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

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**Abstract**

A number of recent studies have challenged the fundamental assumption that longer growing seasons lead to increased tree growth, raising concerns that forecasts of future climate change—which include increased carbon storage through this assumption—may be overly optimistic. In a review of recent literature, we found that 58% of studies supported the assumption of increased growth with longer seasons, while 36% of studies did not. Diverging results remained when holding methodology constant, which suggests the current major challenge is to understand the biological mechanisms that underlie this widespread variation. Studies have proposed a suite of hypotheses for why longer growing seasons may not always increase tree growth, including drought-related constraints and internal limits. These hypotheses and their underlying mechanisms, however, were generally tested in different ways by different fields, making comparisons difficult. We outline how bridging these current divides while simultaneously integrating ecological theory could yield new advances in fundamental biology and build a mechanistic framework for when longer seasons will—or will not—lead to greater growth, with major forecasting implications.

# Introduction

The idea that longer growing seasons lead to increased plant growth is an intuitive tenet across multiple fields of biology, including physiology, dendrochronology and ecosystem ecology (**??**). It is also a foundational assumption of many global carbon cycle models (e.g. **??**). These models project that continued anthropogenic warming will be partly offset by increased carbon sequestration as warming lengthens growing seasons in many forests (**?**), an assumption supported by ecosystem-scale studies (Chen *et al.*, 1999; Keenan *et al.*, 2014; Finzi *et al.*, 2020).

Yet recent work has questioned this longstanding assumption (e.g. Dow *et al.*, 2022; Green & Keenan, 2022; Silvestro *et al.*, 2023), with potentially large implications for future climate change. These recent studies challenge decades of research reporting increased growth with longer seasons, from observations along elevational and latitudinal gradients (**????**), classic experiments in lab settings (**?**), to trends in 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. **??**), including the complex nature of climate change (e.g. drought or heat stress, Dow *et al.*, 2022) and internal limits on plant growth (Zohner *et al.*, 2023).

Here we review methods and metrics used in diverse fields to uncover connections between growing season length and tree growth and identify the potential mechanisms that unite—and could disconnect—these processes. Results suggest that predictable—and substantial—variation in growth $\times$ season length relationships across species exist. However, we also find a pervasive disciplinary split between studies, which often test different mechanisms on different species, and overlook insights from community and phylogenetic ecology (e.g. **???**). We therefore argue that increased cross-disciplinary efforts would allow the field to rapidly develop a unified theoretical framework to predict when, where and how climate change may increase tree growth.

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

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

Multiple fields have long assumed that longer seasons yield more growth. Foundational evidence comes from spatial clines across elevation and latitude, with growth decreasing alongside growing season length at higher elevations (Fig. **??**) and latitudes. Experimentally, this assumption is supported by small-scale field warming studies that find that phenologically advancing species also grow more with warming (**?**), while observationally, ecosystem-scale studies have reported a similar positive relationship between season length and carbon fluxes across decades with global warming (Keenan *et al.*, 2014) or in years with warm, early springs (Chen *et al.*, 1999). However, some recent studies do not support these previous findings. These studies, which often focus on inter-annual correlations with metrics of standardized individual tree growth (Dow *et al.*, 2022; Silvestro *et al.*, 2023), have generated debate about whether future carbon storage forecasts are overestimated and which metrics of growth (Green & Keenan, 2022), or growing season length (**?**), are relevant.

Despite this recent debate, we found little support for a wholesale disconnect between growth and growing season length—instead finding split support for when longer seasons lead to increased growth. Papers spanning 25 years have variously found evidence for—or against—the relationship, with no clear pattern by method or year (Fig. **??** and see 'Literature review methods' in Supplement). For example, carbon assimilation studies were evenly split in finding evidence for or against the relationship (or simply not testing it, Fig. **??**). Diverging results were consistently found within methods, suggesting the drivers of this variation are likely due to biological mechanisms, not solely inconsistent definitions of growth or growing season length (as some, e.g. Green & Keenan, 2022; **?**, have recently suggested).

