

# Why longer seasons with climate change may not increase tree growth

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## Abstract

Recently a growing number of studies have challenged a fundamental assumption of most forecasts of future climate: that longer growing seasons lead to increased tree growth. This has generated alarm—as increased growth is expected to offset carbon emissions—and a number of hypotheses for why longer growing seasons may not always increase tree growth, including drought-related constraints, internal limits, and methodological differences. Here, using a review of recent literature across spatial scales and methods, we find the perception that longer seasons do not lead to increased growth was supported by only 36% of studies, while most—58% of studies—supported the assumption that longer growing seasons lead to increased growth, with persistent variation across methods, species and years of study. The resulting challenge is thus to understand and predict this widespread variation. We found proposed hypotheses were rarely well-tested, especially across methods. Studies of tree ring growth tended to focus on external drivers, such as drought, while physiological studies of biomass or carbon allocation, tended to focus on internal limits, such as effects of photoperiod. We argue that bridging this disciplinary divide and integrating theory from evolutionary biology, community ecology and life history could rapidly help develop and test a mechanistic framework for when longer seasons will—or will not—lead to greater growth.

## 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 (Nobel *et al.*, 1983; Frank *et al.*, 2022). It is also a foundational assumption of most models of the future global carbon cycle (e.g. Friedlingstein *et al.*, 2022; Ito *et al.*, 2020). Most models project that continued anthropogenic warming will be partly offset by increased carbon sequestration, primarily of temperate and boreal forests, as warming lengthens growing seasons, an assumption supported by a suite of ecosystem-scale studies (Chen *et al.*, 1999; Keenan *et al.*, 2014; Finzi *et al.*, 2020).

Yet recent work has questioned this longstanding assumption and suggested that longer growing seasons do not necessarily lead to greater growth (e.g. Dow *et al.*, 2022; Green & Keenan, 2022; Silvestro *et al.*, 2023), with potentially large implications for future climate change. Such findings challenge decades of research that find growth increases with longer seasons, from studies along natural elevational and latitudinal gradients (Myneni *et al.*, 1997; Berdanier & Klein, 2011; King

*et al.*, 2013; Cuapio-Hernández *et al.*, 2022) to classic studies in lab settings (Went, 1957) to studies of ecosystem fluxes with warming (Chen *et al.*, 1999; Keenan *et al.*, 2014; Finzi *et al.*, 2020). Proposed mechanisms for the apparent disconnect are diverse (Fig. 1), including non-linear effects of climate change itself (e.g., drought or heat stresses Dow *et al.*, 2022), internal limits on plant growth (Zohner *et al.*, 2023), as well as inconsistent use of growth metrics (Green & Keenan, 2022).

Here we review the connections between growing season length and plant growth across fields to identify the potential mechanisms that unite—and could disconnect—these processes. Leveraging a systematic literature review, we examine which methods, species and approaches suggest that extended seasons appear to lead to increased growth, and the current proposed hypotheses. We find a pervasive disciplinary split between studies, which may limit progress in identifying the underlying processes and mechanisms. Further, relevant insights from physiology, community ecology, evolutionary and life history theory appear unexamined in recent work. Yet, with increased interdisciplinary collaboration, the field appears primed to develop a holistic theory of when, where and how climate change may increase tree growth—with implications both for forecasts of future climate change and for fundamental science.

## Evidence that longer seasons increase plant growth, or not

The idea that time limits growth is a fundamental principle of most biological fields. Many biological processes, including photosynthesis and many aspects of growth, are rate-limited making time a crucial commodity (Nobel *et al.*, 1983; Cosgrove, 2005; Hilty *et al.*, 2021). Thus, the hypothesis that longer growing seasons should increase growth is intuitive—and pervasive.

Indeed, the hypothesis that longer seasons yield more time for growth was by far the most common hypothesis for why longer seasons should increase growth across our review of growth  $\times$  growing season length studies, with 19 of 59 total studies including it (Fig. 1). Foundational evidence for this relationship comes primarily from spatial clines across elevation and latitude, with growth decreasing alongside growing season length at higher elevations and latitudes (Fig. 2). Mechanistically, this hypothesis is supported by small-scale warming experiments that find that species which advance phenologically with warming also grow more (Cleland *et al.*, 2012), while observationally, ecosystem-scale studies have reported a similar positive relationship between growing season length and carbon fluxes across decades with global warming (Keenan *et al.*, 2014) or in years with warm, early springs (Chen *et al.*, 1999). These findings, however, have not been well supported by recent work that has focused often on inter-annual correlations with metrics of individual tree growth (Dow *et al.*, 2022; Silvestro *et al.*, 2023). This has led to debate about whether future carbon forecasts are overestimated and which metrics of growth (Green & Keenan, 2022), or growing season length (Körner *et al.*, 2023) are relevant.

Despite the recent eruption of this debate, we found little support for reports of a wholesale disconnect between growth and growing season length. Instead, research has generally found split support—across methods—for when longer seasons lead to increased growth. Papers spanning 25 years have variously found evidence for—or against—the relationship, with no clear trend by method (Fig. 3). For example, studies that measured C assimilation were evenly split in finding

evidence for or against the relationship—or simply not testing it (Fig. 3). Diverging results were consistently found within all well-studied methods, suggesting the drivers of this variation are likely due to biological mechanisms, not solely inconsistent definitions or methods (as recently suggested, Körner *et al.*, 2023).

