Why longer seasons with climate change may not increase tree growth

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June 1, 2025

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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

~~A number of recent studies have challenged the assumption~~ Most climate change forecasts assume that longer growing seasons ~~lead to~~ increase carbon storage through increased tree growth, ~~raising concerns that forecasts of future climate change—which include increased carbon storage through this assumption—may be overly optimistic. In a review of recent literature, we found that 58% of studiessupported the assumption of increased growth with longer seasons, while 36% of studies did not. Diverging results remained when holding methodology constant, which suggests the current major challenge is to understand what underlies this widespread variation. Studies have proposed a suite of~~ 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 ~~, including~~ include drought-related ~~constraints and internal limits~~effects and internal constraints. These hypotheses~~and their underlying mechanisms~~, however, ~~were~~ are generally tested in different ways by different fields on different species, ~~making comparisons difficult~~and rarely consider how external drivers and internal constraints interact. We outline how bridging these ~~current divides while simultaneously~~ divides while integrating evolutionary history and ecological theory could ~~yield new advances and~~ help build a unified model across species for when longer seasons will—or will not—lead to greater tree growth, with major forecasting implications.

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), ~~with potentially large implications for future climate change. These recent studies challenge~~ 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 ~~limits~~ constraints on plant growth (16), which alone or interactively may limit plant responses (17).

Here we ~~review~~ 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. ~~Working across multiple definitions (see Box: Growth, growing season length and the challenge of standardized metrics),we find results that suggest~~ We find substantial variation in growth × 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 ~~often~~ test different mechanisms on different species. Current work often lacks a clear mechanistic physiological model (17; 18), and implicitly ignores the ~~importance~~ role of shared evolutionary history and community ecology to plant growth (e.g. 19; 20; 21), which could ~~aid~~ slow the search for a universal model~~when studying different species. We show how increased~~. 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 ~~positive~~ 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).

~~Despite~~ To better understand this recent debate ~~, we found that longer seasons lead to increased growth in a slight majority of papers~~ 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), ~~we found studies have variously found evidence for—or against—the relationship,~~ 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 ~~were consistently found~~ occurred across and within methods, suggesting the drivers of this variation are likely due to biological mechanisms, not solely ~~inconsistent~~ 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 ~~a suite of~~ relevant research from other disciplines.

Controllers on growth × season length relationships

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

External drivers

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

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

~~Positive~~ Other external drivers could counteract positive effects of longer—or warmer—seasons on growth predicted from temperature responses alone~~, however, could be counteracted by other external drivers~~. Moisture deficits from reduced precipitation or higher evaporative demand (commonly invoked in tree ring studies, Fig. 1) can slow or stall growth. Support for this hypothesis comes from negative correlations between growth and precipitation (or other metrics related to plant access to water in tree ring studies, 26; 41), and is well supported by physiological observations that ~~tree~~ water status can be a biophysical limit to growth (i.e., cells cannot expand without sufficient turgor, 42; 43), though ~~we found~~ few physiological studies on season length ~~that~~ 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). ~~Research~~ Within species (intraspecifically) research has repeatedly shown that populations vary in their growth and ~~its~~ responses to extended seasons~~(Fig. 1d)~~, reflecting differences ~~in genetic and developmental controls~~ 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 ~~across years within individuals , as well as~~ 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 masting 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 ~~affect growth~~ 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 ~~photosynthesate~~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 ~~across their range~~ 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). ~~While this diversity may appear to make identifying a common relationship between growth and growing season length more difficult, it may instead offer the path to an improved framework.~~

~~Building a new framework for growth × season length relationships~~

Building a new framework for growth × 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

~~Useful models of tree growthfor climate change forecasting must include a diversity of species, while overcoming the challenges of uneven sampling across species and their contrasting responses. Leveraging the~~ The diversity of responses ~~observed~~ across species is ~~possible by integrating ecological advances in how species~~ 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 this diversity could offer a path to connecting apparently divergent results.