Most studies tested hypothesis that longer seasons with climate change increase growth via either increased time to grow (10 of 36 papers) or because longer seasons are usually warmer (8 papers), although many also considered hypotheses that could disconnect growth from season length. Studies from dendrochronology (the study of tree rings and their dating) and physiology have readily offered explanations for findings that increased growth may not be a universal outcome of longer seasons (Fig. **??**). External climatic drivers that offset the positive growth effects of longer seasons are often reported in tree ring studies (Kolář *et al.*, 2016; de Sauvage *et al.*, 2022; Camarero *et al.*, 2022). In particular, the hypothesis that higher temperatures paired with lower precipitation produce negative correlations of season length with growth appeared in 58% of tree ring studies we reviewed (and was only mentioned once outside of these studies, see also Fig. **??**). In contrast, 45% of lab experimental and wood phenology (xylogenesis) studies suggested fundamental internal constraints that prevent trees from responding to longer seasons (Fig. S1, Cuny *et al.*, 2012; Michelot *et al.*, 2012; Zohner *et al.*, 2023). Yet we found that these hypotheses have been tested in radically different ways, never together, and all ignore a suite of relevant research from other disciplines.

## Controllers on growth × season length relationships

Studies have uncovered a suite of major mechanisms that could limit or disrupt the positive effects of longer growing seasons. These generally fall into two categories: (1) external factors, such as drought, which should impact ecosystem-level trends at regional scales, and (2) internal physiological constraints, which some research suggests are either universal across plants (e.g. Zohner *et al.*, 2023), or species- and population-specific (e.g. Soolanayakanahally *et al.*, 2013). The importance of internal versus external drivers, however, likely vary by species, highlighting the need to integrate perspectives from community and phylogenetic ecology.

### External drivers

Fundamentally, temperature limits many biological processes. Temperatures that are too cool (below 5°C for temperate trees) and too warm (an area of active research, but likely between 35-45°C; **?**Cabon *et al.*, 2022) slow down biological processes and eventually can lead to tissue death (see Fig. **??**, **??**). Between these upper and lower limits, biological processes underpinning growth generally accelerate such that warming can have a direct effect, by accelerating biological time, up until the maximum rate for that particular process. Assuming a common growth response curve to temperature, increased growth should be predictable at an ecosystem level based on the current seasonal temperatures and the amount of warming.

Positive effects of longer seasons on growth, however, could be counteracted by moisture deficits from reduced precipitation or higher evaporative demand (commonly invoked in tree ring studies, Fig. **??**). Support for this hypothesis comes from negative correlations between growth and precipitation or other metrics related to plant access to water in tree ring studies (Kolář *et al.*, 2016; Etzold *et al.*, 2022). While we found drought limitation was far less considered in physiologically-focused studies, the mechanism is well supported by physiological observations that tree water status can be a biophysical limit to growth (i.e., cells cannot expand without sufficient turgor, **??**), driving diel correlations between vapor pressure deficit and growth (**??**).

Even without the complicating factor of soil moisture, the non-linear effect of temperature on photosynthesis can also limit growth responses (Fig. **??**). At very cool temperatures—such as in early spring—a small increase in temperature may have limited effect (or even increase frost risk, Fig. **??**e, **?**), while an increase at warmer temperatures—such as those more common in the summer (e.g. 16 to 18°C)—could have a larger physiological impact. However, warming that pushes plants beyond their optima, where many biological rates crash, could have large negative impacts (**??**). Thus, some studies hypothesize that longer seasons effectively only extend the very cool early-season periods and may have no discernible effect on growth, while other studies—based on tree rings—suggest that any increases in growth due to longer seasons are offset by reduced growth due to high summer temperatures (Fig. **??**, **?**Dow *et al.*, 2022). In contrast, other researchers argue that warmer temperatures have not yet pushed trees above their optima (**?**), and instead have driven increases in growth through accelerated rates, rather than longer seasons (e.g. Ren *et al.*, 2019).

Biotic interactions—including herbivory, disease and competition—can also act as external factors that 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 plant senescence (**?**). Plant pathogens are also known to respond to warming, and can limit productivity (**??**). These biotic drivers were rarely mentioned in studies examining growing season length (we found no mention of them, Fig. **??**e), but could increasingly limit growth as extended growing seasons allow for additional generations of pests and pathogens (**??**).

