Supplement: Why longer seasons with climate change may not increase tree growth

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Literature review methods

We conducted a review to find studies focused on relationships between growing season length and tree wood growth, though contrasting terminology made it challenging to identify papers through one search. After reviewing several recent papers (Dow *et al.*, 2022; Zohner *et al.*, 2023), we searched ISI Web of Science for "growing season length" AND "tree ring*" (ALL FIELDS) on 12 April 2023, which returned 33 citations. We next reviewed abstracts and discarded papers that did not mention the relationship between growing season length and growth. We further reviewed all citations within all papers for additionally relevant papers and included them in our review. In total we report on 36 papers after reviewing over 107 potentially relevant papers and discarding one paper (Bruening *et al.*, 2017, which used tree lines as a metric of both growth and growing season length).

Given the large diversity of metrics we found, we did not extract quantitative estimates of growing season length, growth, or their relationship. Instead, we extracted data on location, species, how they measured growing season length, growth, what relationship they found and what internal and external drivers they mentioned (full dataset with more details available on the Knowledge Network for Biocomplexity at publication).

Papers often reported dozens or more statistical tests from different analyses of data or different types or subsets of data, thus we recorded a unique meta-analytic observation within each paper (which we call a 'study') when papers reported: (1) distinctly different datasets (e.g., a global analyses of observations and a short-term experiment); (2) multiple distinctly different measures of growth (e.g., tree ring width and flux tower) and/or growing season length (e.g., they reported both end of season as budset and end of wood growth through xylogenesis); (3) distinctly different results for growth $\times$ growing season length depending on metric (e.g., using budset for growing season length they find a growth $\times$ growing season length relationship, but using leaf coloring they do not).

We returned to the papers to also assess them for which hypotheses they addressed. For this, we reviewed papers for stated hypotheses and/or analogous research questions that were specifically addressed in the results (e.g. hypothesis testing). After this we grouped each hypothesis to a broader main hypothesis (or hypothesis cluster) displayed in Fig. **??**. We extracted all hypotheses/questions from each paper, resulting in many papers had more than one hypothesis (11 of 36 papers).

Trends with year

Across studies which found support for or against a relationship between growth and growing season length (40 of 59 total studies) the range of years was very similar: spanning 2000 to 2023 with a mean of 2017 for studies that found a positive relationship and spanning 2012 to 2023 with a mean of 2020 for studies that did not. Further, we found no trend through time for finding a positive or negative relationship through logistic regression (slope strongly overlapped 0).

1 Growth × elevation relationships

Using Google Scholar and ISI Web of Science, we searched the literature for studies of tree growth, especially via diameter or ring width, by elevation or latitude. Of 20 papers we found for these relationships, six included clear raw tree data in either scatterplots or tables that we scraped: Oleksyn *et al.* (1998); Huang *et al.* (2010); Cavin & Jump (2017); Wang *et al.* (2017); Zhu *et al.* (2018); Zhou *et al.* (2022).

We could not scrape data from 14 papers for the following reasons:

1. Absence of observational tree growth raw data: Some studies only presented the correlation or the data was modeled.
2. Measures other variables: Some studies examined leaf area index and forest NPP.
3. Standardization of tree growth with other variables: Papers did not present the raw data (e.g., papers presented the data calculated with other variables).
4. Presence of overlapping data points: Data points in the plots presented were not visually identifiable for accurate data scraping.
5. Line graphs: No discrete data points for image processing.
6. Geographical scale: The locations of data collection spread across large longitudinal or latitudinal gradient.

We scraped tree growth data from the selected studies using the Fiji image processing package with the Figure Calibration plugin. We calibrated x and y axis using the Figure Calibration plugin, followed by measuring growth values at different elevation using the measure function in Fiji. Of the six remaining papers, we show results for three, excluding Huang *et al.* (2010) because it included only results for trends by latitude (and most other studies included only trends by elevation), and Cavin & Jump (2017); Zhu *et al.* (2018) because the elevation co-varied with latitude.

Thus, we show data from: Oleksyn *et al.* (1998), which measured 54 populations of *Picea abies* along 8 altitudinal transects in Southern Poland, we present the mean DBH (cm yr^{-1}) of values collected from each population (although 54 populations were monitored, only 42 data points were clearly visible in Figure 2 in the paper); Wang *et al.* (2017), which collected tree cores (37-100 years) collected from 4 different sites across an elevation gradient in the Luyashan Mountains in North China, we present the median of tree ring width values from the collected cores (147 tree cores collected from 73 trees); and Zhou *et al.* (2022), who collected tree ring width data (cores of 60-80 years) of *Pinus yunnar* from 6 altitudinal transects in Yunnan, China; we present the median of tree ring width of each transect.

2 The challenge of metrics: Measuring growth

Tree growth, which can be measured in a variety of ways, highlights how the diversity of current metrics slows a unified model of when growth increases with longer seasons. 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.* (2000b) estimated photosynthese 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.

