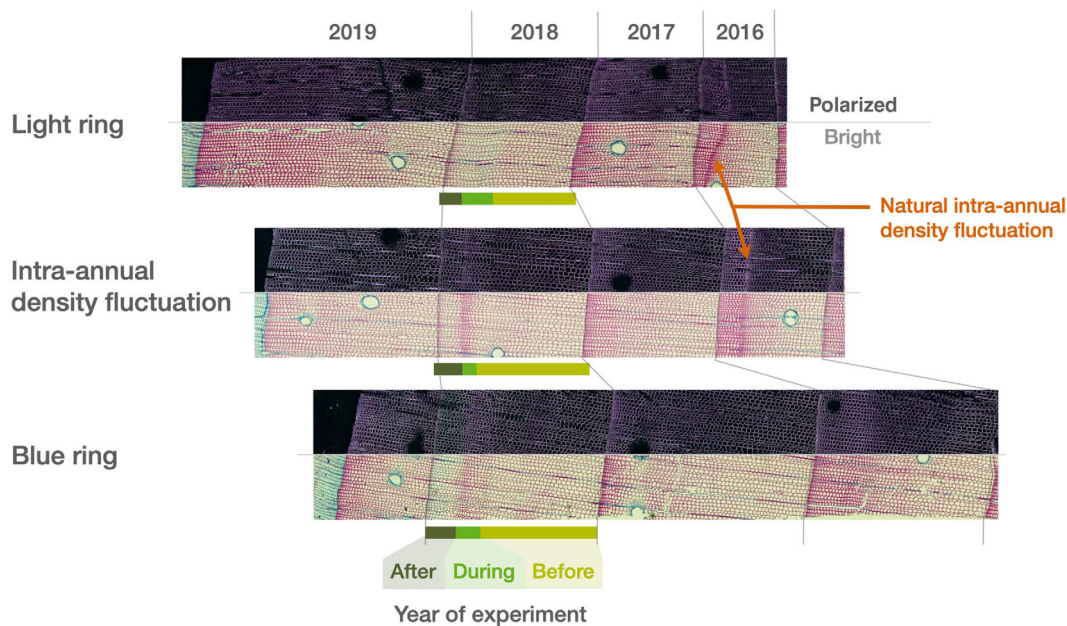


Fig. 3 Novel manipulations can produce novel xylem behaviors. Various anatomical sections of white pine that illustrate experimentally-induced anatomical features: light ring (top panel), an intra-annual density fluctuation or ‘false ring’ (middle panel), and a nonlignified or ‘blue’ ring (bottom panel). The light ring and intra-annual density fluctuation were observed in a stem chilling treatment, while the blue ring occurred in a stem compression experiment. Approximations of the proportion of wood that formed before, during, and after each experimental manipulation are shown with green bars below each image. Images were captured and are shown under polarized (top half) and normal light (bottom half). Some of the trees also showed natural intra-annual density fluctuation in previous years, such as 2016, which coincided with a known drought event.

is contingent on phenology. Cell division and enlargement both require turgor and cell-wall extensibility, the latter upregulated by long day length (Ivakov *et al.*, 2017). Secondary wall deposition and lignification are each disrupted by cold temperatures and enhanced by warm temperatures (Belmecheri *et al.*, 2018). We still lack a precise assessment of the plasticity of these responses across seasons, species, ecosystems, and biomes. For example, which process relationships with climate are universal? How flexible are these phenological routines across variable environments? Selective pressures might change developmental sensitivity to the same environmental factor, even within the same species (Singh *et al.*, 2021). If we are to design effective experiments to answer such questions, an explicit understanding of the endogenous regulation of wood formation processes, particularly factors responsive to anthropogenic forcing and/or disturbances, is essential.

Endogenous controls on wood formation

Sugars are internal cues coordinating plant growth and development with the environment (Aloni, 2021). Particularly, soluble sugars regulate osmotic potentials and fuel all stages of wood formation (Fig. 1). In spring, compared with canopy leaves, radial growth is a low-priority sink (Deslauriers *et al.*, 2009), and carbon reserves then support earlywood, particularly in deciduous angiosperms, such as ring-porous oaks (Barbaroux & Bréda, 2002). Relatively low sugar concentrations and high cell-wall extensibility, due to signaling, slow early-season wall stiffening, allowing turgor-driven cell expansion to continue for weeks (Carteni *et al.*, 2018).

