

Climate change highlights fundamental gaps in plant growth × growing season length relationships

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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 predict increased plant growth will partly offset carbon emissions. A suite of diverse hypotheses, from increased drought and high temperatures, to internal limits on plant growth each year, have generally failed to coalesce around a predictive model of why longer growing seasons do, or do not, increase tree growth. Here, using a systematic literature review spanning regional, continental and global scales, we find an almost even divide in how often increased growing seasons are linked to increase growth—with 57% of all papers finding a positive relationship across XX species and a fundamental disconnect between relevant fields—especially dendrochronology and plant physiology, which currently lead most research. Major hypotheses are generally studied uniquely by one field alone 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 and ecosystem ecology. It is also a foundational assumption of most models of the future global carbon cycle. Most models project that future 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 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 will be limited sinks with increased warming. Such findings challenge decades of research that find growth increases with longer seasons, from large-scale studies along natural elevational gradients to small-scale studies of cell growth in lab settings to previous 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 highly diverse, from previously unknown fundamental internal limits on plant growth (Zohner *et al.*, 2023) to 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. Our approach spans multiple fields, from foundational to recent studies. Leveraging a systematic literature review, we examine which methods, species and approaches 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, the current fields 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 for both 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 tenet across 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.

Total time increasing growth was by far the most common hypothesis for why longer seasons should increase growth, across our systematic review of growth \times growing season length studies, with 19 of XX total studies including it (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. 1). Mechanistically, this hypothesis is supported by warming experiments that find species that 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 relationship across decades (Keenan *et al.*, 2014) or in years with warm, early springs (Chen *et al.*, 1999). Such 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 disconnect between growth and growing season length. Instead the field has generally found split support—across methods—for the when longer seasons lead to increased growth. Papers spanning XX to XX 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. 2). 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. 3). External climatic drivers that offset the positive growth effects of longer seasons are often reported in tree ring studies, suggested when higher temperatures and lower precipitation produce negative correlations with growth. In contrast, several other studies suggested fundamental developmental constraints that prevent trees from responding to longer seasons.

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 consistency of varying results, with no clear pattern by method or even within species—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 unified tests of it, for progress.

Controllers on growth \times growing season length relationships

A suite of mechanisms, both external—including climatic and biotic drivers—and internal could alter any common growth \times season length relationship. Currently, a the lack of integration of several relevant fields and a tendency to focus on only select mechanisms within fields obscures this reality. Below we integrate across the fields of dendrochronology, physiology, phylogenetics and ecology to review the major mechanisms that may limit or disrupt longer growing seasons leading to increased growth, from individual (organismal) to community levels.

External

Temperature & moisture Fundamentally temperature limits biological processes. Temperatures that are too cool (often considered to be below 5°C for temperate trees) and too warm (an area of active research Martinez-Meier *et al.*, 2008; Cabon *et al.*, 2022, see also Fig. 3) slow down biological processes and eventually can lead to tissue death (Larcher, 1980; Kramer, 2012). Between the upper and lower limit 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 (Fig. ??).

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 plant beyond their optima, where many 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 so have no discernible effect on growth, while others suggest observed increases in growth are due only to increased growth rates (not longer seasons) and finally a number tree ring studies seem to suggest an offset of increased growth (due to longer) seasons from high summer temperatures (Gantois, 2022; Dow *et al.*, 2022), though what temperatures are too high is not generally known, and it seems likely current temperatures are below the optima (Schaber & Badeck, 2002).

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. Herbivory can have large impacts on forests, leading to declines in satellite measures of greenness often associated of signals of plant senescence. And disease is well known to determine forest dynamics. These external factors have rarely been mentioned in studies examining growing season length (we found no mention of them in our literature review).