Studies from the disciplines of dendrochronology (the study of tree rings and their dating) and physiology have readily offered mechanisms for the recent results that increased growth may not come with longer seasons. Hypotheses focus on both source (photosynthesis-limited, including  $CO_2$  limitation) and sink limitations (Fig. 4). External climatic drivers that offset the positive growth effects of longer seasons are often reported in tree ring studies (Kolář *et al.*, 2016; de Sauvage *et al.*, 2022; Camarero *et al.*, 2022). In particular, the hypothesis that higher temperatures paired with lower precipitation produces negative correlations with growth appeared in 33% of tree ring studies we reviewed (and was only mentioned once outside of studies measuring radial growth, see also Fig. 1). In contrast, other studies suggested fundamental internal constraints that prevent trees from responding to longer seasons (Cuny *et al.*, 2012; Michelot *et al.*, 2012; Zohner *et al.*, 2023).

Yet we found that these hypotheses have been tested in radically different ways, never together, and ignore a suite of relevant research from other disciplines on this topic. Most tree-ring studies have focused on external climatic drivers limiting growth in annual tree ring studies, while lab experimental and wood phenology (xylogenesis) studies focus on physiological constraints (Fig. ??). Further, the inconsistency of results, with no clear pattern by method or even within species (Figs. 3, ??), suggests that understanding the relationship mechanistically will be critical to accurate predictions. As we outline below, a single mechanism is unlikely to explain all results, requiring a more unified framework, and tests of it, for progress.

## Controllers on growth $\times$ growing season length relationships

A suite of major mechanisms that could limit or disrupt the positive effects of longer growing seasons on growth can be usefully grouped into categories that should operate at different levels. Currently disconnected research has focused on: (1) external factors, such as drought, which should impact community-level trends, and (2) internal physiological limits, such as photoperiod constraints, which should arguably be universal across plants (e.g., Zohner *et al.*, 2023), or population-specific (e.g., Soolanayakanahally *et al.*, 2013). The effects of mechanisms in these two groups, however, are highly likely to vary by species, highlighting the importance of integrating perspectives from phylogenetic and trait ecology, as we review below.

### External

**Temperature & moisture** Fundamentally, temperature limits many biological processes. Temperatures that are too cool (often considered to be below  $5^\circ\text{C}$  for temperate trees) and too warm (an area of active research, Martinez-Meier *et al.*, 2008; Cabon *et al.*, 2022, see also Fig. 4) slow down biological processes and eventually can lead to tissue death (Larcher, 1980; Kramer, 2012). Between the upper and lower limits biological processes underpinning growth generally

accelerate such that warming can have a direct effect, effectively by accelerating biological time, up until the maximum rate for that particular process.

Anthropogenic warming will thus shift a number of biological processes at the same time that it accelerates spring phenology, but how big the shift is due to temperature will depend on the particular response curve and exactly where along that curve warming will push the process. At very cool temperatures, a small increase in warming may have limited effect, while a jump from 10 to 12°C is physiologically more significant, and warming that pushes plants beyond their optima, where many biological rates crash, could have large negative impacts (Nobel *et al.*, 1983; Leuning, 2002). In between, warming would linearly increase rates. Plant growth is likely then to shift with extended growing seasons at the same time it shifts due to changing rates, with some papers suggesting longer seasons effectively only extend the very cool periods and thus have no discernible effect on growth, while others suggest observed increases in growth are due only to increased growth rates (not longer seasons). A number of tree ring studies suggest that any increases in growth due to longer seasons are offset by reduced growth from high summer temperatures (Gantois, 2022; Dow *et al.*, 2022), though which temperatures are too high is not generally known, and it seems unlikely current temperatures have pushed trees above their optima (Schaber & Badeck, 2002), unless other factors, such as drought, reduce those optima (Fig. 1f).

Positive effects of longer seasons on growth could be counteracted by moisture deficits due to reduced precipitation or higher evaporative demand. A suite of tree ring studies confirm this, finding correlations with precipitation or other metrics related to plant access to water (George, 2014; Babst *et al.*, 2019). This is supported by fundamental physiology: because cells cannot expand without sufficient turgor (Cosgrove, 1987, 2023) tree water status an inescapable biophysical limit to growth (Peters *et al.*, 2021), driving diel correlations between vapor pressure deficit and growth (Babst *et al.*, 2019; Zweifel *et al.*, 2021).

**Species interactions** External factors related to species interactions—including herbivory, disease and competition—can also limit growth, and may themselves be responsive to an extended growing season. For example, herbivory can have large impacts on forests, leading to declines in satellite measures of greenness often associated with signals of plant senescence. Plant pathogens are also known to respond to warming, and limit productivity (Sturrock *et al.*, 2011; La Porta *et al.*, 2008). These biotic drivers of growth were rarely mentioned in studies examining growing season length (we found no mention of them, Fig. 1e), but could increasingly limit growth as extended growing seasons allow for additional generation cycles in many pest species (Mitton & Ferrenberg, 2012; Lange *et al.*, 2006).

## Internal

**Universal limits & triggers** When and how growth is initiated and ceases is clearly under genetic and/or developmental control, and thus, plants internal programming could limit growth responses to longer growing seasons (Marchand *et al.*, 2021; McKown *et al.*, 2016; Soolanayakanahally *et al.*, 2013). Some recent studies suggest a novel role for the summer solstice (Zohner *et al.*, 2023) in setting a universal developmental switch between when warming temperatures

hasten or delay leaf senescence (thus influencing growth season length and growth). However, these studies contrast with decades of work showing species-level differences in how and when species grow.

