

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—namely, that longer growing seasons lead to increased tree growth—which can partly offset carbon emissions. A suite of diverse hypotheses, from drought-related late season constraints to internal limits on plant growth, provide diverging explanations of why longer growing seasons do not always increase tree growth. Here, using a literature review spanning regional, continental and global scales, we find an almost even divide in how often increased growing seasons are linked to increased growth—with 58% of all papers finding a positive relationship across over 56 species. We also found a fundamental disconnect between relevant fields—especially the two currently leading most research: dendrochronology and plant physiology. Major hypotheses are generally studied by one field with little interdisciplinary research, limiting any development—or testing—of a mechanistic framework for when longer seasons should lead to greater growth. Leveraging current research, combined with theory from evolutionary biology, community ecology and life history, we outline how progress towards a predictive framework is possible, but will require both new fundamental science, alongside new approaches within and across disciplines.

Introduction

The idea that longer growing seasons lead to increased plant growth is an intuitive tenet across multiple fields of biology, including physiology, dendrochronology (Frank *et al.*, 2022) and ecosystem ecology. 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 called this assumption into question.

A suite of recent studies have suggested longer growing seasons do not always lead to greater tree growth (Dow *et al.*, 2022; Green & Keenan, 2022; Silvestro *et al.*, 2023), with potentially large implications for future climate change. This research suggests that limitations on plant growth mean forests could be limited sinks with increased warming, despite longer growing seasons. Such findings challenge decades of research that find growth increases with longer seasons, from studies along natural elevational gradients to small-scale studies of cell growth

in lab settings 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 previously unknown internal limits on plant growth (Zohner *et al.*, 2023) and the complex effects of climate change itself, such as increased drought or temperatures too high for plant growth (Dow *et al.*, 2022), as well as differences simply due to the metric of growth (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—we argue—limits our ability to identify the underlying processes and mechanisms. Further, we highlight critical insights from physiology, community ecology, evolutionary and life history theory that have been unexamined in recent work. With insights from these other fields and an interdisciplinary focus, research studying connections between growing season length and growth appear 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. From the cellular to ecosystem levels, many biological processes are rate-limited in ways that tie back to time. Thus, the hypothesis that longer growing seasons should increase growth is intuitive—and pervasive.

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 and see Supplement for review details). 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 warming experiments that find that species which advance phenologically with warming also perform better (with performance most often measured by growth, Cleland *et al.*, 2012). With climate change, ecosystem-scale studies have reported a similar positive relationship between growing season length and carbon fluxes across decades (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 not—the relationship, with no clear trend by method, though a surprising number of papers never directly tested the relationship (Fig. 3). Thus, the path to understanding these results is unlikely to emerge solely through improved metrics.

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 (and discussed in XX studies, see Fig. 1), suggesting that higher temperatures paired with lower precipitation produce negative correlations with growth. In contrast, several other studies suggested fundamental internal constraints that prevent trees from responding to longer seasons, even without such external climatic constraints (see Fig. 1).

Yet we found that these hypotheses have been tested in radically different ways, never together, and ignore a suite of research on this topic—including other major possible mechanisms. 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. Further, the inconsistency of results, with no clear pattern by method or even within species (Fig. ??), 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 mechanisms, representing both both external drivers—including climatic and biotic—and internal constraints, could prevent a universally positive growth \times season length relationship. Currently, the lack of integration of several relevant fields and a tendency to focus on only select mechanisms within fields obscures this potential reality. Below we discuss findings across the fields of dendrochronology, physiology, phylogenetics and ecology to review the major mechanisms that may limit or disrupt the positive effects of longer growing seasons on growth, from individual (organismal) to community levels.

External

Temperature & moisture Fundamentally, temperature limits many biological processes. Temperatures that are too cool (often considered to be below $5^\circ C$ 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, whereas warming that pushes plants beyond their optima, where many biological rates crash, could have large impacts. 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 an offset of increased growth (due to longer seasons) from high summer temperatures (Gantois, 2022; Dow *et al.*, 2022), though which temperatures are too high is not generally known, and it seems likely current temperatures are below most plausible optima (Schaber & Badeck, 2002), unless other factors, such as drought, decrease that optima (Fig. 1f).

Positive effects of longer seasons on growth could also be offset by moisture deficits. If warming reduces soil moisture through either reduced precipitation or higher evaporation it could slow growth dramatically. A suite of tree ring studies confirm this, finding correlations with precipitation or other metrics related to plant access to water. The actual relationship between temperature, moisture and tree growth is more complex, as studies finding strong correlations between vapor pressure deficit and growth attest.