Internal

Universal limits Plants internal programming could limit growth responses to longer seasons, with some constraints operating universally across species. These constraints can be genetic or developmental and include fundamental limits on plant processes through biophysical realities (e.g., allometry, chemical reaction limits, and genetic architecture that may limit what trait combinations are possible, Ackerly *et al.*, 2000). Recent studies on how earlier seasons affect tree growth has focused strongly on developmental constraints, suggesting a never-before-heard-of role for the summer solstice to limit how much and when plants can invest in growth (Zohner *et al.*, 2023). This is hypothesized to be universal, somewhat contradicting decades of work showing species-level differences in how and when species grow.

Species-specific limits Much internal programming that would affect growth responses varies by species, as evolution generally drives selection for different constraints and different strategies. Leaf strategies clearly 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.

Ideas of determinism, often used in forest science, intersect with ecological theories of different

plant strategies along which species—especially within communities—assemble. 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.

Imprints of past selection, however, also drive species-level differences, producing phylogenetic patterns that may limit how well species are adapted to current conditions, and constrain plant responses (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, variations from between-populations to within-individuals drive variation in growth and its relationship to growing season length. 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. Within individuals maturity and shifting investment can drive inter-annual variation. Saplings tend to both grow more rapidly and have longer seasons relative to adult trees, where growth and survival are not the only aims. Adult trees then vary depending on investment, most notably in reproduction.

Trade-offs between vegetative and reproductive investments are a paradigm of life history theory and produce important 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 mast 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. 2, S1). 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 a hypothesis for how plants shifts with climate change that we never previously understood well in fundamental biology.

Below we outline a path towards building a mechanistic framework to predict when the longer growing seasons of 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. 4) 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 XX different metrics of start and end of season, and XX of growth—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 aim to report certain relevant drivers (e.g., several temperature and precipitation responses across the growing season) and broaden the metrics they use to encompass a standard set of growth and growing season length metrics (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. 2).

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. 4), highlighting

the need to integrate perspectives from other disciplines with relevant theory and methods.

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 has long assumed growth decreases with shorter seasons (e.g., Bruening *et al.*, 2017) over space (not time), such as higher elevations and latitudes. This assumption is part of why their statistical methods are designed to remove spatial trends. Their methods also generally remove rapid growth phases, where signal of effects of growing season length, and biotic drivers (see below), may be most apparent (Manzanedo & Pederson, 2019). Such 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 much higher, but biases in both fields limit current opportunities. Dendrochronology’s aim for the most climatic response has also 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. 4). 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 given the 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, even though it is foundational to forest dynamics.

Lags & allocation Bridging across disciplines will require bridging across time-scales, 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 would benefit from tackling the challenge of understanding the physiological and/or developmental connections between growing season length and growth. To date, much work has focused on measures of growth and phenology without a clear mechanistic link. This includes current suggestions of constraints that lack any physiological mechanism, but progress in this area is particularly important if want to include constraints in our projections, as extrapolating is especially dangerous when the underlying mechanistic model is wrong. Physiological studies that follow carbohydrate and cell division versus expansion dynamics could yield insights. Similarly, more work on xylogenesis—especially if done with a focus both to extrapolate to long-term tree ring studies and/or in physiological experiments—would help. Expanding beyond the current disciplines focused on this topic, more developmental or genetic expertise may be critical for robust tests of constraints.

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. 4) but almost none have made or tested predictions 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) should form the basis of choosing which species to focus on 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 remove some of the noise 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. *In situ* elevation work suggests no genetic differences (King *et al.*, 2013), while common garden studies across latitudes suggest phenological variation across populations limits growth (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.

The scale of variation across these levels could both refine theory and provide comparisons to the scale 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. 1)—suggesting this is only part of our missing mechanistic understanding.

Where to go in the batmobile, now!

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 now by combining data across fields. 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 (PEP) 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, the dataset together may test for where longer growing seasons will increase growth; based on existing theory, we expect longer growing seasons will increase growth for species with regular reproduction (no masting, see also 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.

More robust tests of population and individual variation could come from existing common garden studies. 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, and could be combined with 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.