3 Extending disciplinary focus to help bridge the internal-external drivers divide

Each field studying growth × growing season length today has its own historical aims, and thus, its own biases towards certain species, methods and metrics. For example, dendrochronology's original focus on using tree growth to estimate climate has led to sampling biases (e.g. to 'climate-sensitive' individual trees, Klesse *et al.*, 2018; Nehrbass-Ahles *et al.*, 2014) and statistical detrending (Rollinson *et al.*, 2021), which may obscure patterns where the signal of longer growing seasons and biotic drivers may be most apparent (such as rapid growth phases, **?**) Dendrochronology also generally focuses on conifers (gymnosperms, Zhao *et al.*, 2019), creating a major split from most studies of leaf phenology, which focus almost entirely on deciduous angiosperm species (see Fig. **??**). By contrast, phenology research has been strongly focused on spring events (e.g. budburst, leafout), with limited data on fall events and thus limited data to calculate growing season length. This focus on spring events may have been justified decades ago, when most shifts from anthropogenic warming occurred in the spring, but less justified as increasing research suggests important complexity in fall shifts (Gill *et al.*, 2015; Zohner *et al.*, 2023) and a need to scale up phenological research to understand tree growth.

These field-specific historical trends limit the opportunities for interdisciplinary insights. For example, dendrochronology studies generally eliminate much of the drivers that physiological studies focus on, while physiological studies often fail to make predictions that scale up (e.g., to adult trees or for diverse species). Opportunities to overlap dendrochronology time records with metrics of growing season length measured through vegetative phenology appear high (Fig. **??**), but sampling biases towards conifers in one and angiosperms in the other field limit current opportunities. All fields could therefore benefit from tackling the challenge of understanding the physiological connections between growing season length and growth, and even the genetic and developmental underpinnings of these connections. To date, much work has focused on measures of growth and phenology without a clear mechanistic understanding of what triggers growth and its cessation, and how these triggers and responses have evolved. Progress in this area could be particularly important for making projections, as extrapolating can be dangerous when the underlying mechanistic model is wrong. Physiological studies that follow carbohydrate balance and cell division (see Locosselli & Buckeridge, 2017) versus growth dynamics could yield insights, as could additional work on xylogenesis—especially if done with a focus both to extrapolate to long-term tree ring studies and/or in physiological experiments (Fang *et al.*, 2020; Simard *et al.*, 2013). Expanding beyond the current disciplines focused on this topic could also be informative. For example, a clearer physiological understanding of which environmental stimuli trigger leaf expansion, senescence, woody growth, and heartwood formation alongside an evolutionary perspective could advance understanding of growth constraints (Baas & Wheeler, 2011; Eckert *et al.*, 2019; Ensminger *et al.*, 2015; Juvany *et al.*, 2013).

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Figures

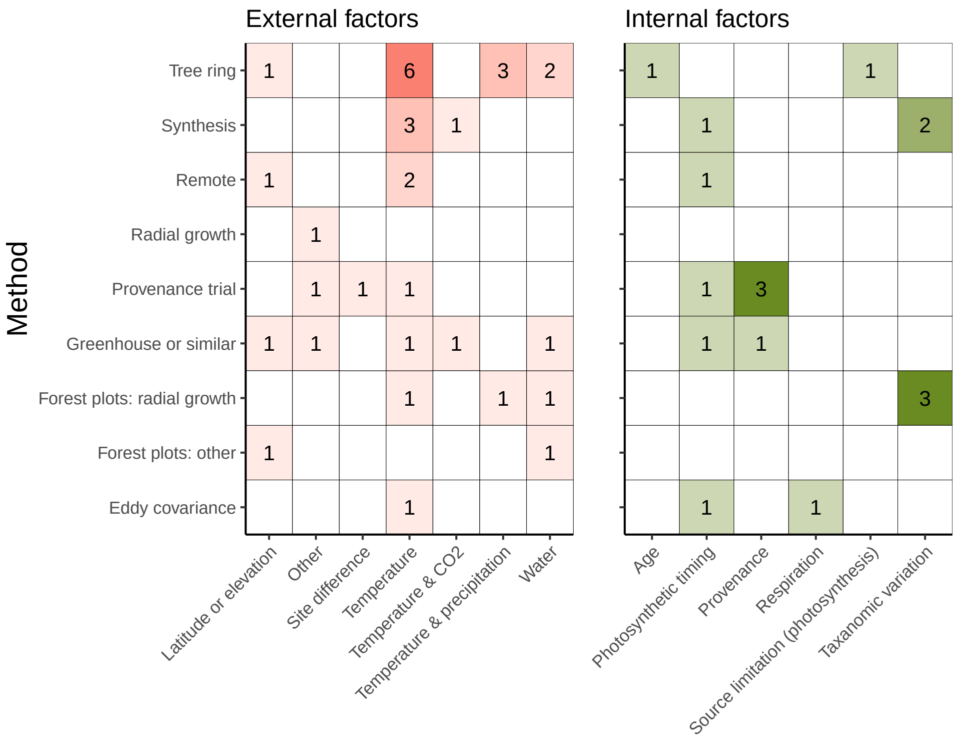

Figure S1: A review of the prevalence of external (left) and internal (right) drivers mentioned in studies from our literature review, grouped by the general methods used. Many studies tested related hypotheses by measuring different drivers (e.g., latitude or elevation), so we combined similar external and internal factors for clearer comparisons.