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. These biotic drivers of growth have rarely been mentioned in studies examining growing season length (we found no mention of them in our literature review, Fig. 1e), but could be increasingly limiting growth in some areas as extended growing seasons allow for additional generation cycles in many pest species (Mitton & Ferrenberg, 2012; Lange *et al.*, 2006).

Internal

Universal limits & triggers Fundamental limits on plant processes through biophysical realities may limit the extent to which growth can increase in response to a greater growing season length (e.g., allometry, chemical reaction limits, and genetic architecture that may limit what trait combinations are possible, Ackerly *et al.*, 2000). Additionally, long-term exposure to early- and late-season risks (e.g. frost) and growth constraints (e.g. low water availability) may have selected for a limited growth response to extended growing seasons. Regardless, 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. 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 contradict

decades of work showing species-level differences in how and when species grow.

Species-specific limits The underlying genetic and developmental drivers of growth varies by species, as evolution generally 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 ‘determinism’ defines a suite of differences in the levels and timing of investment and leaf growth. Determinate species build most of their leaf material the season before and flush most leaf buds all at once at the start of season, while indeterminate species more continually produce new buds and flush them. Such differences can clearly influence the extent to which the growth of different species is influenced by increases in growing season length, even under identical conditions.

Whether and how strongly increased growing seasons result in increased growth can potentially also be understood by considering 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 can grow rapidly and more flexibly 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 be far more likely 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, also 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; Davies *et al.*, 2013). 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).

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—when the end of the season is as defined by budset—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 and have longer seasons relative to adult trees. The response of adult trees may then vary depending on their investment 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 in reproduction.

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. Most fields studying growth \times growing season length relationships consider a limited set of metrics and a small subset of possible drivers (see Figs. 3, ??). Beyond failing to test a suite of highly relevant mechanisms, the lack of interdisciplinary study means we lack coherent tests that compare multiple mechanisms. Taken together, the current landscape of research suggests we may be testing hypotheses for how plants shift with climate change that we never previously understood well in fundamental biology.

Below we outline a path towards building a better mechanistic framework for predicting when the longer growing seasons caused by anthropogenic climate change will increase plant growth. This path 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 and 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).

Bridging the internal-external drivers divide

Standardized measurements will not yield fully comparable estimates—especially on the relative impacts of external and internal drivers—without larger shifts within fields. Major fields studying this relationship—dendrochronology, phenology research and physiology—all need to broaden in specific ways to overlap with one another to facilitate interdisciplinary work. At the same time, all fields have missed certain major hypotheses they could test (Fig. 1), highlighting the need to integrate perspectives from other disciplines with relevant theory and methods.

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 (see Fig. 1) but almost none have 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. Given an increasing number of studies across more species, a careful synthesis of studies across species could further test for the role of evolutionary history.

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 operate 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 major 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) and statistical detrending (of tree ring chronologies), that may obscure patterns where the signal of effects of growing season length and biotic drivers (see below) may be most apparent (such as rapid growth phases, Manzanedo & Pederson, 2019). Unfortunately, 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 higher than for dendrochronology and physiology, but sampling biases in both fields limit current opportunities. Dendrochronology’s aim for prioritizing climatic response has led to a strong focus on conifers (gymnosperms), creating a major split from most studies of leaf phenology, which focus almost entirely on deciduous species, which are mainly angiosperms (see Fig. 1). Phenology research has also been overly 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, 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 are 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, 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 the cessation of growth, and how these triggers and responses have evolved. This includes current suggestions of constraints that lack any physiological mechanism, but 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 and cell division versus expansion 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. Expanding beyond the current disciplines focused on this topic could also be informative. For example, a clearer understanding of which environmental stimuli trigger leaf expansion, senescence, and woody growth, the underlying developmental processes that are triggered, and their evolution, could contribute towards a clearer understanding of growth constraints.

Urgent opportunities

Existing data and networks Expanding the focus of disciplines to help build an interdisciplinary framework for growth \times growing season length relationships will take time, but some hypotheses may be tractably tested by taking advantage of existing data sets and ongoing experiments. We mention three such opportunities here.

First, 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 Hackett-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.

A second opportunity comes from existing common garden studies, from which 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 (as opposed to immediately at the end of the treatment season). While these are most easily done for juvenile trees, they could also be done on adult trees, given the infrastructure investment.

