

Why longer seasons with climate change may not increase tree growth

E.M. Wolkovich¹, Ailene K. Ettinger², Alana Chin³, Catherine J. Chamberlain⁴,
Frederik Baumgarten¹, Kavya Pradhan^{5,6}, Rubén D. Manzanedo⁷⁻⁹ &
Janneke Hille Ris Lambers⁷

January 25, 2025

¹ Forest & Conservation Sciences, Faculty of Forestry, University of British Columbia, 2424 Main Mall, Vancouver, BC V6T 1Z4, Canada

² The Nature Conservancy of Washington, 74 Wall Street, Seattle, WA USA

³ California State Polytechnic University, Humboldt. Department of Biological Sciences. Arcata, CA, USA

⁴ The Nature Conservancy, 334 Blackwell St Ste 300, Durham, NC, USA

⁵ Department of Biology, University of Washington, Seattle, WA, 98195

⁶ Moore Center for Science, Conservation International, Arlington, VA, 22202

⁷ Institute for Integrative Biology, ETH Zürich, 8092 Zürich, Switzerland

⁸ Institute of Plant Sciences, University of Bern, Bern, Switzerland

⁸ Oeschger Center for Climate Change Research, University of Bern, Bern, Switzerland

Author contributions: All authors conceived of the idea, prepared the literature review, edited the manuscript and contributed to designing figures; in addition EMW wrote the manuscript, AKE, AC, CJC and EMW synthesized the literature review, RD led developing Fig. 1 and 5, AKE and EMW developed Figure 2, CJC developed Fig 3, AC, RD and EMW led developing Fig. 4.

Abstract

A number of recent studies have challenged the 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 what underlies 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 on different species, making comparisons difficult. We outline how bridging these current divides while simultaneously integrating evolutionary history and ecological theory could yield new advances and build a unified model across species for when longer seasons will—or will not—lead to greater tree 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 (Nobel *et al.*, 1983; Frank *et al.*, 2022). It is also a foundational assumption of many global carbon cycle models (e.g. Ito *et al.*, 2020; Friedlingstein *et al.*, 2022). These models project that continued anthropogenic warming will be partly offset by increased carbon sequestration as warming lengthens growing seasons in many forests (Friedlingstein *et al.*, 2022), an assumption supported by ecosystem-scale studies (Chen *et al.*, 1999; Keenan *et al.*, 2014; Finzi *et al.*, 2020).

24 Yet recent work has questioned this longstanding assumption (e.g. Dow *et al.*, 2022; Green
 25 & Keenan, 2022; Silvestro *et al.*, 2023), with potentially large implications for future climate
 26 change. These recent studies challenge decades of research reporting increased growth with
 27 longer seasons, from observations along elevational and latitudinal gradients (Myneni *et al.*, 1997;
 28 Berdanier & Klein, 2011; King *et al.*, 2013; Cuapio-Hernández *et al.*, 2022), classic experiments
 29 in lab settings (Went, 1957), to trends in ecosystem fluxes with warming (Chen *et al.*, 1999;
 30 Keenan *et al.*, 2014; Finzi *et al.*, 2020). Proposed mechanisms for the apparent disconnect are
 31 diverse (Fig. 1), including the complex nature of climate change (e.g. drought or heat stress,
 32 Dow *et al.*, 2022) and internal limits on plant growth (Zohner *et al.*, 2023).

33 Here we review how different fields have studied the relationship between growing season length
34 and tree growth to identify the potential mechanisms that unite—and could disconnect—these
35 processes. Working across multiple definitions of growth and growing season length (see Box),
36 we find results that suggest substantial variation in growth \times season length relationships across
37 species. We also find a pervasive disciplinary split between studies, which often test differ-
38 ent mechanisms on different species. Current work often implicitly ignores the importance of

39 community and phylogenetic ecology to plant growth (e.g. Grime, 1977; Webb *et al.*, 2002; Ávila-
40 Lovera *et al.*, 2023), which could aid the search for a universal model when studying different
41 species. We show how increased cross-disciplinary efforts to build a model across species would
42 allow the field to rapidly develop a framework to predict when, where and how climate change
43 may increase tree growth.