### Internal constraints

When and how growth is initiated and ceases is under genetic and developmental control, and thus plants' internal programming could limit growth responses to longer seasons (**?**McKown *et al.*, 2016; Soolanayakanahally *et al.*, 2013). Research has repeatedly shown that populations vary in their growth and its responses to extended seasons (Fig. **??**d), reflecting differences in genetic and developmental controls that likely evolved to limit tissue loss to rare early or late-season events. 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; **?**). This means longer seasons are generally driven by spring phenology, which appears far more flexible, and has advanced more rapidly than fall events (**?**). 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. Within populations, individual trees may also vary in how early or late they initiate (spring) or end (fall) growth. This can be driven by a shifting investment to growth, survival and/or reproduction with growth. For example, saplings, for which growth and survival are paramount, tend to both grow more rapidly (**?**) and have longer seasons relative to adult trees (**???**), which need to also invest in reproduction.

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

### Species-level variation

The effects of these external and internal drivers are likely to vary across species, a reality rarely acknowledged by most studies (Fig. **??**c). Species identity, however, strongly predicts variation in growth × season length relationships (e.g. Cuny *et al.*, 2012; Michelot *et al.*, 2012) and thus is likely critical for understanding the widespread observed variation. Biogeographical patterns in climate and assembly within communities also predict species should evolve towards different optima and different strategies (**??**). For example, leaf strategies (e.g. leaf mass per area, longevity) vary strongly between evergreen and deciduous species, but also within each group—where variation in 'determinacy' defines the timing and investment of shoot growth and leaf

emergence. Determinate species have most of their leaf material prebuilt in overwintering buds, generally unfolding their entire canopy within a few weeks each season, while indeterminate species continue to produce new shoots including leaves over the growing season (**??**). Such differences would influence the extent to which the growth of different species respond to increases in growing season length, even under identical conditions. Current studies span a wide range of species (we found 57 species from 26 genera across 36 papers), making the aim of identifying a common relationship between growth and growing season length with current studies especially difficult.

Phylogenetic ecology provides tools to study imprints of past selection, which often shape species-level differences today—limiting how well species are adapted to current conditions and potentially constraining their responses to rapidly changing conditions (**?**). Most studies testing for such effects of evolutionary history on plant responses find them (e.g. **?**), including new work on physiological traits (**?**), and previous physiological syntheses find results suggestive of strong phylogenetic relationships (e.g. **?**).

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

Predicting when and where longer seasons lead to increased growth may seem overwhelming given the diversity of potential drivers and complexity of species-level differences, but together they offer a set of testable hypotheses that could rapidly advance progress—if tackled with a more cross-disciplinary approach. Such changes may take time, but major hypotheses can be tractably tested now. Taking advantage of existing data sets and ongoing experiments could provide tests of variation in growth at relevant organizing levels—individuals, populations, species and ecosystems—to provide a benchmark when comparing the effect sizes of external drivers of variation (e.g. climate, pest outbreaks). 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. New experiments could also help address this gap and could be designed to directly compare effects of external versus internal drivers on growth. Combining observational and experimental data in models that build up from internal limits to external drivers and include species-level variation would then provide predictions while helping to refine theory. More tractable changes within fields would also help—the high variation in observed growth responses to longer seasons (Figs. **??**, S2) could be partly reduced through standardized measurements (see Box: Standardized measurements) and a broadening of perspective within fields (see 'Extending disciplinary focus' in Supplement).

### Using existing data and networks to partition levels of variation across drivers

Taking advantage of existing ecological and field global change experiments could help bridge across the two major fields currently studying growth × season length relationships—physiology and dendrochronology—and their contrasting timescales. We found most physiological studies of growth × growing season length relationships studied 1-2 years of dynamics, usually of juvenile trees, while tree ring studies focused on synthesizing across decades of adult tree growth.