Integrating more research from ecology and field global change experiments could help test lag effects, and bridge across physiological to dendrochronology scales. Large scale experiments on heat (e.g., SPRUCE), moisture via drought or irrigation (e.g., DroughtNet, Phynwald) and other factors (e.g., CO_2 in FACE) have increasingly been used to test ecological ‘memory’ and could help scale up from smaller and shorter-time scale physiological studies. 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 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 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 provenance 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, and unreplicated experiment. What this often hints at is how much it has highlighted important biology we don't know well, and how much it requires us to rediscover dusty old fundamentals, while also exposing 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 translates directly to improved models of future forest dynamics, and the suite of species and services that depend on them.

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 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 radially 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 simplistic, 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).

2 Figures

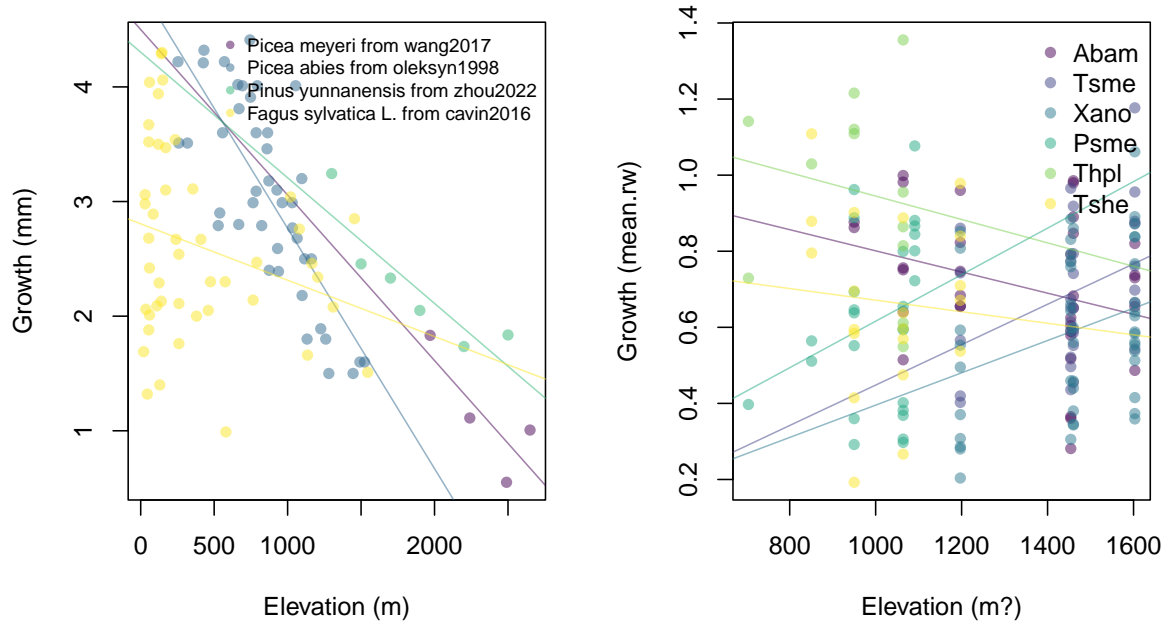


Figure 1: Growth \times elevation studies (from the literature, left) and results from Mount Tahoma/Rainier (right).