44 Evidence that longer seasons increase plant growth, or not

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

49 Foundational evidence comes from spatial clines across elevation and latitude, with growth
50 decreasing alongside growing season length at higher elevations and latitudes (Fig. 2). Ex-
51 perimentally, this assumption is supported by small-scale field warming studies that find that
52 phenologically advancing species also grow more with warming (Cleland *et al.*, 2012), while
53 observationally, ecosystem-scale studies have reported a similar positive relationship between
54 season length and carbon fluxes across decades with global warming (Keenan *et al.*, 2014) or in
55 years with warm, early springs (Chen *et al.*, 1999). However, some recent high-profile studies
56 find no support for this relationship (Dow *et al.*, 2022). These studies, which often focus on
57 inter-annual correlations with metrics of standardized individual tree growth (Dow *et al.*, 2022;
58 Silvestro *et al.*, 2023), have generated debate about whether future carbon storage forecasts are
59 overestimated and which metrics of growth (Green & Keenan, 2022), or growing season length
60 (Körner *et al.*, 2023), are relevant (Fig. , see Box).

61 Despite this recent debate, we found that longer seasons lead to increased growth in a slight
62 majority of papers spanning 25 years. Though the number of papers directly addressing this topic
63 is small, we found studies have variously found evidence for—or against—the relationship, with
64 no clear pattern by method or year (Fig. 3 and see ‘Literature review methods’ in Supplement).
65 For example, carbon assimilation studies were evenly split in finding evidence for or against
66 the relationship (or simply not testing it, Fig. 3). Diverging results were consistently found
67 within methods, suggesting the drivers of this variation are likely due to biological mechanisms,
68 not solely inconsistent definitions of growth or growing season length (as some have recently
69 suggested, e.g. Green & Keenan, 2022; Körner *et al.*, 2023, see also Fig.).

70 Most studies tested the hypothesis that longer seasons with climate change increase growth via
71 either increased time to grow (10 of 36 papers) or because longer seasons are usually warmer (8
72 papers), although many also considered hypotheses that could disconnect growth from season
73 length. Studies from dendrochronology (the study of tree rings and their dating) and physiology
74 have readily offered explanations for findings that increased growth may not be a universal

75 outcome of longer seasons (Fig. 1). External climatic drivers that offset the positive growth
76 effects of longer seasons are often reported in tree ring studies (Kolář *et al.*, 2016; de Sauvage
77 *et al.*, 2022; Camarero *et al.*, 2022). In particular, the hypothesis that higher temperatures paired
78 with lower precipitation produce negative correlations of season length with growth appeared
79 in 58% of tree ring studies we reviewed (and was only mentioned once outside of these studies,
80 see also Fig. 1). In contrast, 43% of lab experimental and wood phenology (xylogenesis) studies
81 suggested fundamental internal constraints that prevent trees from responding to longer seasons
82 (Fig. ??, Cuny *et al.*, 2012; Michelot *et al.*, 2012; Zohner *et al.*, 2023). Yet we found that these
83 hypotheses have been tested in radically different ways on different species, never together, and
84 ignore a suite of relevant research from other disciplines.

85 **Controllers on growth × season length relationships**

86 Major mechanisms that could limit or disrupt the positive effects of longer growing seasons
87 generally fall into two categories: (1) external factors, such as drought, which should impact
88 ecosystem-level trends at regional scales, and (2) internal physiological constraints, which some
89 research suggests are either universal across plants (e.g. Zohner *et al.*, 2023), or species- and
90 population-specific (e.g. Soolanayakanahally *et al.*, 2013). While we address each in turn, these
91 drivers clearly operate together. Further, the importance of internal versus external drivers
92 likely varies by species, highlighting the need to integrate perspectives from community and
93 phylogenetic ecology.

94 **External drivers**

95 Temperature limits many biological processes. Temperatures that are too cool (below 5°C for
96 temperate trees) and too warm (an area of active research, but likely between 35-45°C; Martinez-
97 Meier *et al.*, 2008; Cabon *et al.*, 2022) slow down biological processes and eventually can lead to
98 tissue death (see Fig. 5, Larcher, 1980; Kramer, 2012). Between these upper and lower limits,
99 biological processes underpinning growth generally accelerate such that warming can have a
100 direct effect, by accelerating biological time, up until the maximum rate for that particular
101 process. Assuming a common growth response curve to temperature, possible increased growth
102 should be predictable at an ecosystem level based on the current seasonal temperatures and the
103 amount of warming (Fig. 6).