Many hormones are also involved with wood formation: auxin, cytokinins, strigolactones, and polyamines for cell division; brassinosteroids, abscisic acid, ethylene, and gibberellins for cell elongation and wall deposition (see Buttò *et al.*, 2020 for a review). However, particularly auxin and gibberellin are known to undergo seasonal fluctuations, accounting for interspecific variability in wood anatomy (Kijidani *et al.*, 2021) and have known intra-ring gradients and pathways, making them promising targets for field manipulation. Auxin is produced in buds and leaf primordia, while gibberellin is mostly found in older leaves (Aloni, 2021). Manipulation aimed at interacting with auxin flow during wood formation should consider that strong transport of auxin from buds and leaf primordia promotes cambial division and triggers xylem and phloem differentiation. This polar auxin transport (cell-to-cell) through the phloem is the main driver of the asymmetric gradient of auxin centered on the cambium, decreasing sharply in the phloem and gradually in the xylem (Fig. 1a; Bhalerao & Fischer, 2014). Maturing leaves export reduced levels of auxin but increased levels of gibberellin precursors, rendered bioactive across the developing tree ring (Björklund *et al.*, 2007; Aloni, 2021), and extend cell division by stimulating additional polar auxin transport (Ben-Targem *et al.*, 2021). Thus, even manipulating a single organ, such as leaves (e.g. by defoliation), has multiple effects on various hormones and these need to be taken into consideration during design and interpretation of manipulative experiments.

Interactions among different internal signals, such as sugars and hormones, can be complex. For example, during the late growing

season, low auxin-to-gibberellin ratios enhance secondary wall deposition, simultaneously upregulated by increasing stem soluble sugar concentrations under canopy export (Johnsson *et al.*, 2019). In conifers, stem sugar availability peaks after shoot elongation, and this increased sugar supply is thought to drive the earlywood–latewood transition. Accordingly, higher sugar levels promote secondary wall deposition, influencing cell development to produce smaller cells with thicker walls (Carteni *et al.*, 2018).

As these processes annually accumulate and are driven by environmental factors (such as water availability, temperature, and day length), tree-ring patterns can emerge over longer timescales. Understanding the emergence of observed wood traits will require various internal signals and processes to be considered when designing experiments.

Exogenous (environmental) controls on wood growth

At longer timescales, climate controls on annual tree ring formation have often been studied through relationships among climate and tree-ring time series (Fritts, 1966). Key climate drivers include soil moisture availability, temperature, and atmospheric moisture demand. Larger tree rings are facilitated by sufficient temperature for metabolism (Gantois, 2022), prolonged soil moisture toward transpiration and cell turgor (Liu *et al.*, 2020), and a lack of vapor pressure deficit extremes risking hydraulic dysfunction and carbon starvation (McDowell *et al.*, 2022). Thus results a wider or narrower ring, according to the combination of climate conditions in a given year.

These general relationships belie the nonlinearity and context specificity of a tree's response to climate variation, where species, location, timing, phenology, leaf habit, ontogeny, site, individual tree life history, disturbance, and numerous other factors modify these relationships (McGregor *et al.*, 2021). Elevated temperatures enhance growth during spring cell division, but impede growth during summer latewood formation (Björklund *et al.*, 2019), while winter warming spells may induce freeze–thaw embolisms. At ecotones, within the same stand one species may be moisture-limited, and the other temperature-limited. Thus, despite a proliferation of synthesis studies trying to quantify complex nonlinear tree growth responses to climate (Dannenbergh *et al.*, 2019), trees exhibit remarkable flexibility, or perhaps context specificity in how they actually respond to climate drivers (Klesse *et al.*, 2020).

At short timescales, climate extremes may lead to annually detectable features, most typically from disturbance or altered phenology. Such features include frost rings, fire scars, white rings, false rings or intra-annual density fluctuations, dark rings, or series of small or missing rings (Hartl *et al.*, 2019). But the presence or absence of these features may also depend on tree physiological state and can be contingent on antecedent climate conditions (Babst *et al.*, 2016). That is, additional complexities emerge as longer timescales are considered.

Trees are long-lived organisms, with physiological inertia driving slow variation across their lifespans. Biological memory, autocorrelation, legacy effects, lags, and other related or synonymous phenomena are critical controls on tree growth (Fig. 2).

Trees may exhibit altered growth for many years preceding mortality (Bigler *et al.*, 2007). Droughts or wet years may also limit or enhance growth for multiple years (Jiang *et al.*, 2019). Despite long recognition of such inertia (e.g. 'carryover effects'), the physiological mechanisms have rarely been directly studied. Three classes of explanations include physical (e.g. deep soil moisture storage), structural (e.g. sapwood area loss or canopy dieback), and carbon-mediated mechanisms (e.g. reserve exhaustion) (*sensu* Peltier & Ogle, 2020). Experiments may help to distinguish among these potential explanations for the responses of a given xylogenesis process to past conditions.