Perhaps because of this dichotomy, tree ring studies often study lag effects, while they are rarely mentioned in physiological studies, but current large-scale experiments on heat (e.g. SPRUCE, **?**), moisture via drought or irrigation (e.g. DroughtNet, Pfynwald **?**) and other factors (e.g. $CO_2$ in FACE) have increasingly been used to test ecological 'memory' (e.g. **??**). They thus could help scale up from smaller and shorter-time scales of physiological studies, potentially to ecosystem-level dynamics, such as carbon cycling (**??**). Building on available data and infrastructure could also bridge this gap, for example, adding dendrometers to provenance studies (or other ways to measure growth, e.g., **?**) and locations with established phenological sampling and vice versa. Such efforts may be especially valuable in sites across elevational and latitudinal gradients (e.g. PSP, Feeley elevation network, Forest Inventory and Analysis). These sites in turn could be priority locations for xylogenesis and focused physiological studies.

Existing open data repositories could test predictions from community ecology for species-level variation in responses to external drivers. Combining large-scale databases of tree rings and vegetative phenology (e.g. the International Tree Ring Database, ITRDB, and the Pan European Phenology project, PEP725, see Fig. **??**) would provide a major spatially and temporally diverse dataset to compare how external climatic drivers, species and population together explain growth $\times$ season length relationships. While the low spatial and taxonomic overlap between these databases currently poses challenges (see 'Extending disciplinary focus' in Supplement), combining these datasets with theory from community ecology may also allow us to identify which species will grow more with longer growing seasons. Community ecology predicts trade-offs along an acquisitive to conservative axis, where some species grow rapidly and more flexibly to take advantage of resources, but are less defended against herbivores and compete poorly at low resource levels, whereas other species compete well at low resource levels, but at the expense of growing slower and conservatively (**?**). Integrating these perspectives within a broader framework would provide predictions that researchers could test from combined datasets, specifically that longer growing seasons will increase growth for species with regular reproduction (no masting, see also new masting database in **?**), an acquisitive strategy, from clades that are historically (on an evolutionary timescale) plastic, in locations that are warm—but not too warm—and moist.

### New experiments to tease apart external & internal drivers

Given the complex effects of external drivers and internal constraints on growth $\times$ growing season length relationships, fully disentangling them will likely require new experiments. Changes in growing season length covary with other environmental changes, in particular longer seasons are usually warmer seasons (**?**). Thus, experiments to robustly tease these drivers apart seem a paramount need, especially if done across multiple species spanning diverse strategies. Similarly, factorial experiments that manipulate season length (via early growth or delayed senescence), while additionally manipulating external abiotic (e.g. heat waves, droughts) and/or biotic (e.g. pests, competition) drivers could allow us to compare the effects of these drivers on tree growth. Such experiments could also test for lag effects, if sampled multiple years after the manipulations (versus the common practice of destructive sampling at the end of the treatment growing season). While such experiments are most easily done for juvenile trees, they could also be done on adult

trees, given investment in infrastructure.

Efforts to design and launch such large-scale experiments should start now. Long-term experiments on adult trees that manipulate temperature, precipitation and growing season length could test a suite of drivers at relevant lifestages. Such experiments could robustly compare drivers and become a resource for testing the underlying mechanisms for constraints, if properly measured and designed. This would mean careful measurements of carbon allocation, including to reproductive output, and tissue lost to frost and biotic drivers, and choosing species to maximize divergent strategies and provide the potential for genomic and related studies (e.g. *Populus, Quercus*). Given the potential role of evolutionary history, selecting for these varying strategies within a clade, or—if not feasible—correcting for phylogenetic distance would provide more robust tests of how strategies influence the growth × season length relationship. These highly measured experiments would represent a major investment to tackle this question in one location, and could form part of a broader network of sites to test these relationships at larger spatial scales. 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.

### Models that push forward theory and aid forecasting

Efforts to bridge observational trends with experimental insights will need statistical and more mechanistic models that can bridge across temporal and organismal scales while testing the major hypotheses. New statistical models should include the separate effects of temperature, moisture and growing season length while partitioning individual, population and species-level variation—thereby providing broad-scale estimates of the effects of the major external drivers versus potential internal constraints (which may be apparent as within-season and/or population differences). Including species-level effects while also integrating phylogenetic relationships between species could then test for the role of evolutionary history in shaping responses, while adding in site × year-level effects of biotic disturbances could begin to compare across abiotic and biotic external drivers. Such models should be built alongside a suite of mechanistic process-focused models that scale up. For example, one model could build from carbohydrate balance and cell division (e.g. Locosselli & Buckeridge, 2017) to predict growth dynamics observed in xylogenesis, while another could build from phenology, including frost disturbance and reproduction, to predict growth for different species (e.g. **?**).