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. Combined with careful measurements of carbon allocation, including to reproductive output, and tissue lost to frost and biotic drivers, such an experiment could rapidly compare a suite of drivers. With species carefully chosen to maximize divergent strategies and the potential for genomic and related studies (e.g., *Populus*, *Quercus*), the experiment could also become a resource for studies of underlying mechanisms for constraints. 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, unnatural, accidental, and unreplicated 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

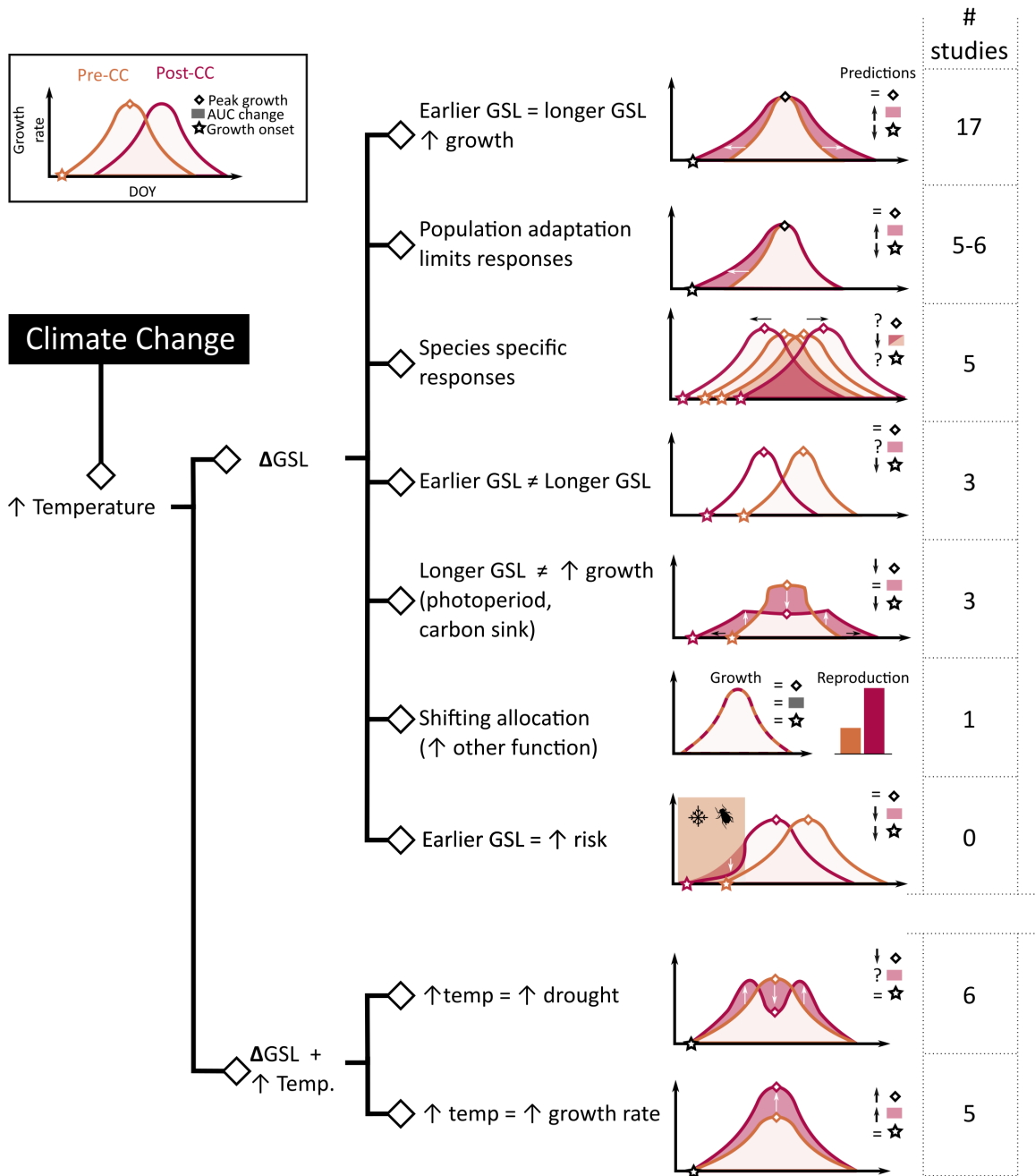


Figure 1: Pathways through which climate change could alter growing season length and growth.

