

Why longer seasons with climate change may not increase tree growth

E.M. Wolkovich¹, Ailene K. Ettinger², Alana Chin³, Catherine J. Chamberlain⁴,
Frederik Baumgarten¹, Kavya Pradhan^{5,6}, Rubén D. Manzanedo⁷⁻⁹ &
Janneke Hille Ris Lambers⁷

June 1, 2025

¹ Forest & Conservation Sciences, Faculty of Forestry, University of British Columbia, 2424 Main Mall, Vancouver, BC V6T 1Z4, Canada

² The Nature Conservancy of Washington, 74 Wall Street, Seattle, WA USA

³ California State Polytechnic University, Humboldt. Department of Biological Sciences. Arcata, CA, USA

⁴ The Nature Conservancy, 334 Blackwell St Ste 300, Durham, NC, USA

⁵ Department of Biology, University of Washington, Seattle, WA, 98195

⁶ Moore Center for Science, Conservation International, Arlington, VA, 22202

⁷ Institute for Integrative Biology, ETH Zürich, 8092 Zürich, Switzerland

⁸ Institute of Plant Sciences, University of Bern, Bern, Switzerland

⁹ Oeschger Center for Climate Change Research, University of Bern, Bern, Switzerland

Author contributions: All authors conceived of the idea, prepared the literature review, edited the manuscript and contributed to designing some of the figures; in addition EMW wrote the manuscript, AKE, AC, CJC and EMW synthesized the literature review, RD led developing Fig. 1, CJC developed Fig 2, EMW developed Fig. 4, and AC, RD and EMW led developing the Box figure and Fig. 3.

Abstract

Most climate change forecasts assume that longer growing seasons increase carbon storage through increased tree growth, but recent findings have challenged this assumption. Here we highlight divergent findings across studies, spanning diverse methods and disciplinary perspectives. Current hypotheses for why longer growing seasons may not always increase tree growth include drought-related effects and internal constraints. These hypotheses, however, are generally tested in different ways by different fields on different species, and rarely consider how external drivers and internal constraints interact. We outline how bridging these divides while integrating evolutionary history and ecological theory could help build a unified model across species for when longer seasons will—or will not—lead to greater tree growth, with major forecasting implications.

1 Introduction

The idea that longer growing seasons lead to increased plant growth is an intuitive tenet across multiple fields of biology, including physiology, dendrochronology and ecosystem ecology (1; 2). It is also a foundational assumption of many global carbon cycle models (e.g. 3; 4). These models project that continued anthropogenic warming will be partly offset by increased carbon sequestration as warming lengthens growing seasons in many forests (4), an assumption supported by ecosystem-scale studies (5; 6; 7).

Yet recent work has questioned this longstanding assumption (e.g. 8; 9; 10), challenging decades of research reporting increased growth with longer seasons, from observations along elevational and latitudinal gradients (11; 12; 13; 14), classic experiments in lab settings (15), to trends in ecosystem fluxes with warming (5; 6; 7). Proposed mechanisms for the apparent disconnect are diverse (Fig. 1), including the complex nature of climate change (e.g. drought or heat stress, 8) and internal constraints on plant growth (16), which alone or interactively may limit plant responses (17).

Here we examine how different fields have studied the relationship between growing season length and tree growth to identify the potential mechanisms that unite—and could disconnect—these processes. We find substantial variation in growth \times season length relationships across different definitions (see Box: Defining the quest for a comprehensive framework across external and internal drivers). We also find a pervasive disciplinary split between studies, which test different mechanisms on different species. Current work often lacks a clear mechanistic physiological model (17; 18), and implicitly ignores the role of shared evolutionary history and community ecology to plant growth (e.g. 19; 20; 21), which could slow the search for a universal model. We argue that a robust answer for whether longer seasons lead to increased growth will require new efforts and shifts in perspectives. Towards that aim, we outline how cross-disciplinary efforts to build a more mechanistic model across species, would allow the field to rapidly develop a framework to predict when, where and how climate change may increase tree growth.

Evidence that longer seasons increase plant growth, or not

The idea that time limits growth is a fundamental principle across biology. Many biological processes—including photosynthesis and aspects of growth—are rate-limited, making time a crucial commodity (1; 22; 23). Thus, the hypothesis that longer growing seasons should increase growth is intuitive—and pervasive.

Foundational evidence comes from spatial clines across elevation and latitude, with growth decreasing alongside growing season length at higher elevations and latitudes (Fig. S1). Experimentally, this assumption is supported by small-scale field warming studies that find that phenologically advancing species also grow more with warming (24), while observationally, ecosystem-scale studies have reported a similar relationship between season length and carbon fluxes across decades with global warming (6) or in years with warm, early springs (5). However, some recent high-profile studies find no support for this relationship (8). These studies, which often focus on inter-annual correlations with metrics of standardized individual tree growth (8; 10), have generated debate about whether future carbon storage forecasts are overestimated and which metrics of growth (9), or growing season length (25), are relevant (see Box).

To better understand this recent debate we examined research spanning 25 years for current advances and potential gaps. Though the number of papers directly addressing this topic is small, a slight majority found that longer seasons lead to increased growth (21 of 36 total papers), with no clear pattern by method or year (Fig. 2 and see ‘Literature review methods’ in Supplement). For example, carbon assimilation studies were evenly split in finding evidence for or against the relationship (or simply not testing it, Fig. 2). Diverging results occurred across and within methods, suggesting the drivers of this variation are likely due to biological mechanisms, not solely due to varying definitions of growth or growing season length (as some have recently suggested, e.g. 9; 25, and see Box).

Most studies tested the hypothesis that longer seasons with climate change increase growth via either increased time to grow (10 of 36 papers) or because longer seasons are usually warmer (8 papers), although many also considered hypotheses that could disconnect growth from season length. Studies from dendrochronology (the study of tree rings and their dating) and physiology have readily offered explanations for findings that increased growth may not be a universal outcome of longer seasons (Fig. 1). External climatic drivers that offset the positive growth effects of longer seasons were often reported in tree ring studies (26; 27; 28). In particular, the hypothesis that higher temperatures paired with lower precipitation produce negative correlations of season length with growth appeared in 58% of tree ring studies we reviewed (and was only mentioned once outside of these studies, see also Fig. 1). In contrast, 43% of lab experimental and wood phenology (xylogenesis) studies suggested fundamental internal constraints that prevent trees from responding to longer seasons (Fig. S2, 29; 30; 16). Yet we found that these hypotheses have been tested in radically different ways on different species, rarely together, and ignore relevant research from other disciplines.

65 **Controllers on growth \times season length relationships**

66 Major mechanisms that could limit or disrupt the positive effects of longer growing seasons
67 generally fall into two categories: (1) external factors, such as drought, which should impact
68 ecosystem-level trends at regional scales, and (2) internal physiological constraints, which some
69 research suggests are either universal across plants (e.g. 16), or species- and population-specific
70 (e.g. 31). While we address each in turn, these drivers can clearly operate together (17), though
71 research rarely teases them apart. Further, the importance of internal versus external drivers
72 likely varies by species, highlighting the need to integrate perspectives from phylogenetic and
73 community ecology (we discuss these gaps further in ‘Building a new framework for growth \times
74 season length’ below).

75 **External drivers**

76 Temperature limits many biological processes (17). Temperatures that are too cool (below 5°C
77 for temperate trees) and too warm (an area of active research, but likely between 35-45°C;
78 32; 33) slow down biological processes and eventually can lead to tissue death (see Fig. 3a,
79 Box, 34; 35). Between these upper and lower limits, biological processes underpinning growth
80 generally accelerate such that warming can have a direct effect by accelerating biological time,
81 up until the maximum rate for that particular process. Assuming a common growth response
82 curve to temperature, possible increased growth should be predictable based on the current
83 seasonal temperatures and the amount of warming (Fig. 3b).