The success of modeling approaches will likely depend on how nimbly they respond to new findings and how well they make predictions for new studies to test, which likely requires bridging across statistical and mechanistic models. As new experiments identify potential internal growth constraints and what level they operate on (universal, population or otherwise), both statistical and physiological process models should be adapted, improved and interconnected. Currently, statistical models are often overly disconnected from our biological understanding of tree growth (for example, using linear models for non-linear processes, Fig. **??**) while process-models are often so complex that they cannot clearly provide testable predictions for empirical data. Together the integration of statistical and more mechanistic process-focused models would provide major insights into the fundamental biology of how tree growth shifts with extended seasons—and

yield a unified model for robust predictions of growth responses to warmer, longer seasons across species and levels of warming.

*Conclusions:* Anthropogenic climate change has often been described as an unfortunate and unplanned experiment. Like many experiments, 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, time and a suite of external and internal drivers affect plant growth. The task may seem large, but bridging across theory and data from dendrochronology, physiology, community and phylogenetic ecology 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 Boxes

### Box. Standardized measurements

Understanding the diverse drivers and testing underlying hypotheses (Fig. **??**) for growth × growing season length relationships requires a common language. We found 14 different metrics of start, 16 metrics of end of season (25 metrics of growing season length), and 21 different metrics of growth across 59 studies—highlighting just part of the problem (see also *The challenge of metrics: Measuring growth* in the Supplement). Definitions and metrics for external and internal drivers were myriad, with papers reporting dozens of tests of different aspects of climate over different temporal windows. Although this is understandable given the differing goals of these papers, it also slows progress.

A common framework for explanatory and response variables 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 × growing season length relationships (Fig. **??**), often instead testing only certain hypothesized indirect relationships (e.g. spring temperature × growth in Dow *et al.*, 2022).

## 2 Figures

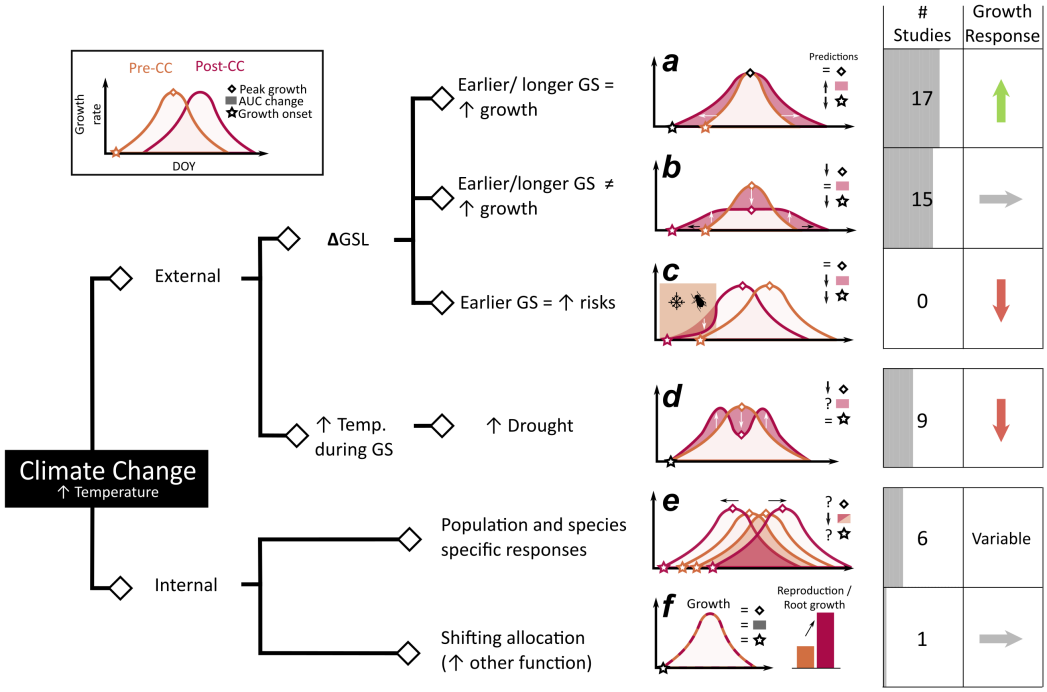


Figure 1: Pathways through which climate change could alter growing season length and growth, with the number of papers we found mentioning each hypothesis from a review of growth × growing season length relationship studies (for more details, see Supplement).