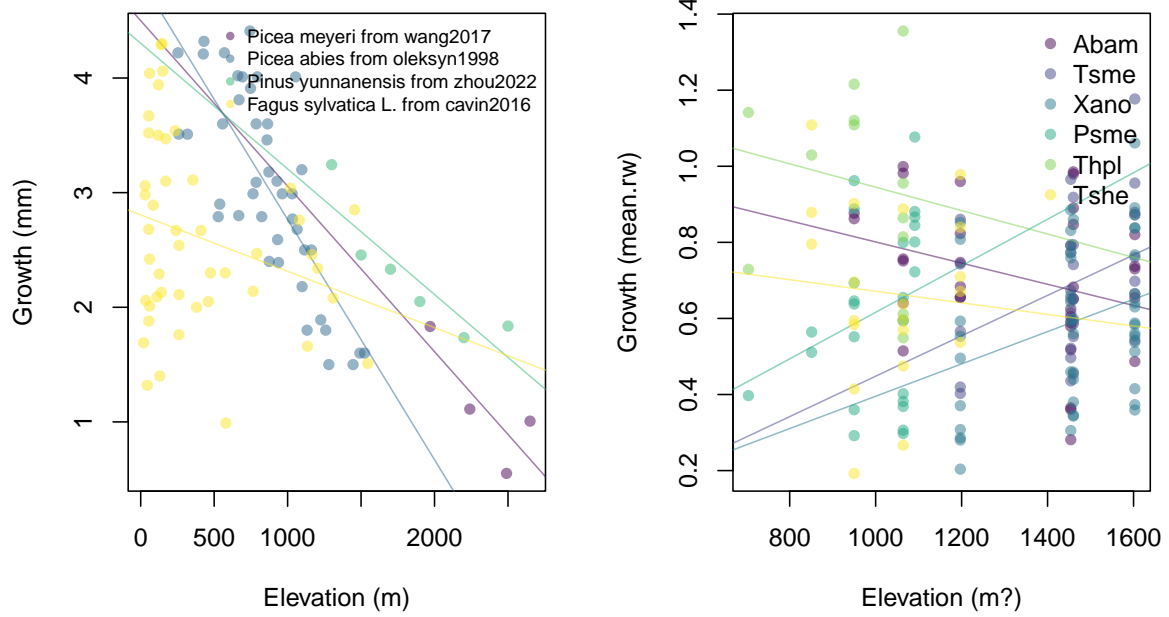


Figure 2: Growth \times elevation studies (from the literature, left) and results from Mount Tahoma/Rainier (right).

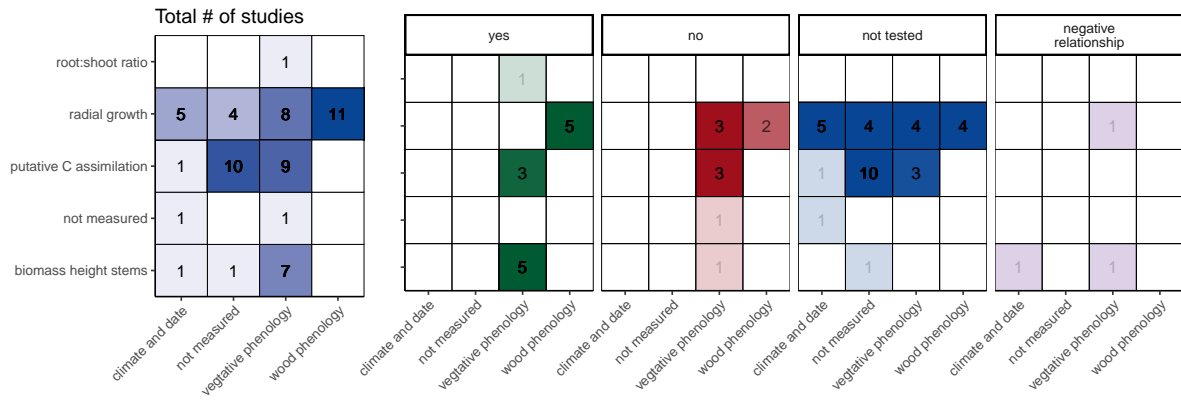


Figure 3: A review of the literature on growth \times growing season length relationships spanned a diversity of methods, but there was no coherency in which methods did or did not find a positive relationship.