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

~~In step with these advances, trait ecology has documented leaf and wood economic spectra that~~

~~suggest major traits to include in these models (with related databases of these traits often available, 76; 77). These 'economics' define a common trade-off along an acquisitive to conservative axis, where some species grow rapidly and more flexibly to take advantage of resources, but are less defended against herbivores and compete poorly at low resource levels, whereas other species compete well at low resource levels, but at the expense of growing slower (19; 76; 77). While these traits likely miss critical components for understanding how growing season length shapes growth, such as when different species invest in shoot and leaf versus wood growth, they provide a baseline from which to build, and a powerful approach to combine data usefully across species. This approach has already been used to identify that early-leafout species often show faster-growing more acquisitive strategies compared to later-leafout species (reviewed in 48)—differences that may also impact how they respond to longer seasons.~~

In addition to naturally organizing species differences, a trait-based phylogenetic comparative approach can help build a more testable and predictable framework. Because this approach can flexibly fit evolutionary history and traits together, it allows clades or species groupings that respond similarly to emerge from the data and models (78), versus being a priori grouped or defined. Similarly traits that co-vary with different responses can be more quickly identified (e.g. 79; 78, see Fig. 4). Both of these benefits could highlight which species or traits to focus additional studies on to gain the most insights, while similarly suggesting areas that should be less studied (e.g. traits that may be too confounded with evolutionary history, 80; 81) or outlier species that may not represent most species (75). This approach may thus redefine debates over which metrics of growth or growing season length are relevant into debates over which metrics are most relevant for which clades and/or traits ~~.~~ (see Box). It could also help guide research to address what we argue are three major open questions.

~~Importantly, trait-mediated phylogenetic models aid the search a universal model that can be useful for global forecasts of how growing season length influences growth . By effectively assuming one model, which is then shaped by evolutionary history and trait differences to produce the divergent responses observed across species today (Fig.4) , this approach yields an overall estimated growth response alongside a response for each species, which can then be variously combined to scale up. For example, species-level estimates combined with data on species abundance across forests (e.g. 82; 83) could predict larger-scale metrics, such as satellite observations of phenology and productivity. This framework also provides an organizing method to re-approach the fundamental question of how external and internal drivers shape growth responses to longer seasons, and a way to tackle what we are argue the three most critical questions in this area.~~

How prevalent are constraints across species and populations?

New evidence suggests inter-annual variation in growth may be limited because of internal constraints that prevent plants from fully using longer seasons (16). If true, this would have major ramifications for how much we expect growth to shift with warming. All plants are limited by internal constraints and how quickly they can build new tissues (84; 85), but selection towards different growth strategies (e.g. acquisitive versus conservative) should drive variation in these constraints across species. Selection should also drive local adaptation in these constraints at the population-level (68; 31), by favoring individuals that match to local environmental optima (86; 87). This appears to be the case for budset—which indicates the end of height growth, though we currently have data on only a few species (53; 88).

New studies could rapidly test for constraints across species and populations to work towards 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 withi . 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 ~~in season length x growth relationships~~ 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 × elevation relationships' in Supplement)~~, providing a~~ 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 ~~of how growth and~~ is a tractable way to help develop a framework for growth × growing season length ~~relate should be a primary goal, and one that seems broadly tractable.~~ relationships. Tree ring studies designed to leverage latitudinal and elevational gradients in climate could quickly provide the raw data (91). 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 ~~and tractable~~ 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. 92; 93) and also extending to the complexity of roots (68; 94). These data can provide a baseline to compare to the scale of shifts over time, which studies of growth × 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 ~~prevalent are~~ do external drivers and internal constraints ~~across species and populations~~interact?

~~New evidence suggests inter-annual variation in growth may be limited because of internal constraints that prevent plants from fully using longer seasons (16). If true, this would have major ramifications for how much we expect growth to shift with warming. All plants are limited by internal constraints and how quickly they can build new tissues (84; 85), but selection towards different growth strategies (e.g. acquisitive versus conservative) should drive variation in these constraints across species. Selection should also drive local adaptation in these constraints at the population-level (68; 31), by favoring individuals that match to local environmental optima (86; 87). This appears to be the case for budset—which indicates the end of height growth, though we currently have data on only a few species (53; 88). New studies could rapidly test for constraints across species and populations, to work towards 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).~~

~~How do external drivers and internal constraints act together?~~

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 ~~both~~ new experiments and observational studies, ideally designed to integrate into trait-mediated phylogenetic models. Studies across space could provide ~~some~~ inference by studying how growing seasons measured by vegetative versus wood phenology vary—and attributing variation through models that nest ~~species within populations~~ 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; 95; 28), making it impossible to tease out actual drivers behind observed trends. Experiments, in contrast, can provide more robust tests ~~. 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 so 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 shift with longer seasons—providing a potentially standardized way to compare constraints across species and populations—and then~~ 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.