84 How much or whether growth increases at all depends on the non-linear effect of temperature
85 on biological processes (Fig. 3a). At very cool temperatures—such as in early spring—a small
86 increase in temperature may have limited effect (or even increase frost risk through early bud-
87 burst, Fig. 1e, 36), while an increase at warmer temperatures—such as those more common in
88 the summer (e.g. 16 to 18°C)—could have a larger physiological impact. However, warming that
89 pushes plants beyond their optima, where many biological rates crash, could have large negative
90 impacts (1; 37). Thus, some studies hypothesize that longer seasons effectively only extend the
91 very cool early-season periods and may have no discernible effect on growth (with varying defi-
92 nitions of growth, see Box), while other studies—based on tree rings—suggest that any increases
93 in growth due to longer seasons can be offset by reduced growth due to high summer temper-
94 atures (Fig. 1, 38; 8). In contrast, other researchers argue that warmer temperatures have not
95 yet pushed trees above their optima (39), and instead have driven increases in growth through
96 accelerated rates, rather than longer seasons (e.g. 40), or through a combination of both.

97 Other external drivers could counteract positive effects of longer—or warmer—seasons on growth
98 predicted from temperature responses alone. Moisture deficits from reduced precipitation or
99 higher evaporative demand (commonly invoked in tree ring studies, Fig. 1) can slow or stall
100 growth. Support for this hypothesis comes from negative correlations between growth and pre-
101 cipitation (or other metrics related to plant access to water in tree ring studies, 26; 41), and is well

supported by physiological observations that water status can be a biophysical limit to growth (i.e., cells cannot expand without sufficient turgor, 42; 43), though few physiological studies on season length considered this effect (Fig. 2). With increasing extremes in both temperature and moisture, understanding these factors (44)—and how they interact—will become increasingly important (45). External biotic factors are also shifting with longer seasons—including herbivory, disease and competition(46; 47; 48)—and can limit productivity (49; 50; 51), though they are missing from the current debate on the impacts of longer seasons on growth (we found no mention of them, Fig. 1e).

Internal constraints

When and how growth is initiated and ceases is under genetic and developmental control, and thus plants' internal programming could limit growth responses to longer seasons (52). Within species (intraspecifically) research has repeatedly shown that populations vary in their growth and responses to extended seasons, reflecting differences that likely evolved to limit tissue loss to rare early or late-season events (46; 47; 48). Populations often vary predictably in their end-of-season phenology, with more poleward populations tending to stop height growth (budset) earlier using locally adapted photoperiod cues (31; 53). This means longer seasons are generally driven by spring phenology, which appears far more flexible, and has advanced more rapidly than fall events (53). Some recent studies suggest novel roles for the summer solstice (16) in setting a fixed universal developmental switch between when warming temperatures hasten or delay leaf senescence, and in determining when warmer temperatures trigger greater reproduction (54).

Trade-offs between vegetative and reproductive investments may produce important growth response differences within individuals and between species. Years of high reproductive output can reduce growth (55; 56). For species that mast—producing abundant cones or fruits in only some years—high reproduction could especially impact measures of wood growth. Higher summer temperatures may trigger mast in the following year (56; 57); if true, then reduced growth in years following warm summers may not indicate temperatures too high for growth, as recent studies have suggested (e.g. 38; 8), but instead shifting investment to reproduction. Such contrasting interpretations of the same pattern highlight the lack of a comprehensive mechanistic model for how internal and external factors may operate—both independently and together—to affect the relationship between growth and season length (see Box, 17).

Species-level variation

The effects of these external and internal drivers are likely to vary across species, with species identity strongly predicting variation in growth \times season length relationships (e.g. 29; 30). Though this reality was rarely acknowledged in studies we reviewed (Fig. 1c), research in dendrochronology, physiology and in phenology often mentions important differences between certain species groups that should affect how longer seasons impact growth (58; 59; 60).

The distinct strategies of deciduous versus evergreen species, including in how and when they invest in leaf and shoot elongation versus cambial growth, can affect how they respond to longer seasons. While evergreen species generally leaf out later than deciduous species they can more immediately photosynthesize with earlier springs, though both types of species generally invest in buds (for new leaves, shoots and flowers) in the preceding year. This means neither can rapidly change their investment in leaf area in response to an earlier spring, but both can have multiple flushes of leaves (61; 31). Wood growth in evergreen species is generally thought to come from current season photosynthates, while deciduous species may more often use stored carbon resources (62; 63). These differences would suggest season length by growth relationships may be most apparent via lagged effects in deciduous species, but this is rarely studied (and not clearly supported to date, see 64; 65).

This division between evergreen and deciduous species hints at a larger suite of traits that predict growth by growing season length relationships among species. Species that budburst earlier and more readily produce additional leaves (e.g. leaf flushes after budset, and other characteristics more common to ‘indeterminate’ species, 66; 67) may grow more with longer seasons (though potentially with a lag, see Box) versus those that budburst later and flush new primary growth only once. Similarly, species adapted to cold, dry or high latitude conditions may have different thresholds for when these external drivers limit or promote growth (e.g. some *Populus* and *Quercus* species, 31; 68; 69; 27, and see Fig.3). Such differences could easily obscure any overall relationship between growth and growing season length. Supporting this possibility, current studies finding divergent results (Fig. S3) span a wide range of species (we found 57 species from 26 genera across 36 papers).

Building a new framework for growth \times season length

Understanding when, how and why longer seasons lead to increased tree growth would benefit from a framework that integrates across external and internal drivers to predict plant growth across species. While our brief review of this literature could not cover all possible mechanisms, it highlights disciplinary divergences and major gaps in our mechanistic model (see Box, and 17; 70; 71) that likely underlie the current debate in whether longer seasons lead to increased tree growth. We argue that a more mechanistic understanding of how these drivers integrate to explain current findings is possible, but will require new approaches that help address major open questions.

Integrate phylogeny and traits to guide research

The diversity of responses across species is a major challenge to building a common framework to predict how growth shifts with growing season length. Different species—especially those with different growth strategies (19)—are unlikely to have the same response to longer seasons, thus results of studies on one species may not easily translate to another. Yet explicitly incorporating

174 this diversity could offer a path to connecting apparently divergent results.

175 New approaches that integrate how species traits and evolutionary history shape responses
176 to climate change (72; 73) could organize responses to provide novel insights and guide new
177 studies. In particular, advances in phylogenetic comparative methods (20) have moved research
178 away from treating species identity as a simple grouping factor where each species is unique
179 (e.g. *Fagus sylvatica* is different from *Quercus robur* and *Pinus sylvestris*) or fits into a limited
180 set of groups (e.g. deciduous versus evergreen) and towards species as suites of correlated
181 observations, separated by their evolutionary distance (e.g. *Fagus sylvatica* is much more closely
182 related to *Quercus robur* compared to *Pinus sylvestris*). This evolutionary distance may explain
183 diverging responses, but can also help identify underlying growth strategies that drive species-
184 and clade-level variation (74; 75). Such models can layer in species-level information, such as
185 traits correlated with differences in growth strategies, while phylogeny can capture additional
186 species differences, which likely capture unmeasured ‘latent’ traits .

187 In addition to naturally organizing species differences, a trait-based phylogenetic comparative
188 approach can help build a more testable and predictable framework. Because this approach can
189 flexibly fit evolutionary history and traits together, it allows clades or species groupings that
190 respond similarly to emerge from the data and models (76), versus being a priori grouped or
191 defined. Similarly traits that co-vary with different responses can be more quickly identified
192 (e.g. 77; 76, see Fig. 4). Both of these benefits could highlight which species or traits to focus
193 additional studies on to gain the most insights, while similarly suggesting areas that should be
194 less studied (e.g. traits that may be too confounded with evolutionary history, 78; 79) or outlier
195 species that may not represent most species (75). This approach may thus redefine debates over
196 which metrics of growth or growing season length are relevant into debates over which metrics
197 are most relevant for which clades and/or traits (see Box). It could also help guide research to
198 address what we argue are three major open questions.

199 **How prevalent are constraints across species and populations?**

200 New evidence suggests inter-annual variation in growth may be limited because of internal
201 constraints that prevent plants from fully using longer seasons (16). If true, this would have
202 major ramifications for how much we expect growth to shift with warming. All plants are limited
203 by internal constraints and how quickly they can build new tissues (80; 81), but selection towards
204 different growth strategies (e.g. acquisitive versus conservative) should drive variation in these
205 constraints across species. Selection should also drive local adaptation in these constraints at
206 the population-level (68; 31), by favoring individuals that match to local environmental optima
207 (82; 83). This appears to be the case for budset—which indicates the end of height growth,
208 though we currently have data on only a few species (53; 84).