**Population- & individual-level limits** Below the species-level, populations and individuals also vary in their growth and its responses to growing season length (Fig. 1d), similarly reflecting differences in genetic and developmental controls. For example, 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 (Soolanayakanahally *et al.*, 2013; Aitken & Bemmels, 2016). This means longer seasons are generally driven by spring phenology, which appears far more flexible, and has advanced more rapidly than fall events (Aitken & Bemmels, 2016). Within populations, individual trees may also vary in how early or late they are for both spring and fall events. This can be driven by maturity and a shifting investment to growth, survival and/or reproduction. Saplings, for which growth and survival are paramount, tend to both grow more rapidly (Hilty *et al.*, 2021) and have longer seasons relative to adult trees (Augspurger & Bartlett, 2003; Rozendaal *et al.*, 2010; Vitasse *et al.*, 2014), which need to also invest in reproduction.

Trade-offs between vegetative and reproductive investments are a paradigm of life history theory and may also produce important growth response differences across years within individuals (as well as between species). Years of high reproductive output can reduce growth (Thomas, 2011; Hacket-Pain *et al.*, 2016a). For species that mast—producing abundant cones or fruits in only some years—high reproduction years could especially impact measures of wood growth. Many hypotheses suggest higher summer temperatures trigger masting in the following year (Hacket-Pain *et al.*, 2016a,b); if true, then reduced growth in years following warm summers may not indicate temperatures too high for growth, as often suggested (e.g., Gantois, 2022; Dow *et al.*, 2022), but instead shifting investment to reproduction.

## 0.1 Species-level variation

These underlying genetic and developmental drivers of growth generally vary by species, as evolution drives selection for different optima and different strategies (Fig. 1c). For example, leaf strategies vary strongly between evergreen and deciduous species, but also within each group—where variation in ‘determinacy’ defines the timing and investment of shoot growth and leaf emergence. Determinate species have most of their leaf material prebuilt in overwintering buds, generally unfolding their entire canopy within few weeks each season, while indeterminate species continue to produce new shoots including leaves over the growing season (??). Such differences can clearly influence the extent to which the growth of different species responds to increases in growing season length, even under identical conditions.

Whether longer growing seasons result in more growth may also related to differences amongst species in their life history strategies. Leaf, wood, fruit and other plant traits show trade-offs along a 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 and conservatively (Grime, 1977; Diaz *et al.*, 2016). These ideas would predict indeterminate acquisitive species, such as poplar, to grow more with longer seasons, while conservative species, such as beech, may not.

Species differences in growing season  $\times$  growth relationships, regardless of their direction, do not always reflect optimal strategies today. Imprints of past selection often drive species-level differences, producing phylogenetic patterns that both limit how well species are adapted to current conditions and especially constrain their responses to rapidly changing conditions (Ackerly, 2009). The legacy of historical evolutionary pressures—including different external drivers—is not easily erased. Thus, many species show evidence of previous selection, seen when evolutionary relationships (usually represented through phylogeny) predict plant responses and lead to clade-level similarities. Most studies testing for such historical effects on plant responses find them (e.g., Davies *et al.*, 2013), and even more physiological syntheses find results suggestive of strong phylogenetic relationships (though they are more rarely formally tested, e.g., Way & Oren, 2010).

## **An interdisciplinary framework for growth $\times$ growing season length relationships**

Predicting when and where longer seasons lead to increased growth may seem overwhelming given the diversity of potential drivers, but together they offer a set of testable hypotheses that could rapidly advance progress—if tackled with a more organized interdisciplinary approach. This approach requires building fundamental biological knowledge in a suite of areas across physiology, dendrochronology, life history, ecology and evolutionary biology. These suggestions thus apply to understanding this relationship at the individual (organismal) level, though they make predictions at larger (e.g., ecosystem) scales, and are highly applicable to ecosystems dominated by one species (e.g., Chen *et al.*, 1999).

### **Standardized measurements**

Tackling the diverse drivers and their underlying hypotheses (Fig. 1) for growth  $\times$  growing season length relationships requires a common language and set of metrics for growing season length (Körner *et al.*, 2023), growth (see Box), and the potential drivers. We found 14 different metrics of start, 16 metrics of end of season (25 metrics of growing season length), and 21 different metrics of growth across 59 studies—highlighting just part of the problem. Definitions and metrics for external and internal drivers were myriad, with many papers reporting dozens of tests of different aspects of climate over different temporal windows. This is understandable, given the complexity of environmental variables and our limited understanding of how they trigger phenology and growth, but also slows progress. A common framework where researchers measure and report common explanatory and response variables (see Supplement) would accelerate research by easing communication between fields and providing a path to comparable quantitative estimates. This should also include expected statistical tests, as we found a number of papers failed to directly test for growth  $\times$  growing season length relationships (Fig. 3).

**Quantify species/population/individual variation** A robust interdisciplinary approach to understanding growth  $\times$  growing season length will need to integrate disciplines that focus on variation at the species-level and below. To date, a handful of studies have mentioned species differences (Fig. 1) but almost none made or tested predictions on how species differ based on existing theory.

Life history theory, community ecology and evolutionary history predict—and find—relevant patterns of species-level variation. Species with acquisitive versus conservative traits, and which differ in their reproductive strategies (i.e., masting or not, fruit size and number) provide an axis of important variation that could be used to identify focal species for further study and to test predictions. Acquisitive species with consistent investment in fruit would show stronger shifts in growth with changing growing season length—assuming no other factors become limiting. Given the potential role of evolutionary history, selecting for these varying strategies within a clade, or—if not feasible—correcting for phylogenetic distance would more robustly test how strategies influence the growth  $\times$  growing season length relationship.