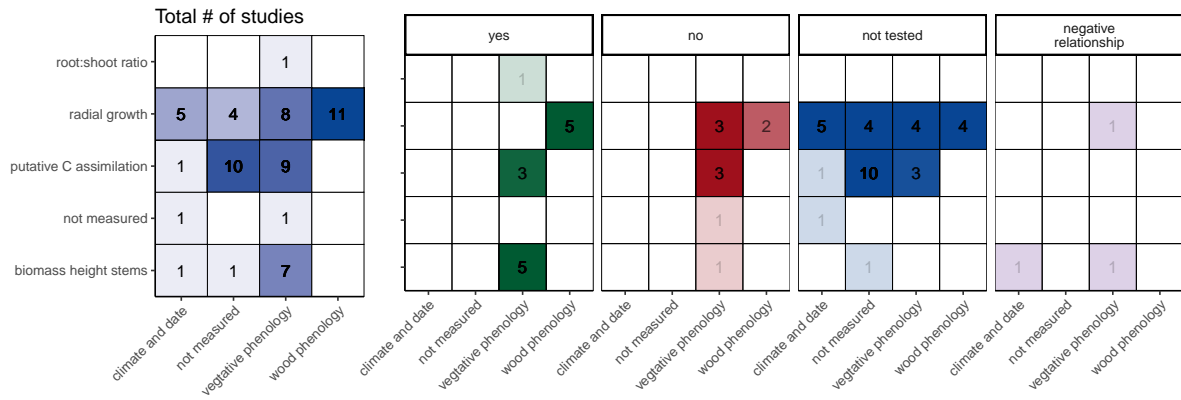


Figure 2: A review of the literature on growth × growing season length relationships spanned a diversity of methods, but there was no coherency in which methods did or did not find a positive relationship.

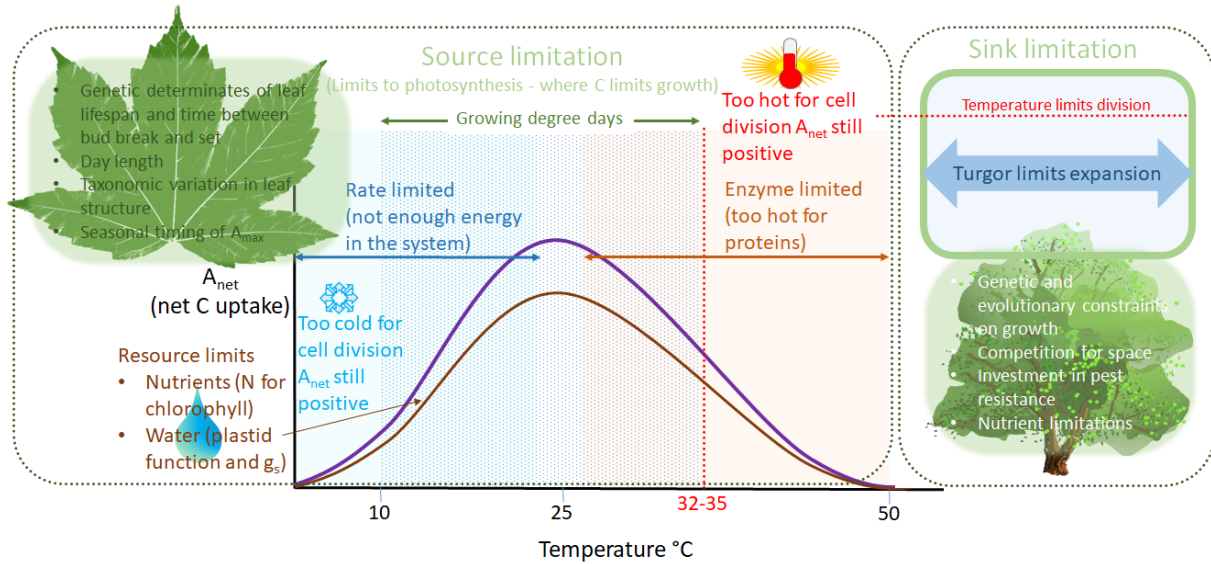


Figure 3: Less simplified version of how temperature works, including lots of limits at high and low temperatures (we need to update to make more asymmetric and to have the language match the language in the paper more ... or we need to add a box to this figure to explain all the terms).