209 New studies could rapidly test for constraints across species and populations to work towards
210 a predictive framework using phylogeny and traits to predict these constraints. This approach

has already yielded useful insights in spring phenology, highlighting which environmental factors consistently drive budburst across species while also showing widely-cited results may not extend beyond one well-studied species (75). Organizing current data for budset and other metrics of start and end of growth (see Box) could identify how variable responses are across populations and species.

The best tests of constraints will likely leverage experiments. Large-scale common garden studies can test for constraints in adult trees, including constraints due to different strategies and from past climatic events (e.g., by selecting species with different growth strategies and/or selecting populations within a species with varying past exposure to damaging early season frosts 85; 86). Such approaches take time, but could be supplemented by manipulative experiments. While juvenile stages of trees are often more flexible than their adult forms, they usually provide predictable inference in differences across species and populations, and thus should be integrated far more into studies of how season length affects growth. Using saplings and controlled environments could quickly test how much growth can—or cannot—shift with longer seasons—providing a potentially standardized way to compare constraints across species and populations.

What is the scale of variation across space and time?

The idea that growing season length influences plant growth is fundamental to plant biology, but we found it is rarely tested in ways relevant to the current debate (see ‘Growth \times elevation relationships’ in Supplement)—a major gap that limits progress. While multiple papers report a lack of relationship between growth and growing season length (Figs. 1, 2), we have no fundamental understanding of what the effect size of this relationship should be, and thus no way to know if we have sufficient power in current studies to detect it.

Identifying the macro-scale pattern is a tractable way to help develop a framework for growth \times growing season length relationships. Tree ring studies designed to leverage latitudinal and elevational gradients in climate could quickly provide the raw data (87). Research will then need to develop models that tease out the effects of warmer temperatures across the season—likely affecting important biological rates (Fig. 3)—versus longer seasons. Disentangling these may require focused efforts to understand xylogenesis across species and climates, but doing so across major climatic gradients could make differences more obvious. Wood growth provides an obvious baseline from which to set expectations of how much growth can vary across space, and links to existing major datasets (Fig. S4). Research will also then need to integrate beyond wood growth, including methods to better characterize changes across the leaf, shoot and wood architecture of different species (e.g. 88; 89) and also extending to the complexity of roots (68; 90). These data can provide a baseline to compare to the scale of shifts over time, which studies of growth \times growing season length to date have focused on (Fig. 2), since the same tree rings measured for understanding spatial variation will also capture inter-annual variation.

How do external drivers and internal constraints interact?

The external and internal factors that affect how longer seasons impact growth are inherently interconnected (1). While research often acknowledges this, modeling these together will require new experiments and observational studies, ideally designed to integrate into trait-mediated phylogenetic models. Studies across space could provide inference by studying how growing seasons measured by vegetative versus wood phenology vary—and attributing variation through models that nest populations within species and include traits while also testing for how climate drives growth.

The complexity of climate change and plant growth in response to longer, warmer seasons makes experiments vital to building useful mechanistic models for understanding current trends and for forecasting. Observational data—used mainly to date to tackle this question (Figs. 2, S2)—generally confounds multiple external drivers, including season length, temperature and precipitation regimes (40; 91; 28), making it impossible to tease out actual drivers behind observed trends. Experiments, in contrast, can provide more robust tests and help understand observational responses. Experiments that we outlined to test for internal constraints in saplings (above) can layer on shifts in external drivers to tease apart this complexity. Combining results from such experiments with observational data from larger-scale well designed networks (see 44) could be transformative.

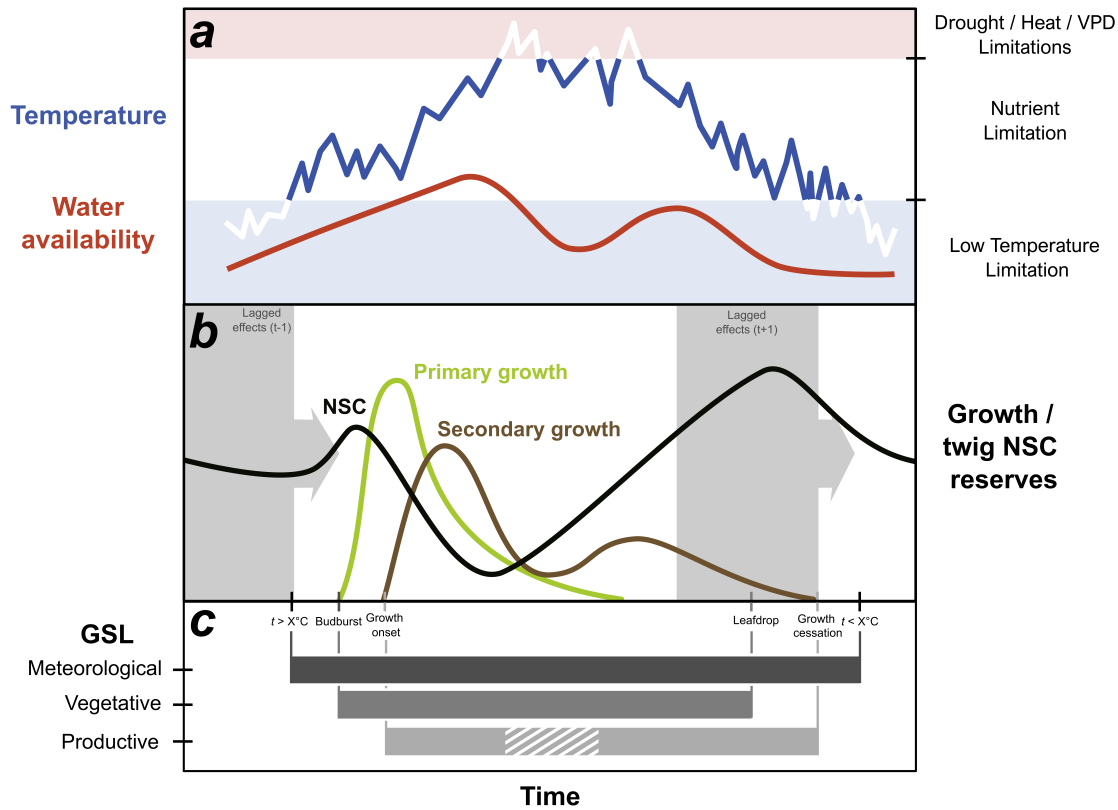
Building a better mechanistic model of tree growth will also require teasing out changes in season length from warming that affects rates; a challenge best addressed by new experiments that decouple these two factors. Such experiments could start on juvenile trees to help inform the underlying model, select representative species to focus on, and develop predictions for large-scale studies. Experiments could also inform a better model of lag effects across species, with small-scale studies sampling saplings multiple years after manipulations (versus the common practice of destructive sampling at the end of the treatment growing season) and large-scale studies following existing efforts to test for ecological ‘memory’ (e.g. 92; 93; 94). These efforts should help bridge across the contrasting timescales of current physiological and dendrochronological studies of growing season length: we found most physiological studies of growth \times growing season length relationships studied 1-2 years of dynamics, usually of juvenile trees, while tree ring studies focused on synthesizing across decades of adult tree growth.

Expanding studies across more species will support development of accurate models that can forecast at relevant scales and to help design large-scale experiments. While experimenting on adult trees is difficult, previous challenges in climate change research have led to large-scale experiments to understand other complex drivers (e.g. SPRUCE, DroughtNet, Pfyndwald, 95; 96; 97). We expect similar experiments will be critical here. Preparing for these large experiments using trait-mediated phylogenetic models to understand responses across species, however, could yield advances well beyond past efforts. By informing which species or clades to study, new experiments could span enough phylogenetic and trait diversity to forecast species

285 beyond the experiment and maximize the information gained (98). Starting now to leverage
286 data across species to inform and design new large-scale studies and experiments will help build
287 accurate models of future forest and related carbon dynamics, with implications for projections
288 of carbon sequestration and carbon markets.