Explicitly including differences between species may explain some of the variation in current studies, and would allow tests of the scale of species versus population, individual, and within-individual variation. Community ecology and life history theory clearly predict that species are unlikely to share a common growth  $\times$  growing season length relationship, but less research addresses how the relationship should shift across populations within species. *In situ* elevation work suggests no genetic differences (King *et al.*, 2013), while common garden studies across latitudes suggest phenological variation across populations can limit growth responses to extended growing seasons (Soolanayakanahally *et al.*, 2013). Current growth responses to anthropogenic climate change mostly operated one level further below these—at the intra-annual (within-individual) level.

Understanding the scale of variation across all these levels could both help to refine theory and provide a benchmark when comparing the effect sizes of other drivers of variation. While multiple papers report a lack of relationship between growth and growing season length, we have no fundamental understanding of what the effect size of this relationship should be, and thus no way to know if we have good power in current studies to detect it. Estimates of how growth shifts with elevation likely include responses from both plasticity (within-individual variation) and local adaptation (population-level variation) and thus could be an upper bound on our expectations, yet elevational trends to date appear relatively weak and noisy (Fig. 2)—suggesting this is only part of our missing mechanistic understanding.

**Extending disciplinary focus** Each field studying growth  $\times$  growing season length (dendrochronology, phenology research and physiology) has its own historical aims, and thus its own biases towards certain species, methods and metrics. Dendrochronology’s original focus on using tree growth to estimate climate has led to certain assumptions and methods that likely obscure the complexity of how growth shifts with growing season length. Fundamentally, the field relies on an assumed relationship that, within individual and populations of trees, growth (measured by annual ring width) is greater when growing conditions are better (Cook & Kairiukstis, 2013, e.g.). Dendrochronologists traditional aim to magnify the climate signal has led to standard

approaches, including sampling biases (e.g., to ‘climate-sensitive’ individual trees, Klesse *et al.*, 2018; Nehrbass-Ahles *et al.*, 2014) and statistical detrending (Rollinson *et al.*, 2021), that may obscure patterns where the signal longer growing seasons and biotic drivers may be most apparent (such as rapid growth phases, Manzanedo & Pederson, 2019). Further, these approaches mean dendrochronology studies are also fundamentally washing out much of what physiological studies focus on, limiting opportunities for interdisciplinary overlap.

Opportunities for overlap between dendrochronology and phenology research are potentially high, but sampling biases in both fields limit current opportunities. Dendrochronology generally focuses on conifers (gymnosperms Zhao *et al.*, 2019), creating a major split from most studies of leaf phenology, which focus almost entirely on deciduous angiosperm species (see Fig. 1). Phenology research has also been strongly focused on spring events (e.g., budburst, leafout), with limited data on fall events and thus limited data to calculate growing season length. This focus on spring events may have been justified decades ago, when most shifts from anthropogenic warming occurred in the spring, but less justified as increasing research suggests important complexity in fall shifts (Gill *et al.*, 2015; Zohner *et al.*, 2023) and a need to scale up phenological research to understand tree growth.

All fields have lacked a focus on the ecology of growth  $\times$  growing season length, generally ignoring impacts of certain external drivers, the complexity of life-history, and species differences. Dendrochronology often uses frost events or insect outbreaks as markers of particular years, but rarely integrates them into patterns of growth. A shift to reporting and estimating effects of frost events, biotic disturbances, and reproduction status of trees (including mast years) could provide new estimates of the effects of these drivers. Physiological studies tend to avoid such complexities through controlled environments and a focus on juvenile plant stages (Poorter *et al.*, 2016), but scaling up between life stages will be critical for useful models of growth, and to bridge to dendrochronology.

**Extending temporal focus: Zooming in and out** Bridging across disciplines will require bridging across timescales, a consistent and thorny issue for research on trees. 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 or longer of adult tree growth. Perhaps because of this dichotomy, tree ring studies often study lag effects, while they are rarely mentioned in physiological studies. Given the complexity of carbon storage in trees (Finzi *et al.*, 2020; Thompson *et al.*, 2023; Anderson-Teixeira & Kannenberg, 2022), and how investment can shift across years (Aubinet *et al.*, 2018; Doughty *et al.*, 2014), studies should more consistently acknowledge and test for lag effects.

All fields could benefit from tackling the challenge of understanding the physiological connections between growing season length and growth, and even the genetic and developmental underpinnings of these connections. To date, much work has focused on measures of growth and phenology without a clear mechanistic understanding of what triggers growth and its cessation, and how these triggers and responses have evolved. Progress in this area is could be particularly important for making projections, as extrapolating can be dangerous when the underlying mechanistic model is wrong. Physiological studies that follow carbohydrate balance and cell di-



vision (see Locosselli & Buckeridge, 2017) versus growth dynamics could yield insights, as could additional work on xylogenesis—especially if done with a focus both to extrapolate to long-term tree ring studies and/or in physiological experiments (Fang *et al.*, 2020; Simard *et al.*, 2013). Expanding beyond the current disciplines focused on this topic could also be informative. For example, a clearer physiological understanding of which environmental stimuli trigger leaf expansion, senescence, woody growth, and heartwood formation alongside an evolutionary perspective could contribute towards a clearer understanding of growth constraints (Baas & Wheeler, 2011; Eckert *et al.*, 2019; Ensminger *et al.*, 2015; Juvany *et al.*, 2013).