Why design experimental manipulations of wood growth?

We summarize three inter-related arguments (attribution, interactions, and forecasting) for why observations of wood growth variation in response to natural environmental fluctuations are useful, but manipulations can often be more valuable, particularly in hypothesis-driven inquiry. First, multiple contemporaneous processes produce new wood (e.g. cell division and lignification) in the context of a broad scope of antecedent conditions (e.g. drought and disturbance) that can modify the rates, durations, and timings of these processes (Fig. 1b). Then, attribution of specific observed changes in resulting wood anatomy is made *a priori* to some causal event, which can be difficult to isolate from other coincident conditions or characteristics of an individual tree. This is particularly true in the context of global change, when anthropogenic warming and accompanying nontransient dynamics are globally superimposed upon our experiments and observations in natural forest systems. Second, well-designed manipulations can attempt to isolate specific physiological processes of interest from other interacting factors or processes. Taking the example of temperature, targeted manipulations could investigate the effects of manipulations on individual organs (roots, cambium, etc.) on spring cambial initiation timing (i.e. heating: Oribe *et al.*, 2003; chilling: Begum *et al.*, 2016). This can also be partly accomplished through counterfactuals in the form of control groups, or regression designs (Hanson *et al.*, 2017), but remains difficult to achieve if we limit ourselves to observations of natural phenomena. Third, experiments can address future conditions with no past analog (forecasting), exceeding the range of historic variation, such as higher drought frequencies, heat waves, pluvials, salt-water intrusions, and other conditions that may be experienced in the future (Hanson *et al.*, 2017).

Future manipulations may target specific wood formation processes (explicitly considering treatment timing), particularly in 'nonmodel' species (e.g. evergreen angiosperms) and forest systems (e.g. tropics) to disentangle wood formation processes across space and time. Importantly, the timing of any manipulation needs to be considered to isolate treatment effects on specific processes of interest, such as lignification. For example, temperature impacts on cell division and deposition vary strongly throughout the season (Balducci *et al.*, 2016). Similarly, in the southwestern United States, winter and summer moisture stress impact different portions of annual ring growth (Belmecheri *et al.*, 2018). Thus,

experimental timing requires prior knowledge of wood phenology for a particular context, which includes factors, such as species, wood porosity, and other traits (Fig. 4). At present, this information is well-characterized for certain species but is clearly not universal (Schmitz *et al.*, 2008), and cambial phenology also likely varies across a species' range and in different years (Zhang *et al.*, 2018).

Comparing the responses of multiple species with contrasting traits (e.g. wood porosity; D'Orangeville *et al.*, 2022) may be particularly important to elucidate universal mechanisms. For example, phenological and physiological differences can become apparent when observing co-occurring species (Chen *et al.*, 2019) and are likely related to differences in resource allocation strategies (e.g. acquisitive vs conservative species). In this sense, acquisitive species might exhibit more opportunistic behaviors than conservative species, tracking environmental changes by adjusting their phenology, which allows for greater plasticity in tree productivity than in conservative species (Chen *et al.*, 2019). These frameworks become extremely useful when selecting species for experimental designs, ensuring that the chosen species appropriately represent a variety of ecological strategies. Other carbon source-sink related traits, such as investment in reproduction or defense (Bentz *et al.*, 2017), fire adaptations, leaf lifespan along with shade tolerance, wood density, bark photosynthesis, and root : shoot ratios, may also affect how trees respond to treatments, allowing for an holistic understanding of resource allocation patterns that enable tree productivity and resilience. In the context of global inference and prediction, insights from model systems may become less useful and exploring the resource acquisition gradient is one useful framework to select species to increase the knowledge gain in any experimental design.

We suggest that mature trees should be a focus for future manipulations of wood growth. A large majority of manipulations have used small, often potted trees in controlled environments. However, ontogeny affects developmental processes, altering carbon allocation priorities, and tree height can constrain or slow water and carbon cycling, making scaling from smaller trees to mature trees fraught (Hartmann *et al.*, 2018). In particular, there is increasing evidence that the primary controls of wood growth may switch from being source- to being sink-limited with size (Walker *et al.*, 2021). Unfortunately, mature, field-grown trees, rather than small, potted trees, are the most important demographic in the forest carbon cycle (Pugh *et al.*, 2019). When mature trees have been manipulated, wood formation was rarely measured. For example, there are now multiple long-standing Free Air CO₂ Enrichment experiments world-wide on mature, field-grown trees (Walker *et al.*, 2021), but to our knowledge, wood formation is rarely monitored closely (partially due to its invasive nature), despite wood being a primary carbon sink. Finally, we rarely continue measurements after the end of the manipulation, despite the fact that trees will often exhibit treatment legacies for years, if not decades. Such information about the postmanipulation trajectories is valuable for predicting future resilience, particularly under altered disturbance frequencies (i.e. more frequent drought; Williams *et al.*, 2022).