~~In particular, mechanistic models will need to tease~~ 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. 96; 97; 98). 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 × 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.

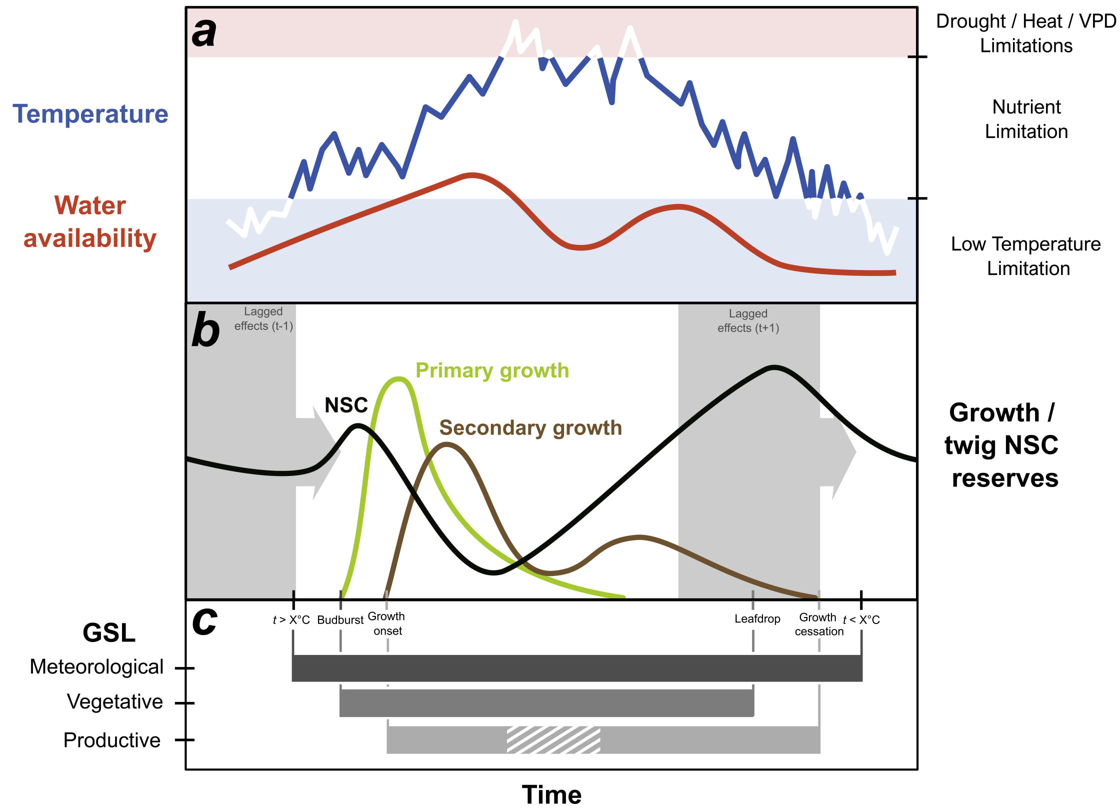
Expanding studies across more species will ~~be critical for useful~~ support development of accurate models that can forecast at relevant scales and to help design large-scale experiments. While experimenting on adult trees is difficult, previous challenges in climate change research have led to large-scale experiments to understand other complex drivers (e.g. SPRUCE, DroughtNet, Pfynwald, 99; 100; 101). 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 ~~advance new experiments~~ 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 ~~to~~ species beyond the experiment and maximize the information gained (102).

~~*Conclusions:* Anthropogenic climate change has often been described as an unfortunate and unplanned experiment. Like many experiments, it has highlighted important biology we do not know well. Understanding when, how and why longer seasons lead to increased tree growth requires an interdisciplinary reckoning with how temperature, time and a suite of external and internal drivers affect plant growth across species. A mechanistic understanding of how these~~

~~drivers integrate over species diverse growth strategies and the imprints of evolutionary history to affect growth today is possible, but will require new approaches.~~ Starting now to leverage data across species to inform and design new large-scale studies and experiments ~~be critical for~~ will help build accurate models of future forest and related carbon dynamics, with implications for projections of carbon sequestration and carbon markets.