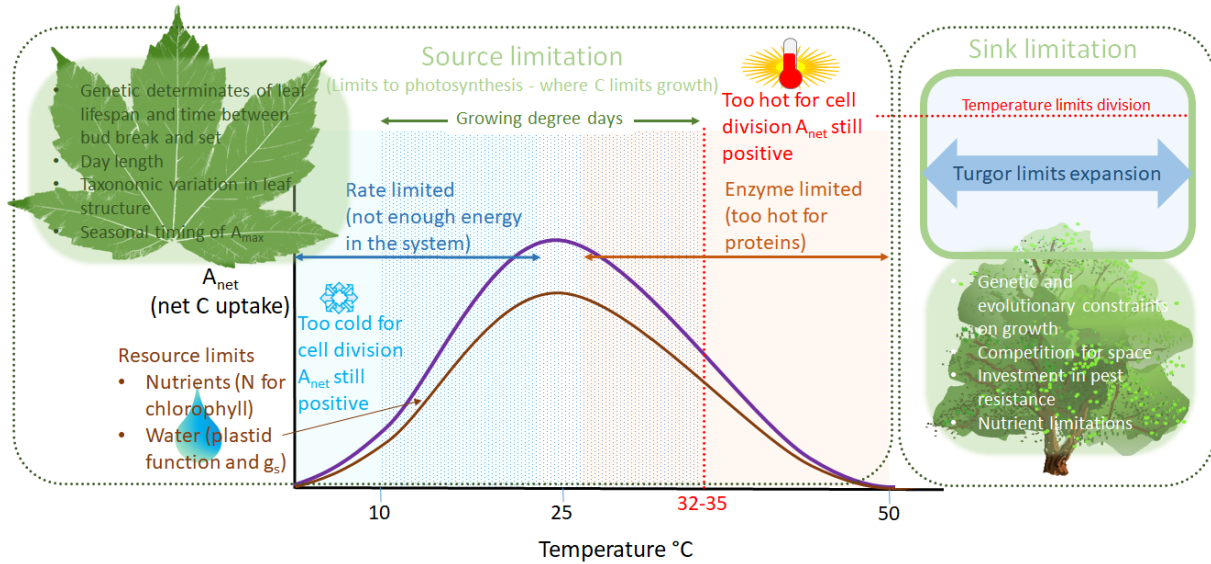


Figure 4: Less simplified version of how temperature works, including lots of limits at high and low temperatures (we need to update to make more asymmetric and to have the language match the language in the paper more ... or we need to add a box to this figure to explain all the terms).