289 *Acknowledgements:* B. Wu for extracting growth \times elevation data; R. Zäch for logistical sup-
290 port; N. Pederson for discussion, J. Davies and three reviewers for comments that improved the
291 manuscript. Support provided by the Rubel Foundation (JHRL), NSERC Discovery (EMW) and
292 the Swiss State Secretariat for education, Research and Innovation (SERI) by a SERI-funded
293 ERC Starting Grant MB23.00011 (RM).

Box. Defining the quest for a comprehensive framework across external and internal drivers



294

295 The idea that plants would not clearly benefit from the temporal opportunity to photosynthesize
 296 more has highlighted the lack of a comprehensive model of tree growth. This has ignited a
 297 series of debates on the fundamental biology of how trees grow, including over the importance
 298 of source (photosynthesis-limited) versus sink limitations (plant growth-limited, but often via
 299 temperature, biophysical constraints, nutrients, and other arguably external factors, 17; 18; 71;
 300 33) and which metrics of growth and growing season length are relevant. Yet the complexity of
 301 each term means that neither can have one simple definition.

302 Here we show the simplified climate of one year (a), which determines rates and timing (b) of
 303 primary growth (root and shoot elongation and leaf production from meristems) and secondary
 304 growth (radial wood and bark growth from cambia), both of which often depend on conditions
 305 determining non-structural carbohydrate (NSC, which are sugars and starch needed for growth
 306 and an important area of study, for more details see 99; 100; 86; 81) production and reserves
 307 and storage from previous seasons. Assuming sufficient available nutrients (17), each of these
 308 types of growth could define the growing season length (GSL, c) but GSL can also be defined
 309 meteorologically (shown here as time, t , above some minimum $X^{\circ}\text{C}$ and below above some
 310 maximum $X^{\circ}\text{C}$, with sufficient soil moisture) or by large-scale measures of plant productivity
 311 (25). Lagged effects (shown in gray in b) are lasting impacts of previous time periods either in

the form of NSC stores or structural legacies influencing productivity.

Of studies in our literature review, the largest proportion used metrics related to secondary growth, quantifying growth by measuring radial growth (e.g. through increment cores or dendrometers, $n = 28$), but a number also looked at metrics related to primary growth, including C assimilation (e.g. net ecosystem productivity or gross primary productivity, $n = 20$). For growing season length, the largest number of studies used vegetative (e.g. budburst to leaf senescence in our figure above, 26 studies) or wood phenology (11 studies) as their definition, while a smaller number used a meteorological definitions or fixed dates (7 studies). We found 14 studies that did not directly measure GSL (e.g. 101; 8; 16).

These different metrics limit any current effort to synthesize results across studies (see ‘The challenge of metrics: Measuring growth and growing season length’ in the Supplement) but also highlight a limited mechanistic framework of tree growth at the physiological level (102; 87). While we cannot integrate over all the proposed mechanisms that could help define these terms to improve our model of growth, research designed to test links between metrics and the physiological processes associated with external drivers and internal constraints would aid progress (103). For example, some meteorological definitions could relate directly to temperatures that limit cell growth, as multiple studies suggest growth stops at below 5°C (104; 70), but we need more studies of the upper limit and a better framework to test for variation across species. Layering on what levels of nitrogen, micronutrients and drought are also critical thresholds for growth (105; 106; 59) should help predict variation across space and species, but a full framework would benefit from an improved understanding of how growth and stress operate at the cellular and molecular levels (107; 108; 71).

1 References

- [1] Nobel, P. S. *et al.* *Biophysical plant physiology and ecology*. (WH Freeman and company, 1983).
- [2] Frank, D., Fang, K. & Fonti, P. Dendrochronology: Fundamentals and innovations. In *Stable Isotopes in Tree Rings: Inferring Physiological, Climatic and Environmental Responses*, 21–59 (Springer International Publishing Cham, 2022).
- [3] Ito, G. *et al.* Global carbon cycle and climate feedbacks in the nasa giss modele2. 1. *Journal of Advances in Modeling Earth Systems* **12**, e2019MS002030 (2020).
- [4] Friedlingstein, P. *et al.* Global carbon budget 2022. *Earth System Science Data Discussions* **2022**, 1–159 (2022).
- [5] Chen, W. *et al.* Effects of climatic variability on the annual carbon sequestration by a boreal aspen forest. *Global Change Biology* **5**, 41–53 (1999).
- [6] Keenan, T. F. *et al.* Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Nature Climate Change* **4**, 598–604 (2014).
- [7] Finzi, A. C. *et al.* Carbon budget of the harvard forest long-term ecological research site: pattern, process, and response to global change. *Ecological Monographs* **90** (2020).
- [8] Dow, C. *et al.* Warm springs alter timing but not total growth of temperate deciduous trees. *Nature* **608**, 552–557 (2022).
- [9] Green, J. K. & Keenan, T. F. The limits of forest carbon sequestration. *Science* **376**, 692–693 (2022).
- [10] Silvestro, R. *et al.* A longer wood growing season does not lead to higher carbon sequestration. *Scientific reports* **13**, 4059 (2023).
- [11] Myneni, R. B., Keeling, C., Tucker, C. J., Asrar, G. & Nemani, R. R. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* **386**, 698–702 (1997).
- [12] Berdanier, A. B. & Klein, J. A. Growing season length and soil moisture interactively constrain high elevation aboveground net primary production. *Ecosystems* **14**, 963–974 (2011).
- [13] King, G. M., Gugerli, F., Fonti, P. & Frank, D. C. Tree growth response along an elevational gradient: climate or genetics? *Oecologia* **173**, 1587–1600 (2013).
- [14] Cuapio-Hernández, L. *et al.* Is there a response pattern between radial growth of trees and elevation gradient? *Tree-Ring Research* (2022).

- [15] Went, F. W. The experimental control of plant growth. *The experimental control of plant growth*. **17** (1957).
- [16] Zohner, C. M. *et al.* Effect of climate warming on the timing of autumn leaf senescence reverses after the summer solstice. *Science* **381**, eadf5098 (2023).
- [17] Körner, C. Paradigm shift in plant growth control. *Current opinion in plant biology* **25**, 107–114 (2015).
- [18] Fatichi, S., Pappas, C., Zscheischler, J. & Leuzinger, S. Modelling carbon sources and sinks in terrestrial vegetation. *New Phytologist* **221**, 652–668 (2019).
- [19] Grime, J. P. Evidence for existence of 3 primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* **111**, 1169–1194 (1977).
- [20] Webb, C. O., Ackerly, D. D., McPeck, M. & Donoghue, M. J. Phylogenies and community ecology. *Annual Review of Ecology and Systematics* **33**, 475–505 (2002).
- [21] Ávila-Lovera, E., Winter, K. & Goldsmith, G. R. Evidence for phylogenetic signal and correlated evolution in plant–water relation traits. *New Phytologist* **237**, 392–407 (2023).
- [22] Cosgrove, D. J. Growth of the plant cell wall. *Nature reviews molecular cell biology* **6**, 850–861 (2005).
- [23] Hilty, J., Muller, B., Pantin, F. & Leuzinger, S. Plant growth: The what, the how, and the why. *New Phytologist* **232**, 25–41 (2021).
- [24] Cleland, E. E. *et al.* Phenological tracking enables positive species responses to climate change. *Ecology* **93**, 1765–1771 (2012).
- [25] Körner, C., Möhl, P. & Hiltbrunner, E. Four ways to define the growing season. *Ecology Letters* (2023).
- [26] Kolář, T. *et al.* Response of the leaf phenology and tree-ring width of european beech to climate variability. *Silva Fennica* **50** (2016).
- [27] de Sauvage, J. C., Vitasse, Y., Meier, M., Delzon, S. & Bigler, C. Temperature rather than individual growing period length determines radial growth of sessile oak in the pyrenees. *Agricultural and Forest Meteorology* **317**, 108885 (2022).
- [28] Camarero, J. J. *et al.* Decoupled leaf-wood phenology in two pine species from contrasting climates: Longer growing seasons do not mean more radial growth. *Agricultural and Forest Meteorology* **327**, 109223 (2022).
- [29] Cuny, H. E., Rathgeber, C. B., Lebourgeois, F., Fortin, M. & Fournier, M. Life strategies in intra-annual dynamics of wood formation: example of three conifer species in a temperate forest in north-east france. *Tree physiology* **32**, 612–625 (2012).