Acknowledgements: B. Wuu for extracting growth × elevation data; R. Zäch for logistical support; N. Pederson for discussion, J. Davies and three reviewers for comments that improved the manuscript. Support provided by the Rubel Foundation (JHRL), NSERC Discovery (EMW) and the Swiss State Secretariat for education, Research and Innovation (SERI) by a SERI-funded ERC Starting Grant MB23.00011 (RM).

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



~~A major challenge in determining how growth responds to longer growing seasons is~~ The idea that plants would not clearly benefit from the temporal opportunity to photosynthesize more has highlighted the lack of a comprehensive model of tree growth. This has ignited a series of debates on the fundamental biology of how trees grow, including over the importance of source (photosynthesis-limited) versus sink limitations (plant growth-limited, but often via temperature, biophysical con and which metrics of growth and growing season length are relevant. Yet the complexity of each ~~, which~~ term means that neither can have one simple definition.

Here we show the simplified climate of one year (a), which ~~drives variation~~ determines rates and timing (b) ~~in~~ of primary growth (root and shoot elongation and leaf production from meristems) and secondary growth (radial wood and bark growth from cambia), both of which often depend on conditions determining non-structural ~~carbohydrates (NSC, which are sugars and starch needed for growth an~~ ~~and~~ carbohydrate (NSC, which are sugars and starch needed for growth and an important area of study, for mor production and reserves and storage from previous seasons. ~~Each~~ Assuming sufficient available nutrients (17), each of these types of growth could define the growing season length (GSL, c) but GSL can also be defined meteorologically (shown here as time, t, above some minimum X°C and below above some maximum X°C, with sufficient soil moisture) or by large-scale measures of plant productivity (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~~(e.g. vessel diameter)~~.

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). ~~A smaller number used metrics that reflect combined primary and secondary growth, including biomass, height, or number of stems (n =9), and root:shoot ratio (n =1), while others used various modeled estimates potentially related to growth.~~ 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. 105; 8; 16). ~~Further, these definitions of GSL are simplified and could not be easily aligned, as we found 14 different metrics of start of season and 16 metrics of end of season, resulting in 25 metrics of growing season length. See also~~

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 (106; 91). 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 (107). For example, some meteorological definitions could relate directly to temperatures that limit cell growth, as multiple studies suggest growth stops at below 5°C (108; 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 (109; 110; 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 (111; 112; 71).