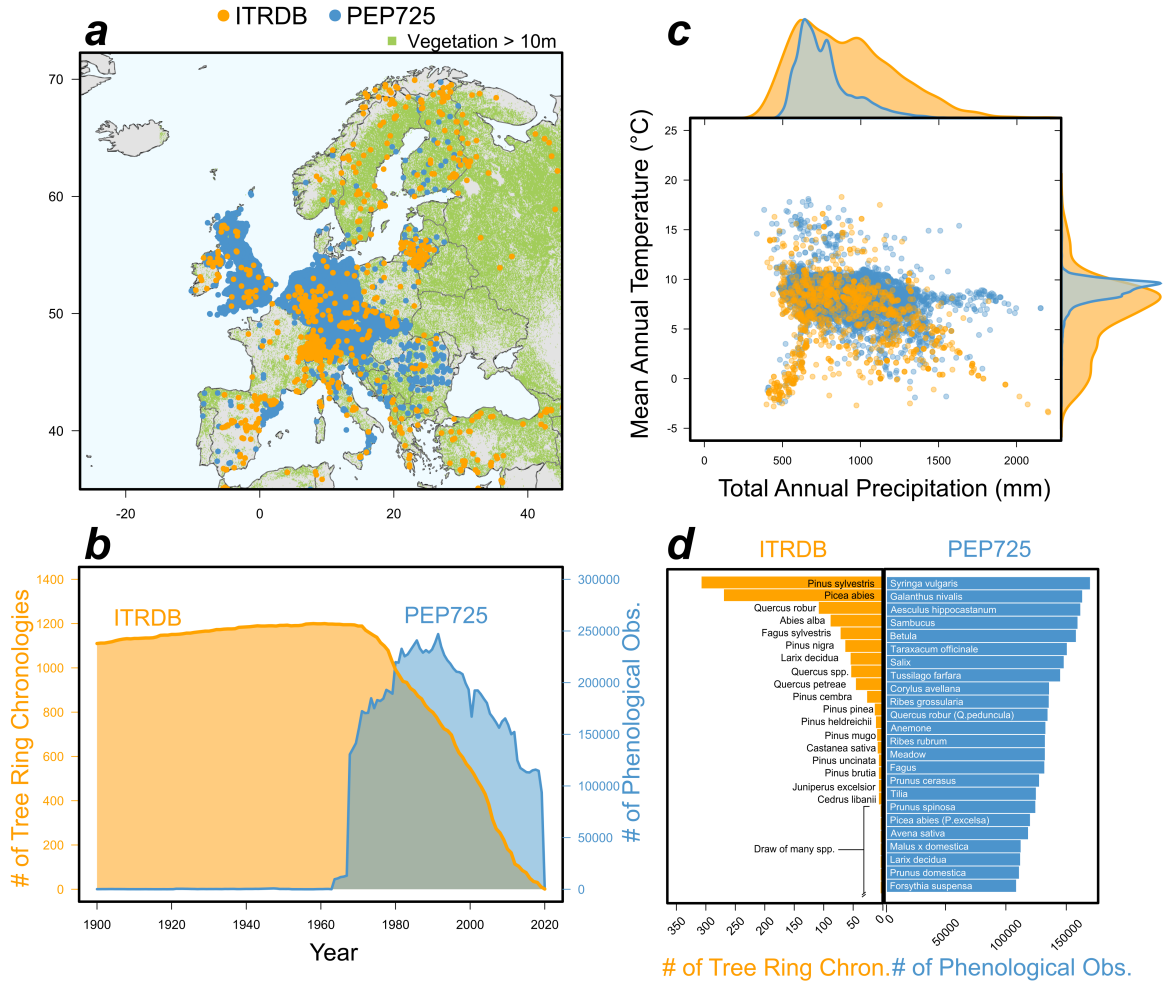


Figure 5: Data overlap between the two major databases of growth (International Tree Ring Data Bank, ITRDB, orange) and plant phenology (Pan European Phenology Project, PEP725, blue). Both databases are compared in terms of their spatial distributions (a), temporal overlaps (b), coverage of environmental 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

- Ackerly, D. (2009) Conservatism and diversification of plant functional traits: Evolutionary rates versus phylogenetic signal. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 19699–19706.
- Ackerly, D.D., Dudley, S.A., Sultan, S.E., Schmitt, J., Coleman, J.S., Linder, C.R., Sandquist, D.R., Geber, M.A., Evans, A.S., Dawson, T.E. *et al.* (2000) The evolution of plant ecophysiological traits: recent advances and future directions: new research addresses natural selection, genetic constraints, and the adaptive evolution of plant ecophysiological traits. *Bioscience* **50**, 979–995.
- Aitken, S.N. & Bemmels, J.B. (2016) Time to get moving: assisted gene flow of forest trees. *Evol Appl* **9**, 271–90.
- Anderson-Teixeira, K.J. & Kannenberg, S.A. (2022) What drives forest carbon storage? the ramifications of source–sink decoupling. *New Phytologist* **236**.
- Cabon, A., Kannenberg, S.A., Arain, A., Babst, F., Baldocchi, D., Belmecheri, S., Delpierre, N., Guerrieri, R., Maxwell, J.T., McKenzie, S. *et al.* (2022) Cross-biome synthesis of source versus sink limits to tree growth. *Science* **376**, 758–761.
- Chen, W., Black, T., Yang, P., Barr, A., Neumann, H., Nesic, Z., Blanken, P., Novak, M., Eley, J., Ketler, R. *et al.* (1999) Effects of climatic variability on the annual carbon sequestration by a boreal aspen forest. *Global Change Biology* **5**, 41–53.
- Chen, W., Chen, J., Liu, J. & Cihlar, J. (2000) Approaches for reducing uncertainties in regional forest carbon balance. *Global Biogeochemical Cycles* **14**, 827–838.
- Cleland, E.E., Allen, J.M., Crimmins, T.M., Dunne, J.A., Pau, S., Travers, S.E., Zavaleta, E.S. & Wolkovich, E.M. (2012) Phenological tracking enables positive species responses to climate change. *Ecology* **93**, 1765–1771.
- Cook, E.R. & Kairiukstis, L.A. (2013) *Methods of dendrochronology: applications in the environmental sciences*. Springer Science & Business Media.
- Davies, T.J., Wolkovich, E.M., Kraft, N.J.B., Salamin, N., Allen, J.M., Ault, T.R., Betancourt, J.L., Bolmgren, K., Cleland, E.E., Cook, B.I., Crimmins, T.M., Mazer, S.J., McCabe, G.J., Pau, S., Regetz, J., Schwartz, M.D. & Travers, S.E. (2013) Phylogenetic conservatism in plant phenology. *Journal of Ecology* **101**, 1520–1530.
- Diaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Prentice, I.C., Garnier, E., Bonisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Wright, S.J., Sheremet’ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Gunther, A., Falczuk, V., Ruger, N., Mahecha, M.D. & Gorne, L.D. (2016) The global spectrum of plant form and function. *Nature* **529**, 167–U73.