Lastly, a focus on ultimate (rather than proximal) explanations for wood formation (Segovia-Rivas & Olson, 2023), while

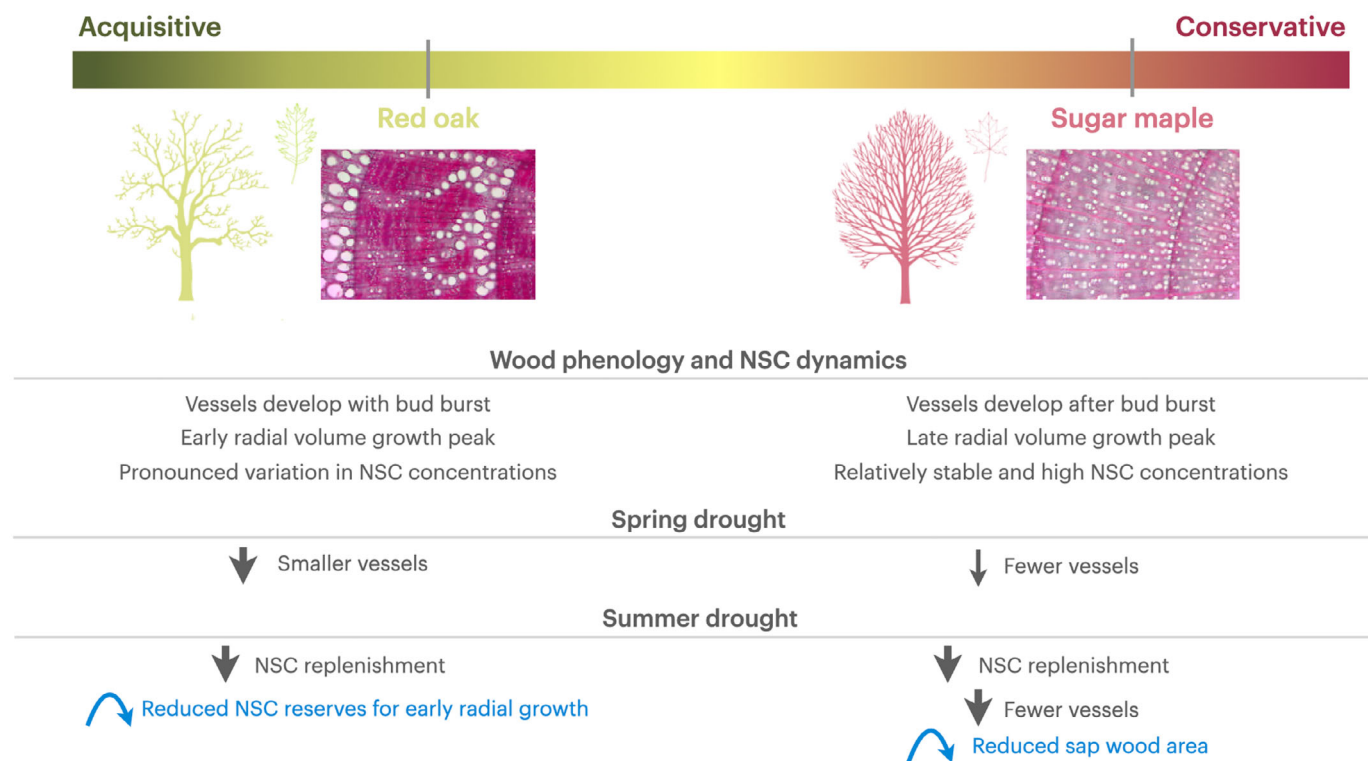


Fig. 4 Example placement of two species with different traits (canopy structure, leaf characteristics, and wood porosity) along a resource acquisition gradient ranging from more acquisitive species to more conservative species, and how each might integrate a spring vs a summer drought event. Grey arrows symbolize negative effects with their size roughly indicating the strength of the effect. Blue arrows symbolize potential carryover effects, for example in nonstructural carbohydrate (NSC) reserve pools.

recognizing the diversity of conditions encountered by trees in terrestrial forests, could be useful. For example, why do trees invest more or less carbon in wood formation? And what are the fitness benefits of different allocation strategies (Fig. 4)? Our own discussions exposed distinctly regional answers to such questions: In temperate and boreal forests, competition for light and space is a primary explanation, while trees in the southwestern United States may benefit from regular replacement of embolized xylem (Trugman *et al.*, 2018).