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2 Figures

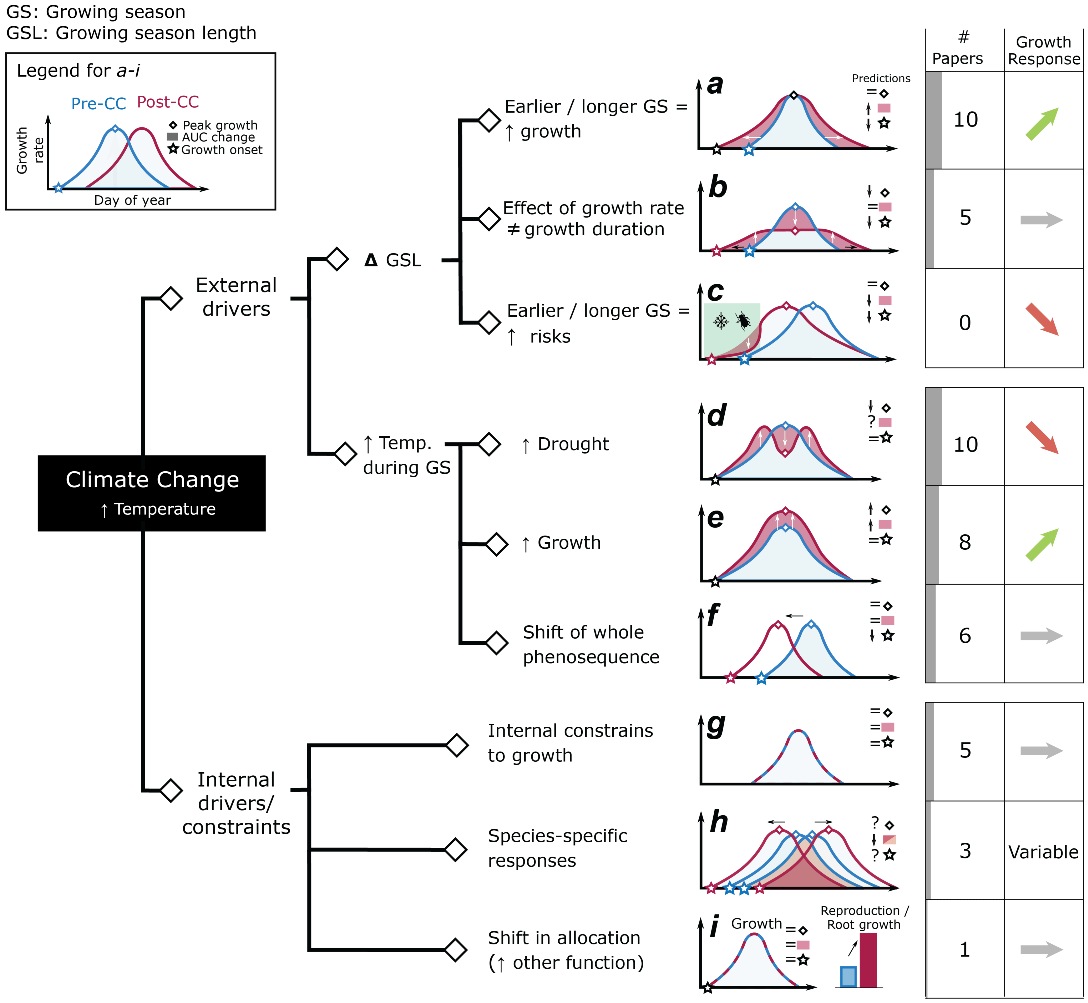

Figure 1: Climate change may alter growing season length (GSL), which can then affect growth through diverse pathways. We review hypotheses for these pathways showing the number of papers (from a review of papers studying growth × growing season length) that mentioned each hypothesis (width of the shaded areas of left column is proportional to the number of papers with the number also given, right column shows the expected growth response for each hypothesis). We group hypotheses as focused on mechanisms moderated by the environment ('external') versus those focused on internal physiological constraints, which span both source (photosynthesis-limited) and sink limitation, and could act together. For more details, see Supplement.