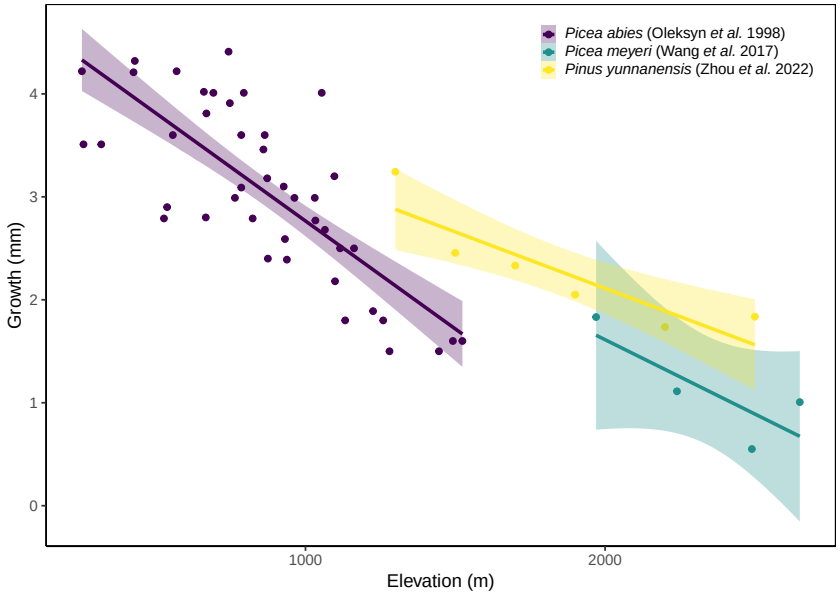


Figure 2: Growth × elevation relationships from the literature with simple linear regression fits shown with 89% confidence intervals. Oleksyn *et al.* (1998) measured growth (mm) as diameter at breast height increments, while the other studies (Wang *et al.*, 2017; Zhou *et al.*, 2022) measured it as ring width. See Supplement for more methods details.