- [30] Michelot, A., Simard, S., Rathgeber, C., Dufrêne, E. & Damesin, C. Comparing the intra-annual wood formation of three European species (*Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris*) as related to leaf phenology and non-structural carbohydrate dynamics. *Tree physiology* **32**, 1033–1045 (2012).
- [31] Soolanayakanahally, R. Y., Guy, R. D., Silim, S. N. & Song, M. Timing of photoperiodic competency causes phenological mismatch in balsam poplar (*populus balsamifera* l.). *Plant, cell & environment* **36**, 116–127 (2013).
- [32] Martinez-Meier, A., Sanchez, L., Pastorino, M., Gallo, L. & Rozenberg, P. What is hot in tree rings? the wood density of surviving douglas-firs to the 2003 drought and heat wave. *Forest Ecology and Management* **256**, 837–843 (2008).
- [33] Cabon, A. *et al.* Cross-biome synthesis of source versus sink limits to tree growth. *Science* **376**, 758–761 (2022).
- [34] Larcher, W. *Plant Physiological Ecology* (Springer-Verlag, 1980).
- [35] Kramer, P. *Physiology of woody plants* (Elsevier, New York, 2012).
- [36] Chamberlain, C. J., Cook, B. I., Morales-Castilla, I. & Wolkovich, E. M. Climate change reshapes the drivers of false spring risk across european trees. *New Phytologist* **229**, 323–334 (2021).
- [37] Leuning, R. Temperature dependence of two parameters in a photosynthesis model. *Plant, Cell & Environment* **25**, 1205–1210 (2002).
- [38] Gantois, J. New tree-level temperature response curves document sensitivity of tree growth to high temperatures across a us-wide climatic gradient. *Global Change Biology* **28**, 6002–6020 (2022).
- [39] Schaber, J. & Badeck, F.-W. Evaluation of methods for the combination of phenological time series and outlier detection. *Tree Physiology* **22**, 973–982 (2002).
- [40] Ren, P. *et al.* Growth rate rather than growing season length determines wood biomass in dry environments. *Agricultural and Forest Meteorology* **271**, 46–53 (2019).
- [41] Etzold, S. *et al.* Number of growth days and not length of the growth period determines radial stem growth of temperate trees. *Ecology Letters* **25**, 427–439 (2022).
- [42] Peters, R. L. *et al.* Turgor—a limiting factor for radial growth in mature conifers along an elevational gradient. *New Phytologist* **229**, 213–229 (2021).
- [43] Cosgrove, D. J. Structure and growth of plant cell walls. *Nature Reviews Molecular Cell Biology* 1–19 (2023).

- [44] Schuldt, B. *et al.* A first assessment of the impact of the extreme 2018 summer drought on central european forests. *Basic and Applied Ecology* **45**, 86–103 (2020).
- [45] Charrier, G. *et al.* Interaction of drought and frost in tree ecophysiology: rethinking the timing of risks. *Annals of Forest Science* **78**, 1–15 (2021).
- [46] Mitton, J. B. & Ferrenberg, S. M. Mountain pine beetle develops an unprecedented summer generation in response to climate warming. *The American Naturalist* **179**, E163–E171 (2012).
- [47] Lange, H., Økland, B. & Krokene, P. Thresholds in the life cycle of the spruce bark beetle under climate change. *Interjournal for Complex Systems* **1648**, 1–10 (2006).
- [48] Cleland, E. E. & Wolkovich, E. Effects of phenology on plant community assembly and structure. *Annual Review of Ecology, Evolution, and Systematics* **55**, 471–492 (2024).
- [49] Sturrock, R. *et al.* Climate change and forest diseases. *Plant pathology* **60**, 133–149 (2011).
- [50] La Porta, N. *et al.* Forest pathogens with higher damage potential due to climate change in europe. *Canadian Journal of Plant Pathology* **30**, 177–195 (2008).
- [51] Senf, C., Seidl, R. & Hostert, P. Remote sensing of forest insect disturbances: Current state and future directions. *International journal of applied earth observation and geoinformation* **60**, 49–60 (2017).
- [52] Howe, G. T. *et al.* From genotype to phenotype: unraveling the complexities of cold adaptation in forest trees. *Canadian Journal of Botany* **81**, 1247–1266 (2003).
- [53] Aitken, S. N. & Bemmels, J. B. Time to get moving: assisted gene flow of forest trees. *Evol Appl* **9**, 271–90 (2016).
- [54] Journé, V. *et al.* Summer solstice orchestrates the subcontinental-scale synchrony of mast seeding. *Nature Plants* **10**, 367–373 (2024). URL <https://www.nature.com/articles/s41477-024-01651-w>.
- [55] Thomas, S. C. Age-related changes in tree growth and functional biology: The role of reproduction. In MEINZER, F. C., Lachenbruch, B. & Dawson, T. E. (eds.) *Size- and Age-Related Changes in Tree Structure and Function*, chap. 2, 33–64 (Springer, 2011).
- [56] Hacket-Pain, A., Friend, A., Lageard, J. & Thomas, P. Tree rings and masting: considering reproductive phenomena when interpreting tree rings? *Tree Rings in Archaeology, Climatology and Ecology* **14**, 78–85 (2016).
- [57] Hacket-Pain, A. J., Cavin, L., Friend, A. D. & Jump, A. Consistent limitation of growth by high temperature and low precipitation from range core to southern edge of european beech indicates widespread vulnerability to changing climate. *European Journal of Forest Research* **135**, 897–909 (2016).