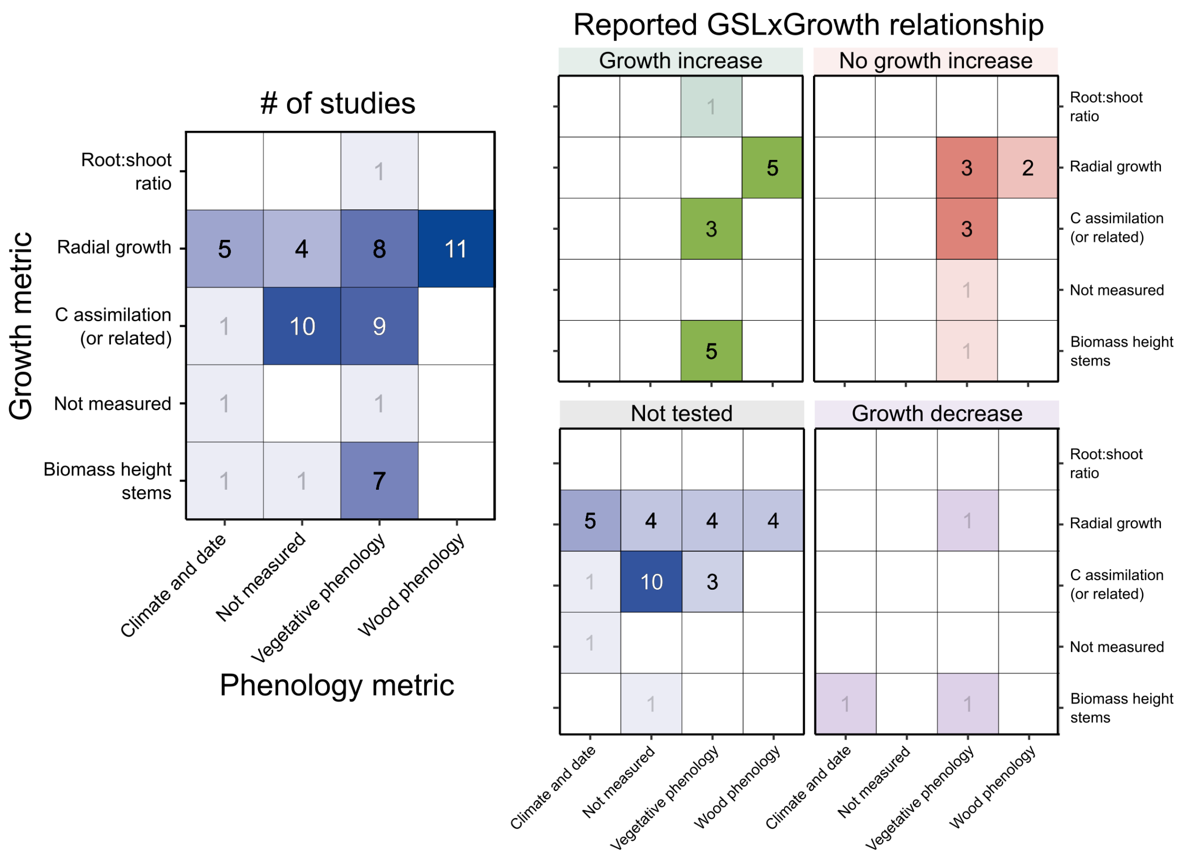

Figure 2: A review of growth × growing season length relationship studies spanned a diversity of methods, but there was no coherency in which methods did or did not find a positive relationship. A number of studies tested relationships possibly related to growth × growing season length (e.g. they tested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

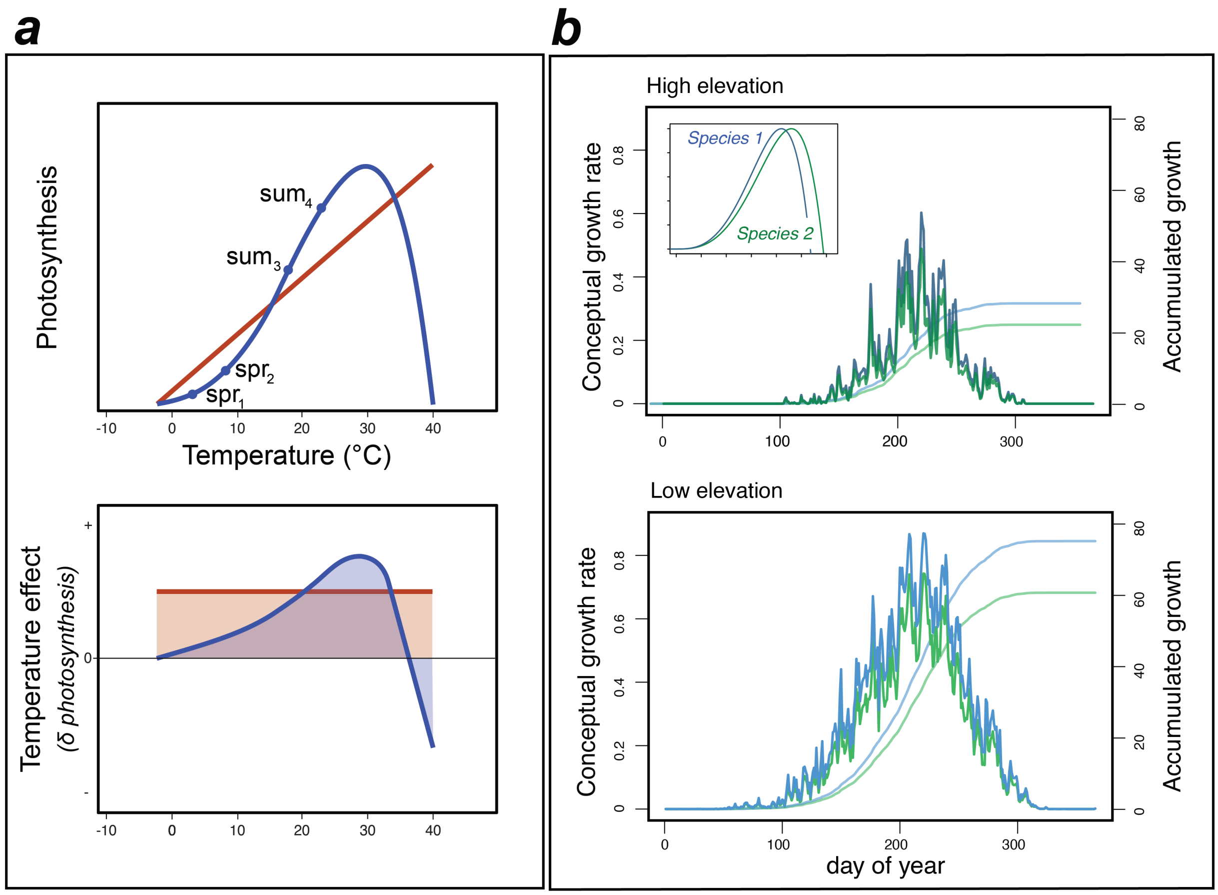

Figure 3: Understanding how longer seasons with climate change affect growth requires teasing out effects of longer seasons versus warmer seasons, which generally co-vary in observational data. Here we show two examples of this complexity. In (a) we show a general net photosynthesis response curve (top panel), which has a non-linear response to temperature (blue curve, adapted from meta-analysis of 113), 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.