## Current & urgent opportunities

Expanding the focus of disciplines to help build an interdisciplinary framework for growth  $\times$  growing season length relationships will take time, but major hypotheses may be tractably tested now. Taking advantage of existing data sets and ongoing experiments could provide tests of variation across individual to species scales and lag effects, while new experiments are likely required—but urgently needed—to compare effects of external versus internal drivers on growth.

**Existing data and networks** Both dendrochronology and phenology research have large freely-available repositories of data, with the International Tree Ring Database (ITRDB) and the Pan European Phenology project (PEP725) being two of the largest. While each dataset reflects the biases previously mentioned, they also provide a major spatially and temporally diverse dataset to compare how external climatic drivers, species and population explain growth  $\times$  growing season length relationships. Depending on the data overlap, these datasets may also allow us to identify where longer growing seasons will increase growth and for which types of species. Based on existing theory, we expect longer growing seasons will increase growth for species with regular reproduction (no masting, see also new masting database in Hacket-Pain *et al.*, 2022), an acquisitive strategy, from clades that are historically (on an evolutionary timescale) plastic, in locations that are warm—but not too warm—and moist.

Existing common garden studies provide an opportunity for more robust tests of population and individual variation could come. Given that many common garden studies have some data on phenology and are designed to tease out population versus inter-annual variation, collecting tree ring data from them seems a rapid way to estimate variation across these two levels. Repeating such measurements for multiple common gardens would also allow for an exploration of species level variation. Common gardens not collecting regular phenology, or annual growth data, could start. Given how old some common gardens are, research may also be able to examine impacts of biotic and abiotic disturbances or effects of climatic variation.

Finally, taking advantage of existing ecological and field global change experiments could help test lag effects, and bridge from physiological to dendrochronology scales. Large scale experiments on heat (e.g., SPRUCE, Hanson *et al.*, 2017), moisture via drought or irrigation (e.g., DroughtNet, Phynwald Smith *et al.*, 2016) and other factors (e.g.,  $CO_2$  in FACE) have increasingly been used to test ecological ‘memory’ (e.g., Flinker *et al.*, 2021; Schweiger *et al.*, 2022) and could help scale up from smaller and shorter-time scale physiological studies, potentially

to ecosystem-level dynamics such as carbon cycling (Ding *et al.*, 2021; Jensen *et al.*, 2019). Building on available data and infrastructure could also bridge this gap, for example, adding dendrometers to locations with phenological sampling and vice versa. Such efforts may be especially valuable in sites across elevational and latitudinal gradients (e.g., PSP, Feeley elevation network, Coweeta). These sites in turn could be priority locations for xylogenesis and focused physiological studies.

**Next experiments** Disentangling the effects of major drivers on growth  $\times$  growing season length relationships will also require new experiments, across multiple levels. Teasing out the effects of warmer temperatures versus longer seasons can only be robustly done with experiments, and seems a paramount need, especially if done across multiple species spanning diverse strategies. Similarly, experiments to compare impacts of extended seasons (via early growth or delayed senescence), and differentiating between external abiotic (e.g., heat waves, droughts) and biotic (e.g., pests, competition) drivers could provide comparable estimates and test lag effects, when sampled multiple years after the manipulations. While these are most easily done for juvenile trees, they could also be done on adult trees, given investment in infrastructure.

Efforts to design and launch such large-scale experiments should start now. A long-term experiment on adult trees that manipulates temperature, precipitation and growing season length, would test a suite of drivers at the relevant lifestage. It could robustly compare drivers and become a resource for studies of underlying mechanisms for constraints, if properly measured and designed. This would mean careful measurements of carbon allocation, including to reproductive output, and tissue lost to frost and biotic drivers, and choosing species to maximize divergent strategies and provide the potential for genomic and related studies (e.g., *Populus*, *Quercus*). At a larger spatial scale, distributed experiments to measure growth and phenology (ideally wood and vegetative) of multiple provenances of multiple species across sites could estimate variation—and potential constraints—that operate at different organizing levels.

*Conclusions:* Anthropogenic climate change has often been described as an unfortunate experiment. It has highlighted important biology we don't know well, requiring us to rediscover dusty old fundamentals, and also expose their limits—and thus our limits of understanding. Understanding when, how and why longer seasons lead to increased tree growth requires an interdisciplinary reckoning with how temperature, growth and a suite of external and internal drivers affect plant growth. The task may seem large, but bridging across theory and data from dendrochronology, phenology research, physiology, evolutionary and life-history theory could rapidly advance fundamental biology in ways that translate directly to improved models of future forest dynamics, and the suite of species and services that depend on them.

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## 1 Box. “Growth”, measured how, exactly?

Tree growth can be measured in a variety of ways. Our literature review found that most studies quantified growth by measuring radial growth (e.g., through increment cores or dendrometers,  $n=28$ ), but a number also looked at metrics related to C assimilation (e.g. net ecosystem productivity or gross primary productivity,  $n=20$ ), while a smaller number examined biomass, height, or number of stems ( $n=9$ ), or root:shoot ratio ( $n=1$ ). Some studies used modeled estimates of photosynthesis (e.g., Smith *et al.* (2014) relied on daily photosynthesis estimates derived from the LPJ-GUESS photosynthesis model, while Chen *et al.* (2000) estimated photosynthesis using the Integrated Terrestrial Ecosystem C-budget model, InTEC). Others measured photosynthesis at the leaf level, through flux towers, or used greenness metrics (NDVI).