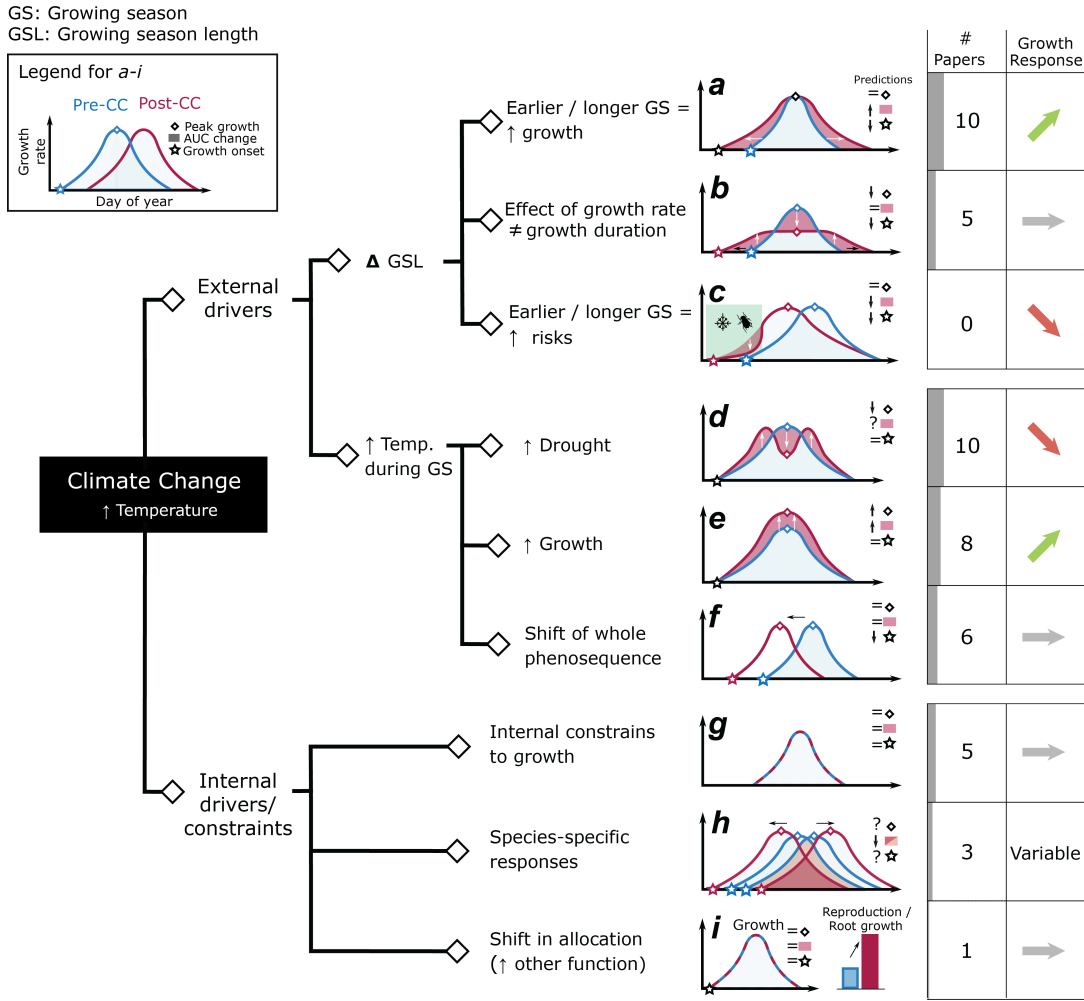
- [58] Camarero, J. J., Gazol, A., Sangüesa-Barreda, G., Oliva, J. & Vicente-Serrano, S. M. To die or not to die: early warnings of tree dieback in response to a severe drought. *Journal of Ecology* **103**, 44–57 (2015).
- [59] Fu, Y. H. *et al.* Nutrient availability alters the correlation between spring leaf-out and autumn leaf senescence dates. *Tree physiology* **39**, 1277–1284 (2019).
- [60] Puchalka, R., Prislan, P., Klisz, M., Koprowski, M. & Gričar, J. Tree-ring formation dynamics in *fagus sylvatica* and *quercus petraea* in a dry and a wet year. *Dendrobiology* **91**, 1–15 (2024).
- [61] Day, M. E. & Greenwood, M. S. Regulation of ontogeny in temperate conifers. In *Size-and age-related changes in tree structure and function*, 91–119 (Springer, 2011).
- [62] Gordon, J. C. & Larson, P. R. Seasonal course of photosynthesis, respiration, and distribution of ^{14}C in young *pinus resinosa* trees as related to wood formation. *Plant Physiology* **43**, 1617–1624 (1968).
- [63] Monson, R. K., Szejner, P., Belmecheri, S., Morino, K. A. & Wright, W. E. Finding the seasons in tree ring stable isotope ratios. *American journal of botany* **105**, 819–821 (2018).
- [64] Coulthard, B. L., George, S. S. & Meko, D. M. The limits of freely-available tree-ring chronologies. *Quaternary Science Reviews* **234**, 106264 (2020).
- [65] Klesse, S. *et al.* Legacy effects in radial tree growth are rarely significant after accounting for biological memory. *Journal of Ecology* **111**, 1188–1202 (2023).
- [66] Kikuzawa, K. Leaf survival and evolution in *betulaceae*. *Annals of Botany* **50**, 345–353 (1982).
- [67] Lechowicz, M. J. Why do temperate deciduous trees leaf out at different times - adaptation and ecology of forest communities. *American Naturalist* **124**, 821–842 (1984).
- [68] McKown, A. D., Guy, R. D. & Quamme, L. K. Impacts of bud set and lammas phenology on root: shoot biomass partitioning and carbon gain physiology in poplar. *Trees* **30**, 2131–2141 (2016).
- [69] Delpierre, N., Guillemot, J., Dufrêne, E., Cecchini, S. & Nicolas, M. Tree phenological ranks repeat from year to year and correlate with growth in temperate deciduous forests. *Agricultural and Forest Meteorology* **234**, 1–10 (2017).
- [70] Rossi, S. *et al.* Critical temperatures for xylogenesis in conifers of cold climates. *Global Ecology and Biogeography* **17**, 696–707 (2008).
- [71] Rademacher, T. *et al.* Insights into source/sink controls on wood formation and photosynthesis from a stem chilling experiment in mature red maple. *New Phytologist* **236**, 1296–1309 (2022).

- [72] Cornwell, W. & Nakagawa, S. Phylogenetic comparative methods. *Current Biology* **27**, R333–R336 (2017).
- [73] Harmon, L. *Phylogenetic Comparative Methods* (University of Idaho, 2024). URL [https://bio.libretexts.org/Bookshelves/Evolutionary_Developmental_Biology/Phylogenetic_Comparative_Methods_\(Harmon\)](https://bio.libretexts.org/Bookshelves/Evolutionary_Developmental_Biology/Phylogenetic_Comparative_Methods_(Harmon)).
- [74] Pearse, W. D., Legendre, P., Peres-Neto, P. R. & Davies, T. J. The interaction of phylogeny and community structure: Linking the community composition and trait evolution of clades. *Global Ecology and Biogeography* **28**, 1499–1511 (2019).
- [75] Morales-Castilla, I. *et al.* Phylogenetic estimates of species-level phenology improve ecological forecasting. *Nature Climate Change* 1–7 (2024).
- [76] Davies, T. J., Regetz, J., Wolkovich, E. M. & McGill, B. J. Phylogenetically weighted regression: A method for modelling non-stationarity on evolutionary trees. *Global ecology and biogeography* **28**, 275–285 (2019).
- [77] Willis, C. G., Ruhfel, B., Primack, R. B., Miller-Rushing, A. J. & Davis, C. C. Phylogenetic patterns of species loss in thoreau’s woods are driven by climate change. *Proceedings of the National Academy of Sciences* **105**, 17029–17033 (2008).
- [78] Cornwell, W. K. *et al.* Functional distinctiveness of major plant lineages. *Journal of Ecology* **102**, 345–356 (2014).
- [79] Westoby, M., Yates, L., Holland, B. & Halliwell, B. Phylogenetically conservative trait correlation: quantification and interpretation. *Journal of Ecology* **111**, 2105–2117 (2023).
- [80] Marchand, L. J. *et al.* Timing of spring xylogenesis in temperate deciduous tree species relates to tree growth characteristics and previous autumn phenology. *Tree Physiology* **41**, 1161–1170 (2021).
- [81] Luo, Y. *et al.* Internal physiological drivers of leaf development in trees: Understanding the relationship between non-structural carbohydrates and leaf phenology. *Functional Ecology* (2024).
- [82] Colautti, R. I., Eckert, C. G. & Barrett, S. C. H. Evolutionary constraints on adaptive evolution during range expansion in an invasive plant. *Proceedings of the Royal Society B-Biological Sciences* **277**, 1799–1806 (2010). Colautti, Robert I. Eckert, Christopher G. Barrett, Spencer C. H.
- [83] McKown, A. D. *et al.* Geographical and environmental gradients shape phenotypic trait variation and genetic structure in populus trichocarpa. *New Phytologist* **201**, 1263–1276 (2014). URL <GotoISI>://WOS:000338510200022. McKown, Athena D. Guy, Robert D. Klapste, Jaroslav Gerales, Armando Friedmann, Michael Cronk, Quentin C. B. El-Kassaby, Yousry A. Mansfield, Shawn D. Douglas, Carl J.