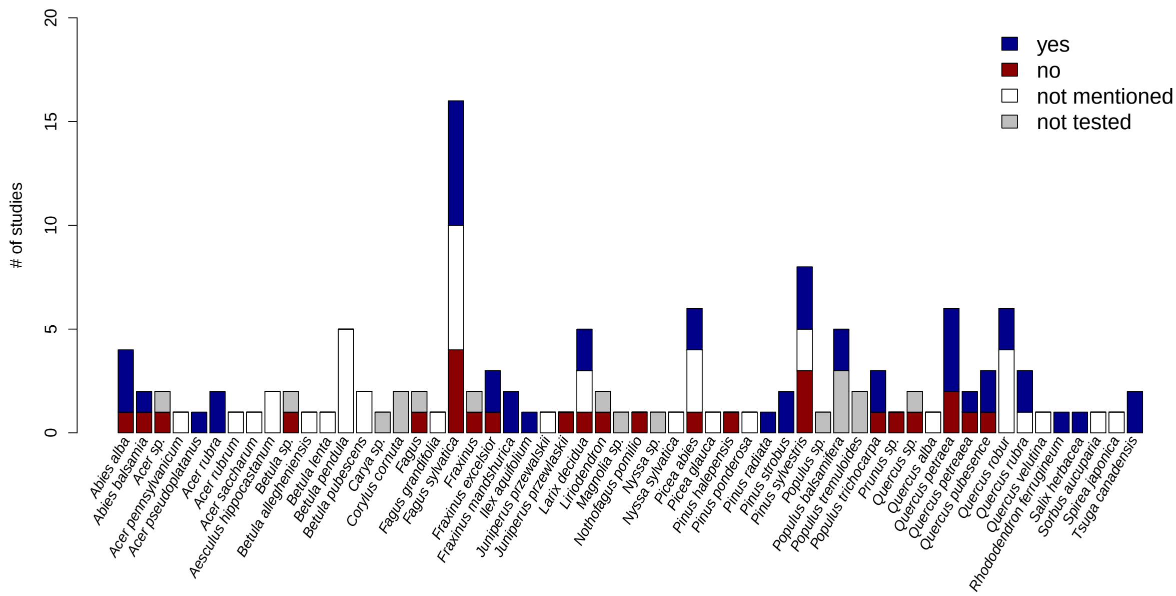

Figure S2: Results of whether studies found a relationship between growth and growing season length were generally inconsistent across and within species. 'Yes' indicates a study found a positive growth × growing season length relationship, while a 'no' means they did not. A number of studies tested 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, which are indicated by 'not tested.'

Table S1: **Hypotheses and references for studies in our database.**

Hypothesis	Number of Studies	References
Longer growing season = more growth	10	(Camarero *et al.*, 2022; Chen *et al.*, 2000a; Čufar *et al.*, 2015; Delpierre *et al.*, 2017; de Sauvage *et al.*, 2022; Gao *et al.*, 2022; Grossiord *et al.*, 2022; Keenan *et al.*, 2014; Silvestro *et al.*, 2023; Wheeler *et al.*, 2016)
More temp = more drought (drought limitation)	10	(Brand *et al.*, 2022; Buermann *et al.*, 2018; Camarero *et al.*, 2022; de Sauvage *et al.*, 2022; Drew & Downes, 2018; Eckes-Shephard *et al.*, 2021; Etzold *et al.*, 2022; Kolář *et al.*, 2016; Oddi *et al.*, 2022; **?**)
Higher temp = more growth (temp limitation)	8	(Camarero *et al.*, 2022; Dow *et al.*, 2022; Finzi *et al.*, 2020; Moser *et al.*, 2010; Richardson *et al.*, 2010; Soolanayakanahally *et al.*, 2013; Stridbeck *et al.*, 2022; Zhang *et al.*, 2021)
shift of whole pheno sequence	6	(Delpierre *et al.*, 2017; de Sauvage *et al.*, 2022; Richardson *et al.*, 2010; Soolanayakanahally *et al.*, 2013; Zani *et al.*, 2020; Zohner *et al.*, 2020)
effect of growth rate not equal to growth duration	5	(Cuny *et al.*, 2012; de Sauvage *et al.*, 2022; Francon *et al.*, 2020; Michelot *et al.*, 2012; Ren *et al.*, 2019)
internal constraints (including pop, photo)	5	(Moser *et al.*, 2010; Sebastian-Azcona *et al.*, 2020; Soolanayakanahally *et al.*, 2013; Vitasse *et al.*, 2009; Zohner *et al.*, 2023)
Carbon fertilization	3	(Chen *et al.*, 1999; Finzi *et al.*, 2020; Oddi *et al.*, 2022)
species-specific responses	3	(Cuny *et al.*, 2012; Etzold *et al.*, 2022; Michelot *et al.*, 2012)
shift in allocation	1	(McKown *et al.*, 2016)