- Ding, W., Cong, W.F. & Lambers, H. (2021) Plant phosphorus-acquisition and-use strategies affect soil carbon cycling. *Trends in Ecology & Evolution* **36**, 899–906.
- Dow, C., Kim, A.Y., D’Orangeville, L., Gonzalez-Akre, E.B., Helcoski, R., Herrmann, V., Harley, G.L., Maxwell, J.T., McGregor, I.R., McShea, W.J. *et al.* (2022) Warm springs alter timing but not total growth of temperate deciduous trees. *Nature* **608**, 552–557.
- Finzi, A.C., Giasson, M.A., Plotkin, A.A.B., Aber, J.D., Boose, E.R., Davidson, E.A., Dietze, M.C., Ellison, A.M., Frey, S.D., Goldman, E., Keenan, T.F., Melillo, J.M., Munger, J.W., Nadelhoffer, K.J., Ollinger, V. S., Orwig, D.A., Pederson, N., Richardson, A.D., Savage, K., Tang, J., Thompson, J.R., Williams, C.A., Wofsy, S.C., Zhou, Z. & Foster, D.R. (2020) Carbon budget of the harvard forest long-term ecological research site: pattern, process, and response to global change. *ECOLOGICAL MONOGRAPHS* **90**.
- Flinker, R.H., Cardenas, M.B., Caldwell, T.G., Flerchinger, G.N., Roy, R. & Reich, P.B. (2021) Promise and pitfalls of modeling grassland soil moisture in a free-air co2 enrichment experiment (biocon) using the shaw model. *Pedosphere* **31**, 783–795.
- Frank, D., Fang, K. & Fonti, P. (2022) Dendrochronology: Fundamentals and innovations. *Stable Isotopes in Tree Rings: Inferring Physiological, Climatic and Environmental Responses*, pp. 21–59, Springer International Publishing Cham.
- Friedlingstein, P., O’sullivan, M., Jones, M.W., Andrew, R.M., Gregor, L., Hauck, J., Le Quéré, C., Luijkx, I.T., Olsen, A., Peters, G.P. *et al.* (2022) Global carbon budget 2022. *Earth System Science Data Discussions* **2022**, 1–159.
- Gantois, J. (2022) 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.
- Gill, A.L., Gallinat, A.S., Sanders-DeMott, R., Rigden, A.J., Gianotti, D.J.S., Mantooth, J.A. & Templer, P.H. (2015) Changes in autumn senescence in northern hemisphere deciduous trees: a meta-analysis of autumn phenology studies. *Annals of Botany* **116**, 875–888.
- Green, J.K. & Keenan, T.F. (2022) The limits of forest carbon sequestration. *Science* **376**, 692–693.
- Grime, J.P. (1977) Evidence for existence of 3 primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* **111**, 1169–1194.
- Hacket-Pain, A., Foest, J.J., Pearse, I.S., LaMontagne, J.M., Koenig, W.D., Vacchiano, G., Bogdziewicz, M., Caignard, T., Celebias, P., Van Dormolen, J. *et al.* (2022) Masttree+: Time-series of plant reproductive effort from six continents. *Global Change Biology* **28**, 3066–3082.
- Hacket-Pain, A., Friend, A., Lageard, J. & Thomas, P. (2016a) Tree rings and masting: considering reproductive phenomena when interpreting tree rings? *Tree Rings in Archaeology, Climatology and Ecology* **14**, 78–85.