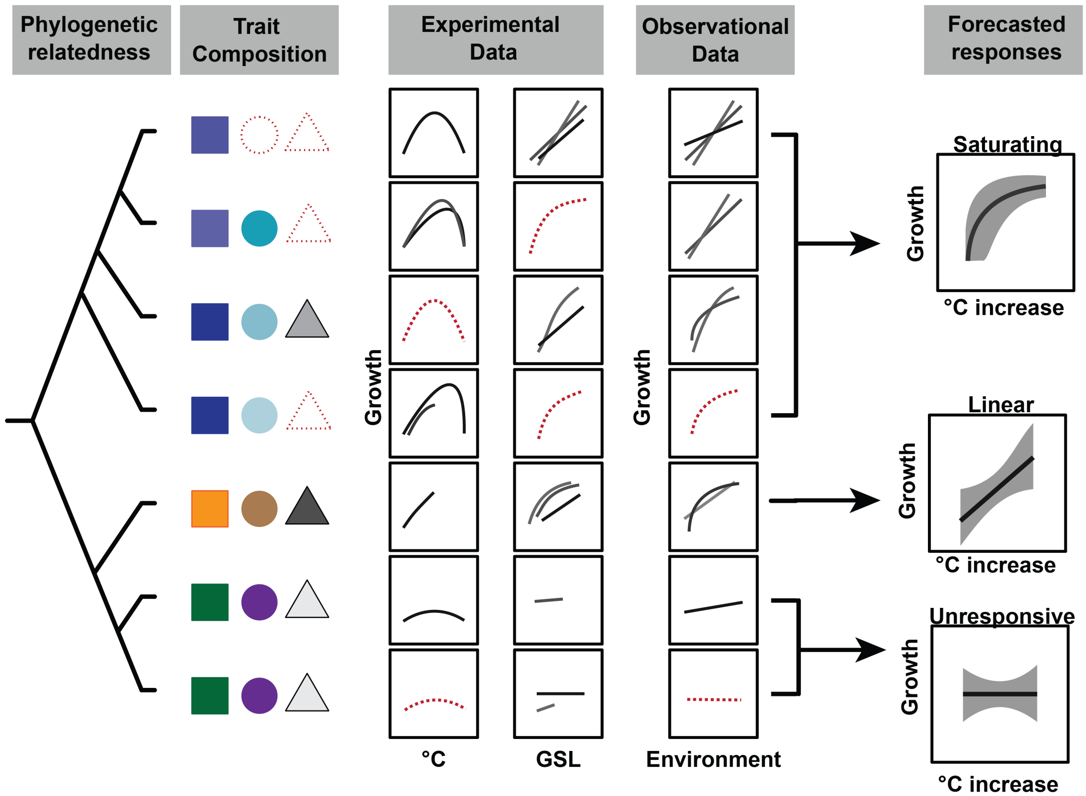

Figure 4: A trait-based phylogenetic model ~~provides a way to~~ can naturally organize species (and, not shown, populations~~, which nest within species~~) responses to predict how they respond to longer seasons. This approach estimates a universal model that is then shaped by species evolutionary history (shown at left via a phylogenetic tree) and traits to ~~estimate how each~~ produce the divergent responses observed across species ~~should uniquely respond~~today. We argue this framework can organize and guide experiments that separate out changes in temperature from changes in growing season length (°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 × season length~~relationships~~’ section for more details). ~~In this~~ It also can be useful for global forecasts. For example, species-level estimates combined with data on species abundance across forests (e.g. 82; 83) 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)~~.~~ ~~Estimating responses across species through a phylogenetic model has the additional benefit of robustly estimating responses given~~ , while handling uneven sampling and missing data (the dashed red lines represent that the model will predict a response for each species~~, informed to various degrees—with the degree determined by the model—by the traits and phylogeny~~).