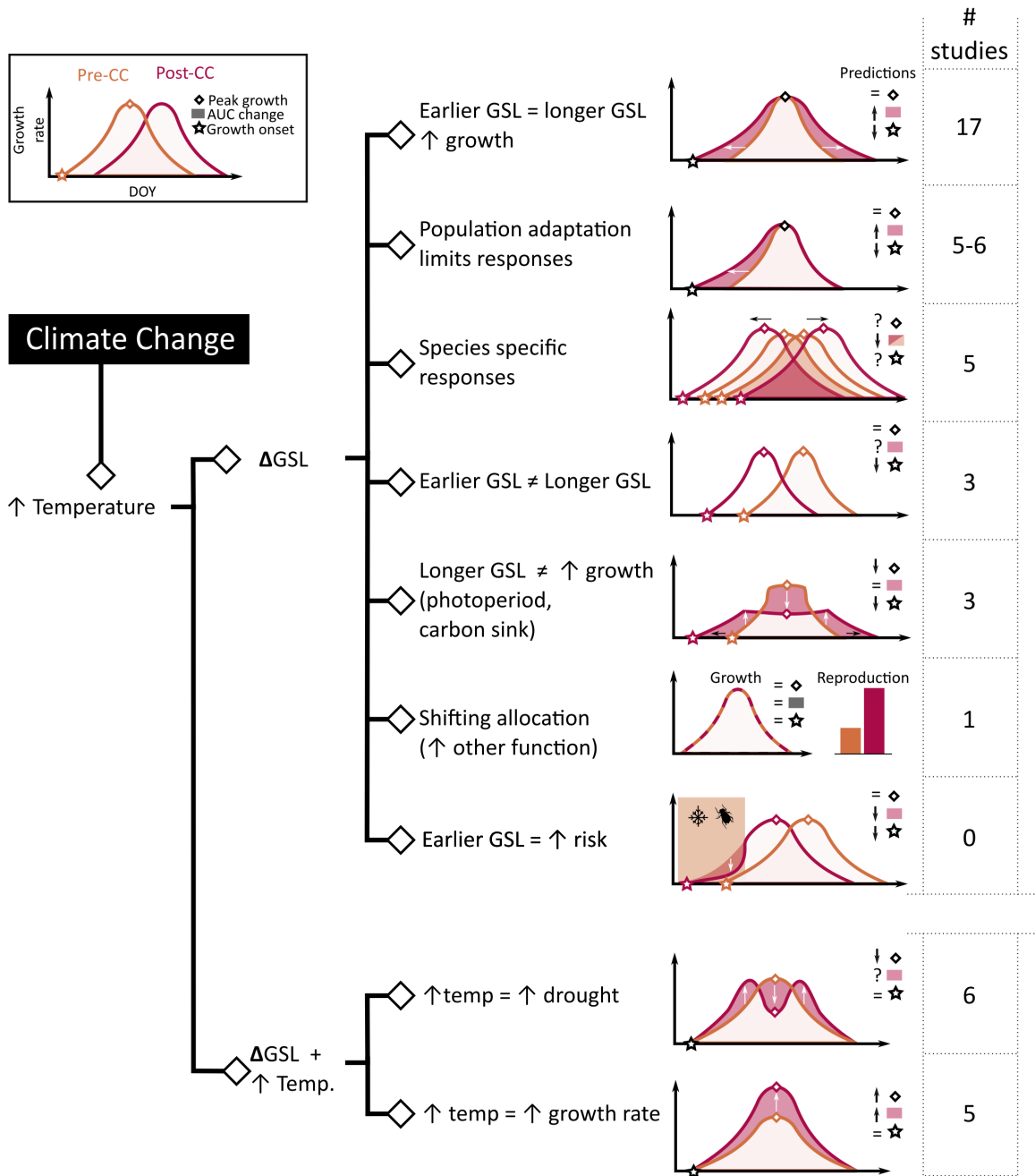


Figure 4: Pathways through which climate change could alter growing season length and growth.