Growth measurements vary across disciplines and study types, posing a further challenge to an interdisciplinary approach to understanding how growing season length relates to growth. Greenhouse or growth chamber studies and provenance trials were more likely to measure height or biomass, whereas larger scale syntheses and remote-sensed studies are more likely to use metrics of carbon assimilation.

Aligning across the range and scale of growth metrics will be critical for an integrated understanding of growth-growing season length relationships and implications under continued climate change. There is decoupling among some metrics of growth. For example, vegetation photosynthesis may be poorly correlated with tree radial growth, and this relationship can vary seasonally (Cabon *et al.*, 2022). Further, tree radial growth is not a perfect indicator of whole tree growth, since plants allocate carbon to their roots, leaves, reproductive structures, and stores in addition to aboveground biomass. Relationships among different metrics of growth are not simple, so selecting relevant ones and aligning across the most widely used ones will be necessary, though not easy: the relationship between photosynthesis, radial growth, and carbon uptake has large implications for future carbon sequestration and it remains widely debated (Green & Keenan, 2022). Further, there is a need to understand how to scale up across these varying metrics- from leaf and individual level to populations, communities, and ecosystems- while incorporating the variation that exists within and across levels.

## 2 Figures

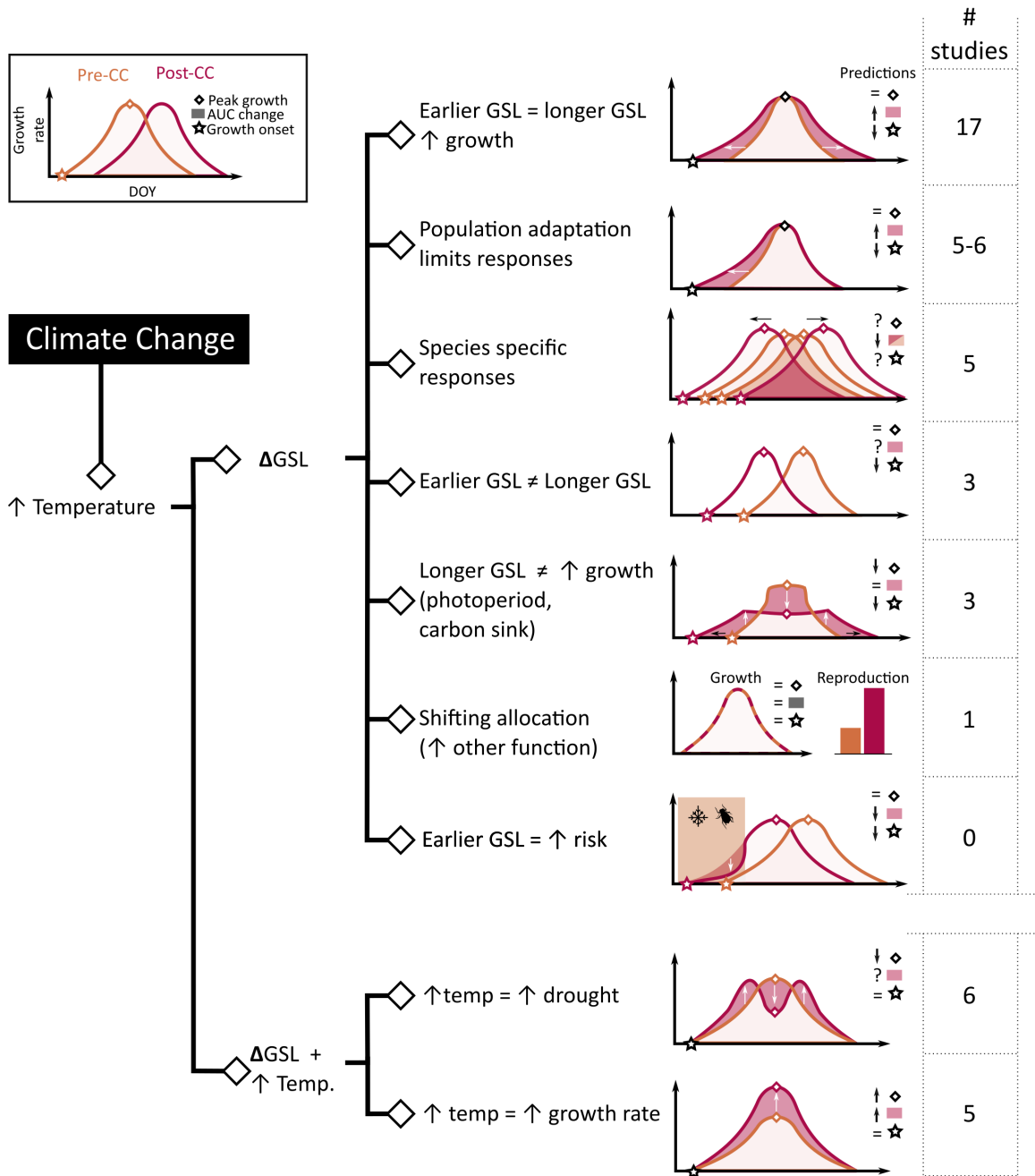


Figure 1: Pathways through which climate change could alter growing season length and growth.