- [84] Zeng, Z. A. & Wolkovich, E. M. Weak evidence of provenance effects in spring phenology across europe and north america. *New Phytologist* (2024).
- [85] Charrier, G., Ngao, J., Saudreau, M. & Améglio, T. Effects of environmental factors and management practices on microclimate, winter physiology, and frost resistance in trees. *Frontiers in plant science* **6**, 259 (2015).
- [86] Tixier, A. *et al.* Comparison of phenological traits, growth patterns, and seasonal dynamics of non-structural carbohydrate in mediterranean tree crop species. *Scientific Reports* **10**, 347 (2020).
- [87] Manzanedo, R. D. *et al.* Moving ecological tree-ring big data forwards: Limitations, data integration, and multidisciplinary. *Science of The Total Environment* **955**, 177244 (2024).
- [88] Puletti, N., Grotti, M., Ferrara, C. & Chianucci, F. Lidar-based estimates of aboveground biomass through ground, aerial, and satellite observation: a case study in a mediterranean forest. *Journal of Applied Remote Sensing* **14**, 044501–044501 (2020).
- [89] Sillett, S. C., Graham, M. E., Montague, J. P., Antoine, M. E. & Koch, G. W. Ground-based calibration for remote sensing of biomass in the tallest forests. *Forest Ecology and Management* **561**, 121879 (2024).
- [90] Radville, L., McCormack, M. L., Post, E. & Eissenstat, D. M. Root phenology in a changing climate. *Journal of Experimental Botany* **67**, 3617–3628 (2016).
- [91] Canadell, J. *et al.* *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (Cambridge University Press, New York, NY, 2021).
- [92] Flinker, R. H. *et al.* Promise and pitfalls of modeling grassland soil moisture in a free-air co2 enrichment experiment (biocon) using the shaw model. *Pedosphere* **31**, 783–795 (2021).
- [93] Schweiger, A., Awdamet, F. T., Drenckhan, W. & Berauer, B. J. Transgenerational effects of elevated co 2: Downregulation of photosynthetic efficiency and stomatal sensitivity to drought (2022).
- [94] Chin, A. R. *et al.* The memory of past water abundance shapes trees 7 years later. *American Journal of Botany* e16452 (2025).
- [95] Norby, R. J. & Zak, D. R. Ecological lessons from free-air co2 enrichment (face) experiments. *Annual review of ecology, evolution, and systematics* **42**, 181–203 (2011).
- [96] Hanson, P. J. *et al.* Attaining whole-ecosystem warming using air and deep-soil heating methods with an elevated co 2 atmosphere. *Biogeosciences* **14**, 861–883 (2017).

- [97] Smith, M. D. *et al.* Drought-net: A global network merging observations, experiments, and modeling to forecast terrestrial ecosystem sensitivity to drought. In *AGU Fall Meeting Abstracts*, vol. 2016, B11J-06 (2016).
- [98] Cadotte, M. W., Davies, T. J. & Peres-Neto, P. R. Why phylogenies do not always predict ecological differences. *Ecological Monographs* **87**, 535–551 (2017).
- [99] Hartmann, H. & Trumbore, S. Understanding the roles of nonstructural carbohydrates in forest trees—from what we can measure to what we want to know. *New phytologist* **211**, 386–403 (2016).
- [100] Martínez-Vilalta, J. *et al.* Dynamics of non-structural carbohydrates in terrestrial plants: a global synthesis. *Ecological monographs* **86**, 495–516 (2016).
- [101] Zhu, L. *et al.* Different response of earlywood vessel features of *fraxinus mandshurica* to rapid warming in warm-dry and cold-wet areas. *Agricultural and Forest Meteorology* **307**, 108523 (2021).
- [102] Körner, C. Tools shape paradigms of plant-environment interactions. *Progress in Botany Vol. 82* 1–41 (2021).
- [103] Vieira, J., Carvalho, A. & Campelo, F. Tree growth under climate change: evidence from xylogenesis timings and kinetics. *Frontiers in Plant Science* **11**, 90 (2020).
- [104] Körner, C. A re-assessment of high elevation treeline positions and their explanation. *Oecologia* **115**, 445–459 (1998).
- [105] Körner, C. The forest’s nutrient cycle drives its carbon cycle. *Tree Physiology* **42**, 425–427 (2022).
- [106] El Omari, B. Accumulation versus storage of total non-structural carbohydrates in woody plants. *Trees* 1–13 (2022).
- [107] Nilsson, J. *et al.* Dissecting the molecular basis of the regulation of wood formation by auxin in hybrid aspen. *The Plant Cell* **20**, 843–855 (2008).
- [108] Ye, Z.-H. & Zhong, R. Molecular control of wood formation in trees. *Journal of experimental botany* **66**, 4119–4131 (2015).
- [109] Rezende, E. L. & Bozinovic, F. Thermal performance across levels of biological organization. *Philosophical Transactions of the Royal Society B* **374**, 20180549 (2019).
- [110] Forest Service - United States Department of Agriculture. Forest Inventory and Analysis (FIA) database. URL <http://www.srsfia.usfs.msstate.edu/ewdata/ewrec.htm>.
- [111] Fischer, C., Traub, B. *et al.* *Swiss National Forest Inventory-methods and models of the fourth assessment* (Springer, 2019).

2 Figures



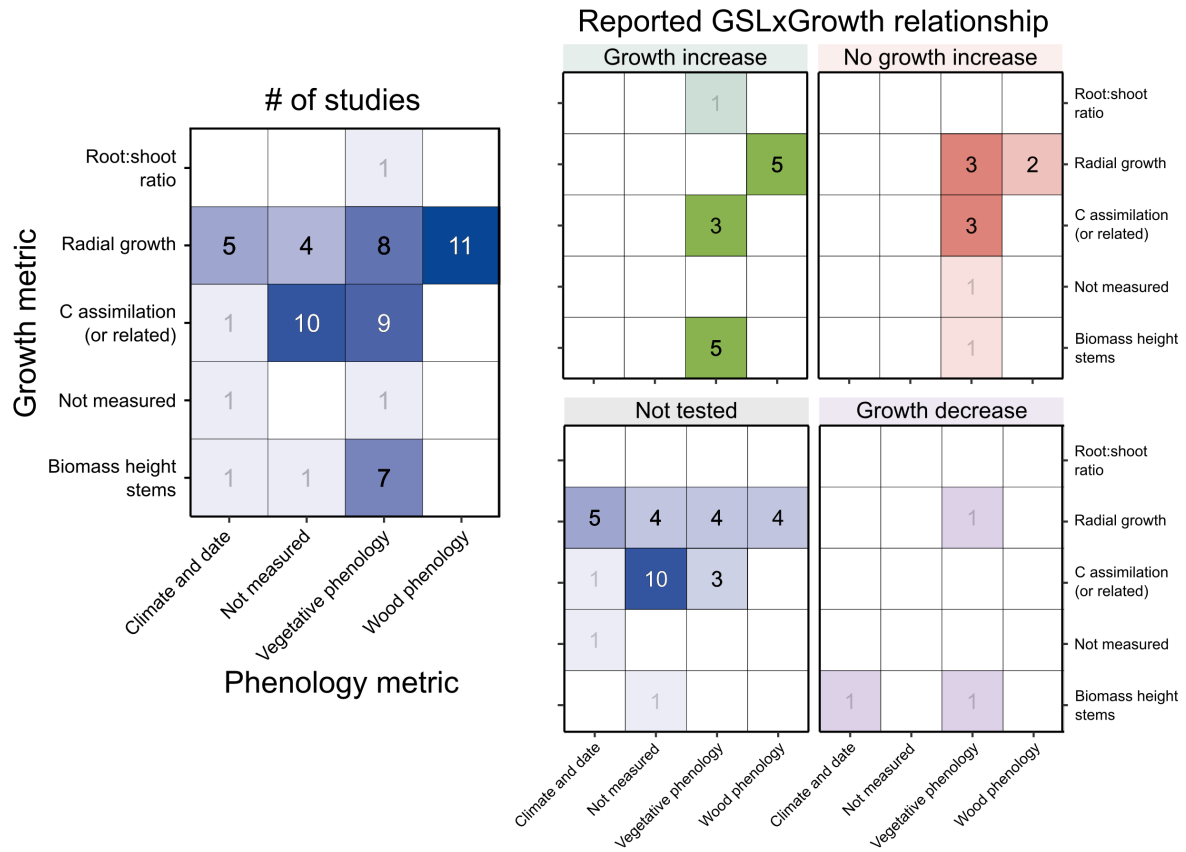


Figure 2: A review of growth \times growing season length relationship studies spanned a diversity of methods, but there was no coherency in which methods did or did not find a positive relationship. A number of studies tested relationships possibly related to growth \times growing season length (e.g. they tested how spring temperatures related to growth) but never directly growth \times growing season length, thus ‘not tested’ was surprisingly common across methods. See Supplement for review details.