A new generation of wood formation manipulations

There remains ample room to leverage manipulation experiments to better understand wood formation across timescales. Diverse physiological experiments, such as defoliation, manipulations of ambient CO₂ concentrations, water supply, and temperature (high and low), with a focus on wood formation promise to yield a better understanding of this integral process. To understand context specificity, regression and factorial designs might prove particularly powerful to identify specific thresholds or shapes of response curves, as well as how antecedent conditions may alter cambial responses to manipulations. For example, heating and chilling trees after sequentially exposing them to high and low water supply could identify critical thresholds among different wood formation behaviors to temperature and water supply. While under strong regulatory and environmental control, wood formation outcomes

remain idiosyncratic and difficult to predict (Dow *et al.*, 2022), perhaps because considering the appropriate timescales of drivers is tricky and sometimes neglected. In this context, replication of previous experiments in multiple ecosystems, species, ontogenetic stages, and phenophases will also be crucial to derive universal principles of wood formation. While model species are useful, there is also much to be learned at the extremes, for example, very tall tree-tops (Koch *et al.*, 2004), evergreen oaks (Campelo *et al.*, 2023), deciduous conifers (Saderi *et al.*, 2019), and aseasonal tropical systems, presently a very active area of research where cloudiness and flooding may be key drivers of cambial phenology (Giraldo *et al.*, 2023). Flooding or cloudiness manipulations outside of the tropics could be instructive to understand the generality of wood formation responses to such drivers and may have unexpected relevance to novel stressors like persistent wildfire smoke (Orozco *et al.*, 2024).

To highlight some diversity of potential avenues for directly manipulating specific wood growth processes, we propose three example experiments and hypotheses (but see Fig. 1a inset). Tapping (as for maple sugar production) could be a promising avenue for independent manipulation of carbon supply to wood formation independent of other aspects of carbon and water status. While a single tap is generally recommended for the sustainable practice of maple sugaring (Rademacher *et al.*, 2023), trees could be intentionally over-tapped (e.g. multiple tap holes along the stem) to substantially reduce stem soluble sugar reserves before the growing

season and monitor the effects of wood formation, in particular onset, rate, and duration of cell division in the early growing season. We might hypothesize that such a treatment would have limited impacts on early-season cell division but constrain late-season cell-wall thickening and lignification, which is more carbon intensive (Fig. 1a). Early-season snow removal (Zhang *et al.*, 2019), along with monitoring of the timing, rate, and duration of cell division and enlargement rates across multiple species, would allow determining the effects of reduced water availability on early-season wood formation processes (cell division) and investigating the degree of influence on later stages of wood formation. Using multiple species, ideally with different rooting depths, would ensure that the effects of the reduced water availability could be differentiated from potential collateral effects of fine root frost damage due to the removal of the protective snow cover. Application of exogenous auxin (Nahas *et al.*, 2024) late in the growing season, directly to the cambium, could test whether auxin levels orchestrate differences between conservative and acquisitive strategies. If combined with stem heating, we hypothesize that cell division could be (re-)promoted, perhaps even after lignification had begun, producing false rings (such as in Fig. 3). The above three experiments manipulating carbon, water, and hormonal supply could provide insights into how each modulates different phases of xylem differentiation, shedding light on the interactions of resources, turgor, and regulation in driving wood formation across a growing season.

Conclusions

During wood formation, the effect of short-term environmental fluctuations is strongly modulated by internal signaling, which coordinates plant growth at the inter-organ level. This complex process, with its multiple dependencies, has evolved under ecosystem-specific dynamics and climate, where the functioning of this nested regulatory system is constrained or enhanced by multi-annual variability in climate and environmental conditions. Observational studies are thus useful but insufficient to make sense of this complex and context-specific process, where tree species, life stage and history, driver strength, timing and duration, and climate each contribute to unique outcomes. To make sense of these interactions, physiological manipulation experiments that quantify wood growth appear to be a potent tool to target individual processes in a context-specific manner. The Rosetta Stone was crucial for deciphering ancient languages, targeted manipulation experiments of individual wood formation processes could help to integrate understanding across subfields, toward a comprehensive understanding of wood formation across timescales. We now have the tools to quantify wood formation, but to understand its underlying causality, we need to (learn to) manipulate it.

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Competing interests

None declared.

Author contributions

VB, DMPP and TR conceived of the ideas, wrote the manuscript, and revised it collaboratively. VB, DMPP and TR are joint first authors.

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