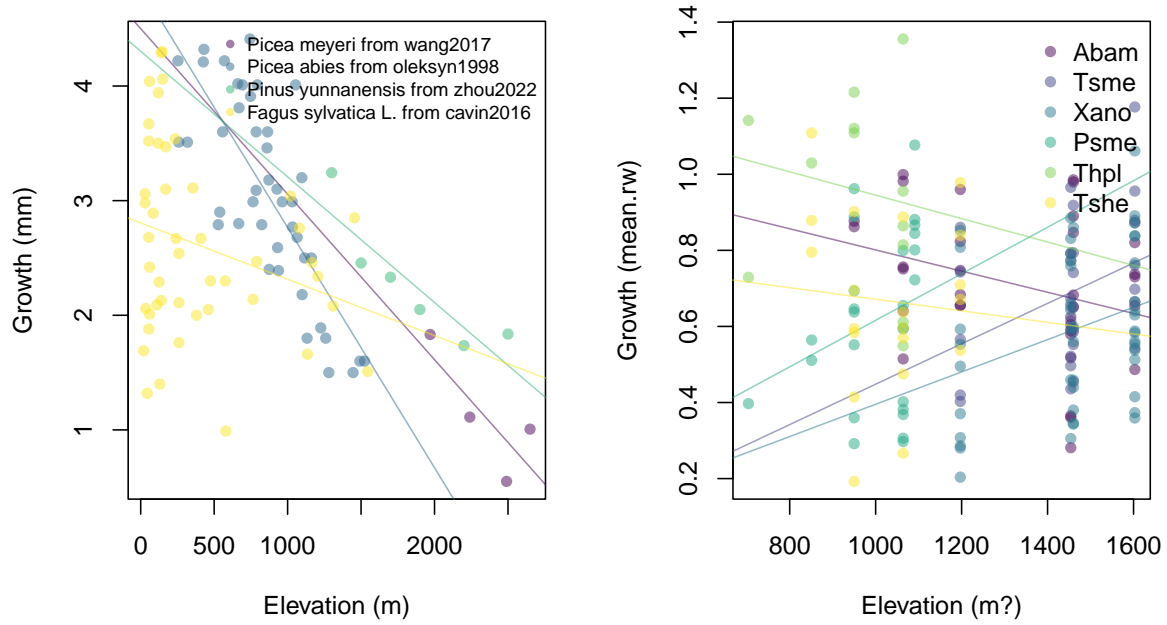


Figure 2: Growth  $\times$  elevation studies (from the literature, left) and results from across species at one location—Mount Tahoma/Rainier (right).

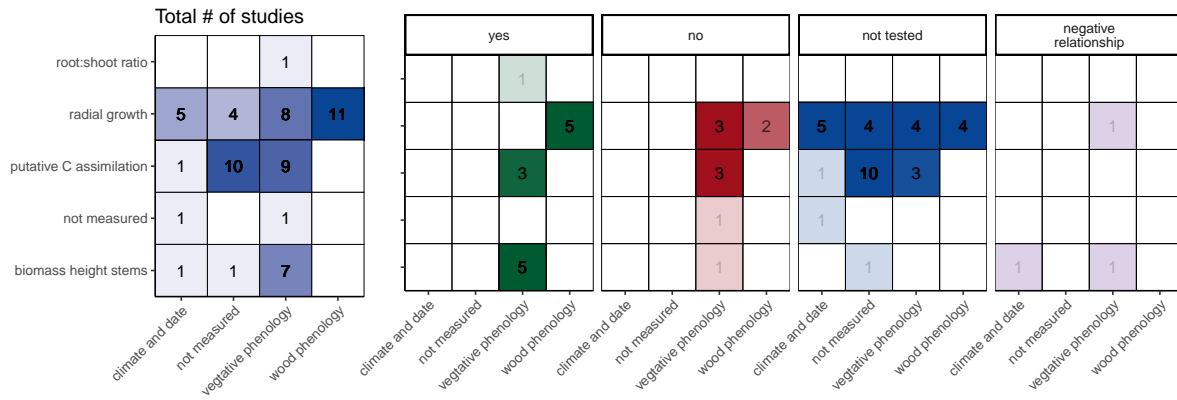


Figure 3: A review of growth  $\times$  growing season length relationship studies spanned a diversity of methods, but there was no coherency in which methods did or did not find a positive relationship. Not directly testing for the relationship was surprisingly common across methods. See Supplement for review details.