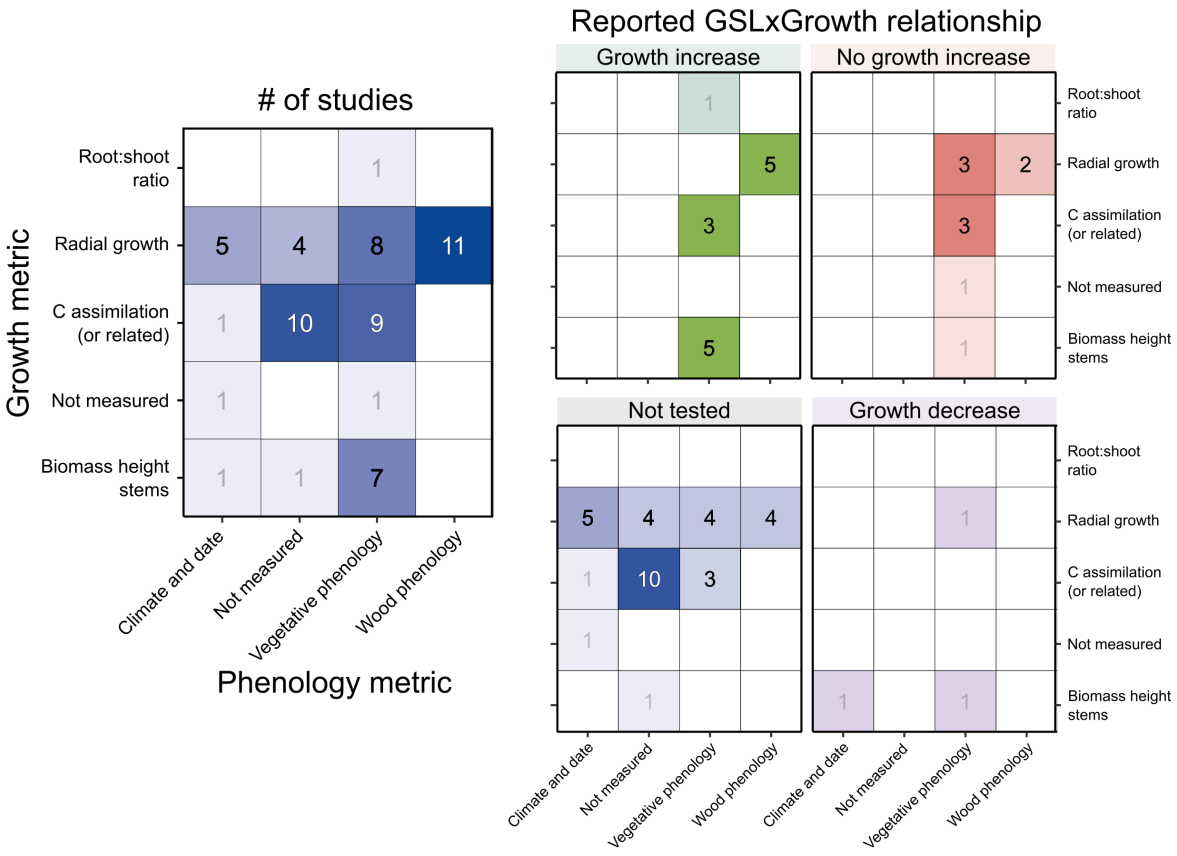


Figure 3: A review of growth × growing season length relationship studies spanned a diversity of methods, but there was no coherency in which methods did or did not find a positive relationship. A number of studies tested relationships possibly related to growth × growing season length (e.g., they tested how spring temperatures related to growth) but never directly growth × growing season length, thus 'not tested' was surprisingly common across methods. See Supplement for review details.

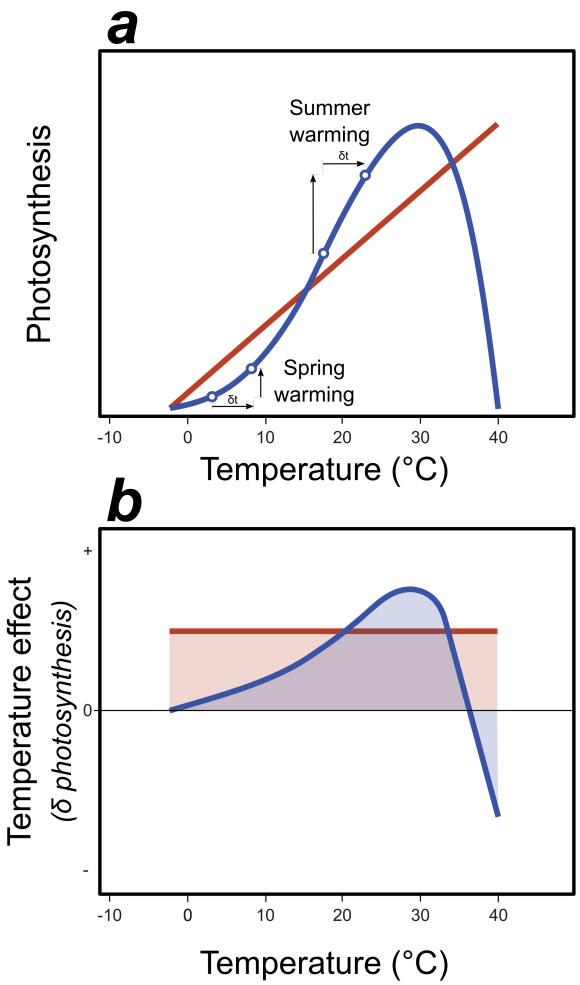


Figure 4: (a) Growth responses to temperature depends on a suite of complex factors and is often represented as net photosynthesis, which has a non-linear response to temperature (blue curve, adapated from meta-analysis of **?**), though it is often modeled as linear (red). (b) This non-linearity means that increases in lower temperatures—such as those in the spring when much of growing season extensions may happen–have a lower absolute increase in photosynthesis compared to increases in later-season (e.g., summer) warmer temperatures, while a linear response assumes a constant scale of effect across low to high temperatures.