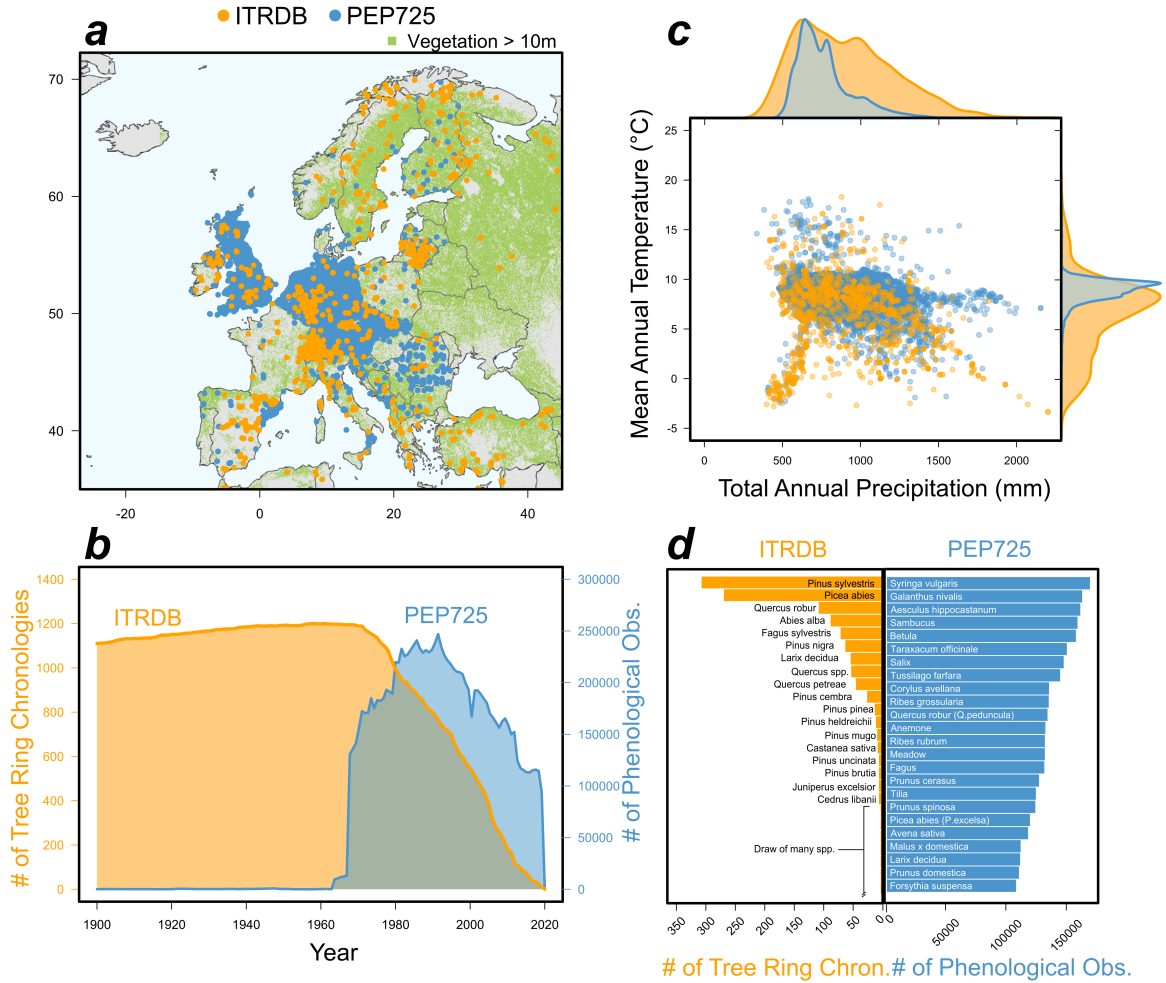


Figure 5: Data overlap between the two major databases of growth (International Tree Ring Data Bank, ITRDB, orange) and plant phenology (Pan European Phenology Project, PEP725, blue). Both databases are compared in terms of their spatial distributions (a), temporal overlaps (b), coverage of environmental 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**.
- Bruening, J.B., Tran, T.J., Bunn, A.G., Weiss, S.B. & Salzer, M.W. (2017) Fine-scale modeling of bristlecone pine treeline position in the great basin, usa. *ENVIRONMENTAL RESEARCH LETTERS* **12**.
- 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.
- 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.
- 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**.
- 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) Mastree+: 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.
- 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.
- 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.
- Schaber, J. & Badeck, F.W. (2002) Evaluation of methods for the combination of phenological time series and outlier detection. *Tree Physiology* **22**, 973–982.
- 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.
- 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., Mirzagholi, 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.