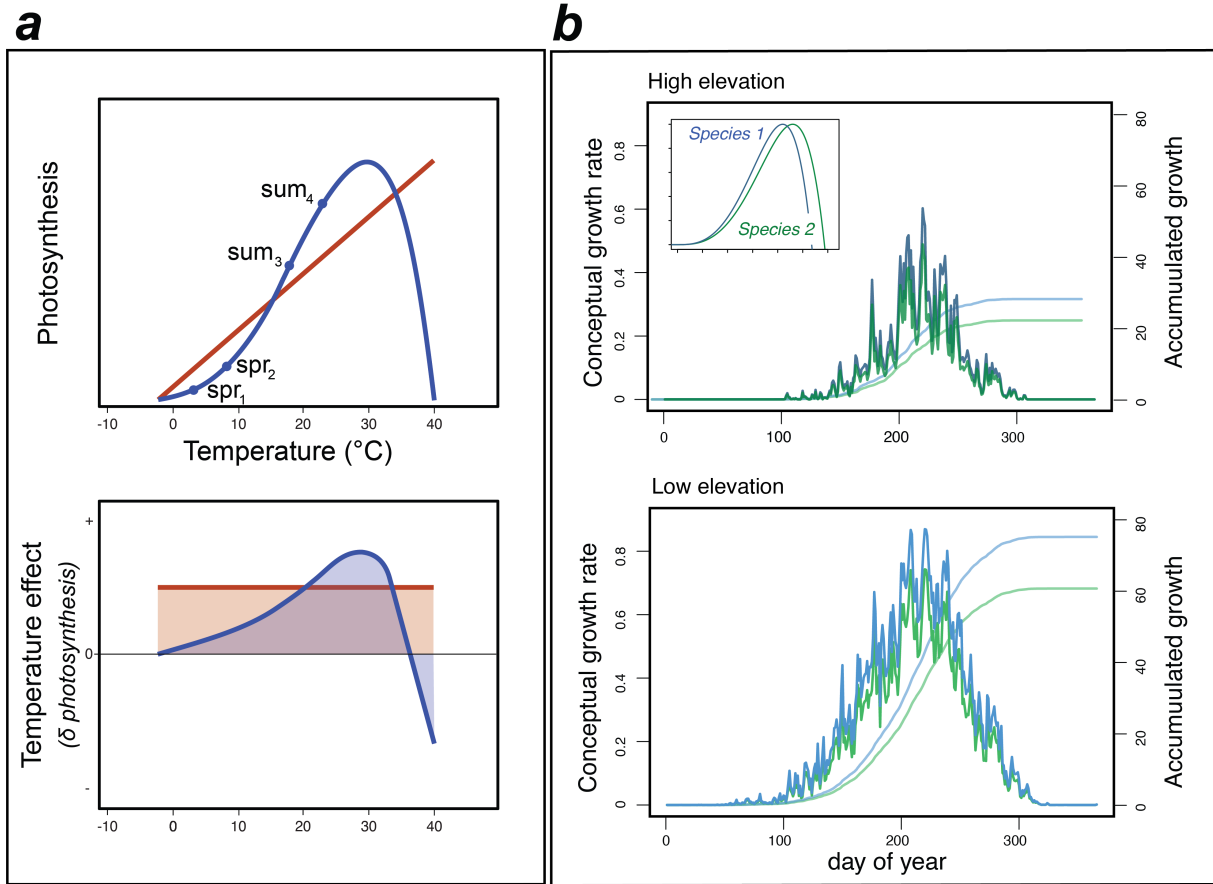


Figure 3: Understanding how longer seasons with climate change affect growth requires teasing out effects of longer seasons versus warmer seasons, which generally co-vary in observational data. Here we show two examples of this complexity. In (a) we show a general net photosynthesis response curve (top panel), which has a non-linear response to temperature (blue curve, adapted from meta-analysis of 109), though it is often modeled as linear (red). This non-linearity means that increases in lower temperatures—such as those in the spring when much of growing season extensions may happen—have lower absolute increases in photosynthesis compared to increases in later-season (e.g. summer) warmer temperatures, while a linear response assumes a constant scale of effect across low to high temperatures (bottom). In (b) we show conceptual growth responses to temperature for two different species with different growth rate responses to temperature (top, inset), which impacts their growth across the season, leading to small absolute differences in accumulated growth at a conceptual high elevation site (top) versus larger differences in accumulated growth low elevation site (bottom). Testing how growth varies across larger spatial gradients of growing season length, as we conceptualize here (b) could help establish a baseline expectation of the scale of temporal—especially inter-annual variation—and force a greater reckoning with drivers that shift alongside growing season length.

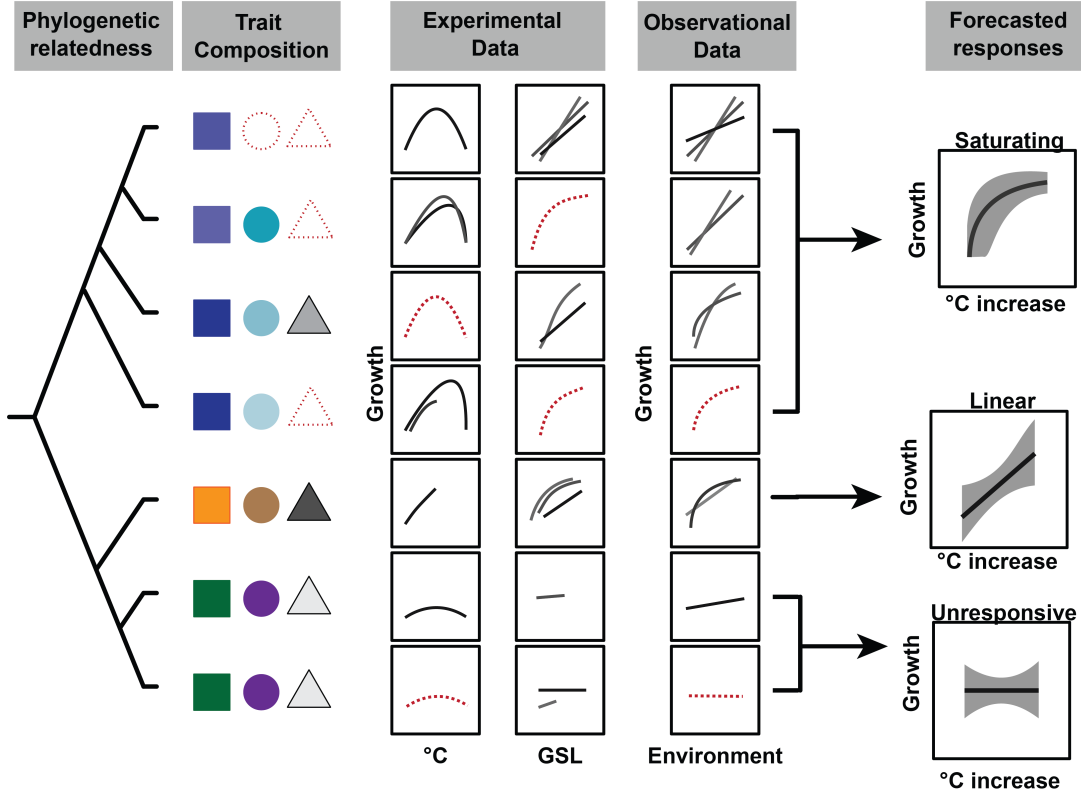


Figure 4: A trait-based phylogenetic model can naturally organize species (and, not shown, populations) responses to predict how they respond to longer seasons. This approach estimates a universal model that is then shaped by species evolutionary history (shown at left via a phylogenetic tree) and traits to produce the divergent responses observed across species today. We argue this framework can organize and guide experiments that separate out changes in temperature from changes in growing season length ($^{\circ}\text{C}$ and GSL in see middle panels) to better integrate observational data and identify different responses by species that can help forecast (see ‘Building a new framework for growth \times season length’ section for more details). It also can be useful for global forecasts. For example, species-level estimates combined with data on species abundance across forests (e.g. 110; 111) could predict larger-scale metrics, such as satellite observations of phenology and productivity. Here, we show how this approach can identify one clade (top) with a common response to longer seasons that also shares a suite of similar traits, and can identify a unique response by one species in a clade where that species also has a unique trait compared to other species with the same common ancestor (lower clade), while handling uneven sampling and missing data (the dashed red lines represent that the model will predict a response for each species).