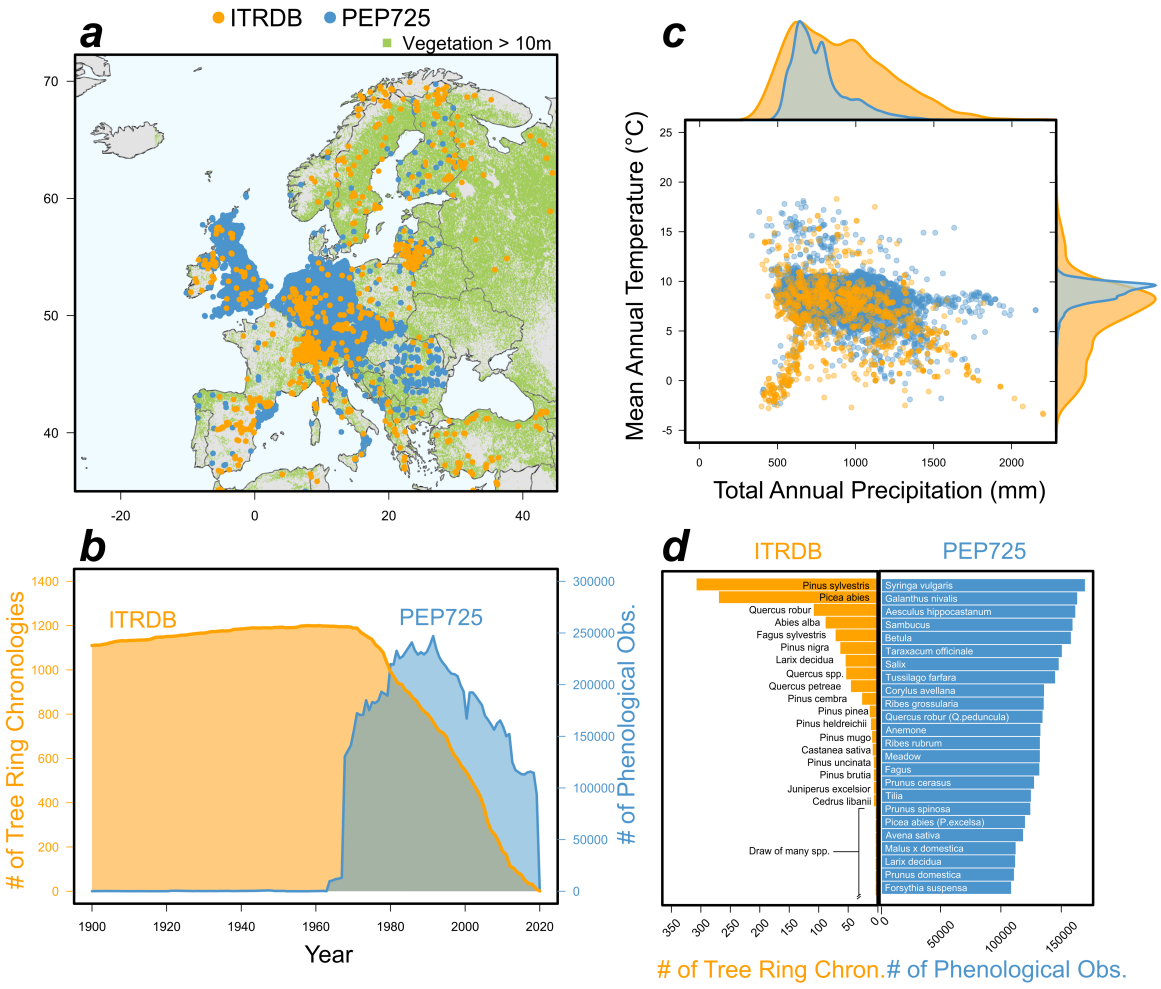


Figure 5: Data overlap between the two major databases of growth (International Tree Ring Data Bank, ITRDB, orange) and plant phenology (Pan European Phenology Project, PEP725, blue). Both databases are compared in terms of their spatial distributions (a), temporal overlaps (b), coverage of environmental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

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