- Hacket-Pain, A.J., Cavin, L., Friend, A.D. & Jump, A. (2016b) 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.
- Hanson, P.J., Riggs, J.S., Nettles, W.R., Phillips, J.R., Krassovski, M.B., Hook, L.A., Gu, L., Richardson, A.D., Aubrecht, D.M., Ricciuto, D.M. *et al.* (2017) Attaining whole-ecosystem warming using air and deep-soil heating methods with an elevated co₂ atmosphere. *Biogeosciences* **14**, 861–883.
- Ito, G., Romanou, A., Kiang, N.Y., Faluvegi, G., Aleinov, I., Ruedy, R., Russell, G., Lerner, P., Kelley, M. & Lo, K. (2020) Global carbon cycle and climate feedbacks in the nasa giss modele2. 1. *Journal of Advances in Modeling Earth Systems* **12**, e2019MS002030.
- Jensen, A.M., Warren, J.M., King, A.W., Ricciuto, D.M., Hanson, P.J. & Wullschleger, S.D. (2019) Simulated projections of boreal forest peatland ecosystem productivity are sensitive to observed seasonality in leaf physiology. *Tree Physiology* **39**, 556–572.
- Keenan, T.F., Gray, J., Friedl, M.A., Toomey, M., Bohrer, G., Hollinger, D.Y., Munger, J.W., O’Keefe, J., Schmid, H.P., Wing, I.S. *et al.* (2014) Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Nature Climate Change* **4**, 598–604.
- King, G.M., Gugerli, F., Fonti, P. & Frank, D.C. (2013) Tree growth response along an elevational gradient: climate or genetics? *Oecologia* **173**, 1587–1600.
- Körner, C., Möhl, P. & Hiltbrunner, E. (2023) Four ways to define the growing season. *Ecology Letters* .
- Kramer, P. (2012) *Physiology of woody plants*. Elsevier, New York.
- Lange, H., Økland, B. & Krokene, P. (2006) Thresholds in the life cycle of the spruce bark beetle under climate change. *Interjournal for Complex Systems* **1648**, 1–10.
- Larcher, W. (1980) *Plant Physiological Ecology*. Springer-Verlag.
- Manzanedo, R.D. & Pederson, N. (2019) Towards a more ecological dendroecology. *Tree-Ring Research* **75**, 152–159.
- Martinez-Meier, A., Sanchez, L., Pastorino, M., Gallo, L. & Rozenberg, P. (2008) 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.
- Mitton, J.B. & Ferrenberg, S.M. (2012) Mountain pine beetle develops an unprecedented summer generation in response to climate warming. *The American Naturalist* **179**, E163–E171.
- Schaber, J. & Badeck, F.W. (2002) Evaluation of methods for the combination of phenological time series and outlier detection. *Tree Physiology* **22**, 973–982.

- Schweiger, A., Awdamet, F.T., Drenckhan, W. & Berauer, B.J. (2022) Transgenerational effects of elevated CO_2 : Downregulation of photosynthetic efficiency and stomatal sensitivity to drought .
- Silvestro, R., Zeng, Q., Buttò, V., Sylvain, J.D., Drolet, G., Mencuccini, M., Thiffault, N., Yuan, S. & Rossi, S. (2023) A longer wood growing season does not lead to higher carbon sequestration. *Scientific reports* **13**, 4059.
- Smith, B., Wårlind, D., Arneth, A., Hickler, T., Leadley, P., Siltberg, J. & Zaehle, S. (2014) Implications of incorporating N cycling and N limitations on primary production in an individual-based dynamic vegetation model. *Biogeosciences* **11**, 2027–2054.
- Smith, M.D., Wilcox, K., Sala, O., Phillips, R., Luo, Y., Knapp, A. & Lemoine, N.P. (2016) Drought-net: A global network merging observations, experiments, and modeling to forecast terrestrial ecosystem sensitivity to drought. *AGU Fall Meeting Abstracts*, vol. 2016, pp. B11J–06.
- Soolanayakanahally, R.Y., Guy, R.D., Silim, S.N. & Song, M. (2013) Timing of photoperiodic competency causes phenological mismatch in balsam poplar (*populus balsamifera* L.). *Plant, cell & environment* **36**, 116–127.
- Thomas, S.C. (2011) Age-related changes in tree growth and functional biology: The role of reproduction. *Size- and Age-Related Changes in Tree Structure and Function* (eds. F.C. MEINZER, B. Lachenbruch & T.E. Dawson), chap. 2, pp. 33–64, Springer.
- Thompson, R.A., Adams, H.D., Breshears, D.D., Collins, A.D., Dickman, L.T., Grossiord, C., Manrique-Alba, À., Peltier, D.M., Ryan, M.G., Trowbridge, A.M. *et al.* (2023) No carbon storage in growth-limited trees in a semi-arid woodland. *Nature Communications* **14**, 1959.
- Way, D.A. & Oren, R. (2010) Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. *Tree physiology* **30**, 669–688.
- Zohner, C.M., Mirzaghali, L., Renner, S.S., Mo, L., Rebindaine, D., Bucher, R., Palouš, D., Vitasse, Y., Fu, Y.H., Stocker, B.D. *et al.* (2023) Effect of climate warming on the timing of autumn leaf senescence reverses after the summer solstice. *Science* **381**, eadf5098.