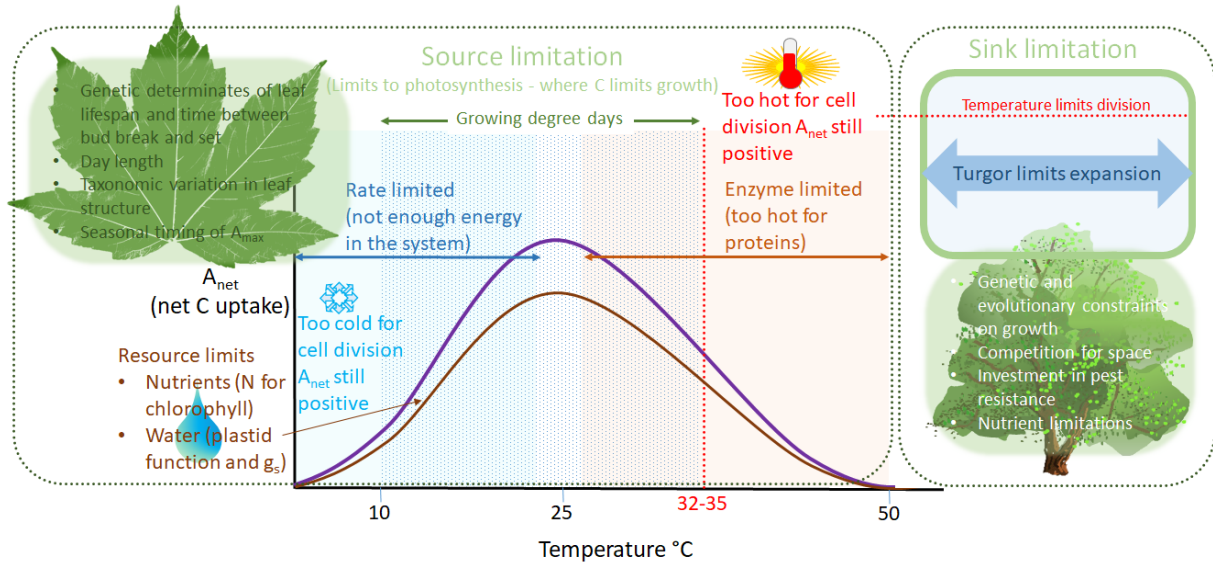


Figure 4: Less simplified version of how temperature works, including lots of limits at high and low temperatures (we need to update to make more asymmetric and to have the language match the language in the paper more ... or we need to add a box to this figure to explain all the terms).



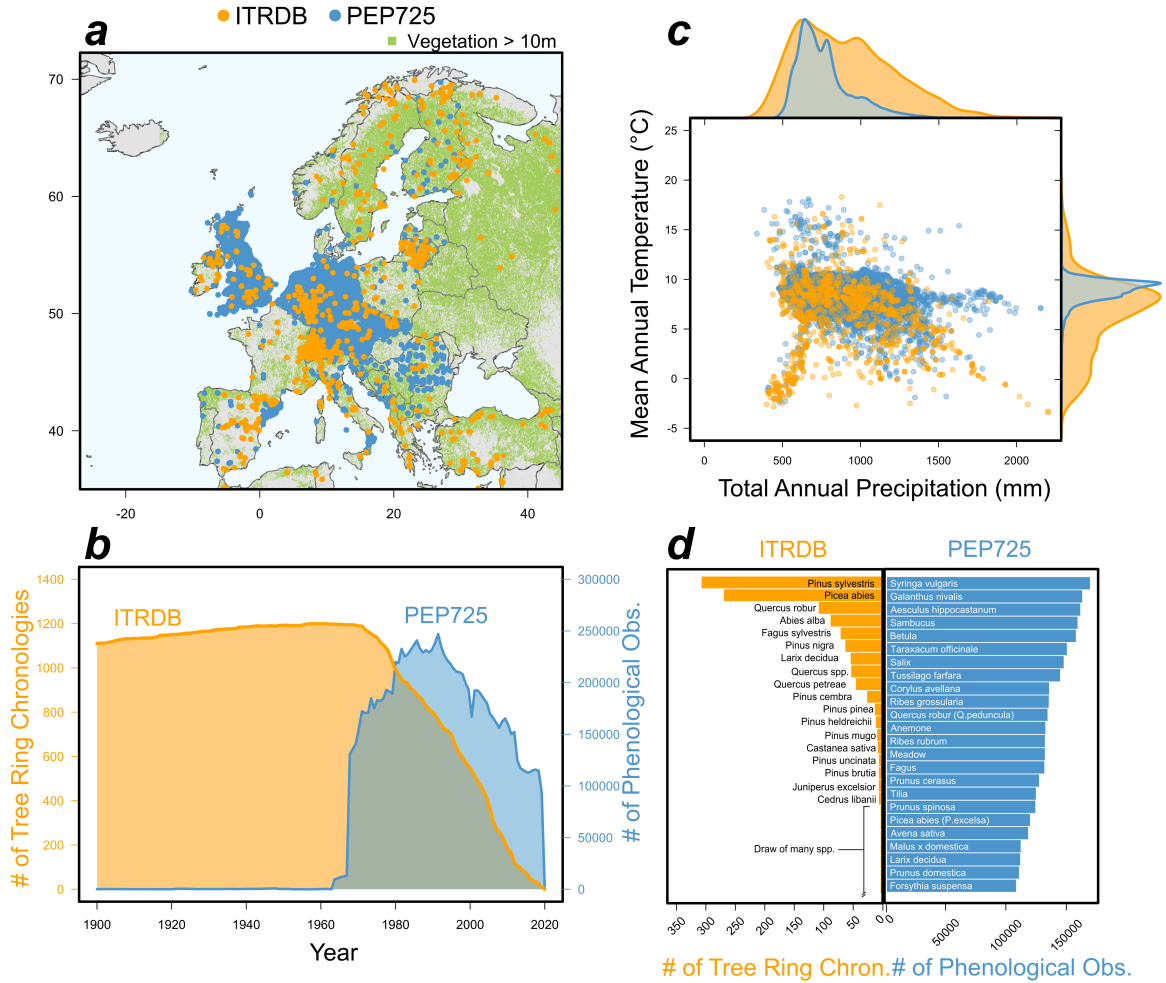


Figure 5: Data overlap between the two major databases of growth (International Tree Ring Data Bank, ITRDB, orange) and plant phenology (Pan European Phenology Project, PEP725, blue). Both databases are compared in terms of their spatial distributions (a), temporal overlaps (b), coverage of environmental conditions in climate space (c) and taxonomical representation (d). Note that the number of tree ring chronologies in (b) are composed by multiple trees per site, typically 10-20. Climatic data from Worldclim database ver. 2.1 at 2.5°grid resolution. PEP725 records in d) show the largest records for any given phenophase per species.

### 3 References

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