104 How much or whether growth increases at all depends on the non-linear effect of temperature
105 on biological processes (Fig. 5). At very cool temperatures—such as in early spring—a small in-
106 crease in temperature may have limited effect (or even increase frost risk through early budburst,
107 Fig. 1e, Chamberlain *et al.*, 2021), while an increase at warmer temperatures—such as those
108 more common in the summer (e.g. 16 to 18°C)—could have a larger physiological impact. How-
109 ever, warming that pushes plants beyond their optima, where many biological rates crash, could
110 have large negative impacts (Nobel *et al.*, 1983; Leuning, 2002). Thus, some studies hypothesize

that longer seasons effectively only extend the very cool early-season periods and may have no discernible effect on growth (with varying definitions of growth, see Box), while other studies—based on tree rings—suggest that any increases in growth due to longer seasons can be offset by reduced growth due to high summer temperatures (Fig. 1, Gantois, 2022; Dow *et al.*, 2022). In contrast, other researchers argue that warmer temperatures have not yet pushed trees above their optima (Schabier & Badeck, 2002), and instead have driven increases in growth through accelerated rates, rather than longer seasons (e.g. Ren *et al.*, 2019), or through a combination of both.

Positive effects of longer—or warmer—seasons on growth predicted from temperature responses alone, however, could be counteracted by other external drivers. Moisture deficits from reduced precipitation or higher evaporative demand (commonly invoked in tree ring studies, Fig. 1) can slow or stall growth. 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), and 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, Peters *et al.*, 2021; Cosgrove, 2023), though we found few physiological studies on season length that considered this effect (Fig. 3). External biotic factors are also shifting with longer seasons—including herbivory, disease and competition (Mitton & Ferrenberg, 2012; Lange *et al.*, 2006; Cleland & Wolkovich, 2024)—and can limit productivity (Sturrock *et al.*, 2011; La Porta *et al.*, 2008; Senf *et al.*, 2017), though they are missing from the current debate on the impacts of longer seasons on growth (we found no mention of them, Fig. 1e).

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 (Howe *et al.*, 2003). Research has repeatedly shown that populations vary in their growth and its responses to extended seasons (Fig. 1d), reflecting differences in genetic and developmental controls that likely evolved to limit tissue loss to rare early or late-season events (Mitton & Ferrenberg, 2012; Lange *et al.*, 2006; Cleland & Wolkovich, 2024). Populations often vary predictably in their end-of-season phenology, with more poleward populations tending to stop height growth (budget) earlier using locally adapted photoperiod cues (Soolanayakanahally *et al.*, 2013; Aitken & Bemmels, 2016). This means longer seasons are generally driven by spring phenology, which appears far more flexible, and has advanced more rapidly than fall events (Aitken & Bemmels, 2016). Some recent studies suggest novel roles for the summer solstice (Zohner *et al.*, 2023) in setting a fixed universal developmental switch between when warming temperatures hasten or delay leaf senescence, and in determining when warmer temperatures trigger greater reproduction (Journé *et al.*, 2024).

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

149 reproductive output can reduce growth (Thomas, 2011; Hacket-Pain *et al.*, 2016a). For species
150 that mast—producing abundant cones or fruits in only some years—high reproduction could
151 especially impact measures of wood growth. Higher summer temperatures may trigger masting
152 in the following year (Hacket-Pain *et al.*, 2016a,b); if true, then reduced growth in years following
153 warm summers may not indicate temperatures too high for growth, as recent studies have
154 suggested (e.g. Gantois, 2022; Dow *et al.*, 2022), but instead shifting investment to reproduction.

155 Species-level variation

156 The effects of these external and internal drivers are likely to vary across species, with species
157 identity strongly predicting variation in growth \times season length relationships (e.g. Cuny *et al.*,
158 2012; Michelot *et al.*, 2012). Though this reality was rarely acknowledged in studies we reviewed
159 (Fig. 1c), research in dendrochronology, physiology and in phenology often mentions important
160 differences between certain species groups that should affect how longer seasons affect growth.

161 The distinct strategies of deciduous versus evergreen species, including in how and when they
162 invest in leaf and shoot elongation versus cambial growth, can affect how they respond to longer
163 seasons. While evergreen species generally leaf out later than deciduous species they can more
164 immediately photosynthesize with earlier springs, though both types of species generally invest
165 in buds (for new leaves, shoots and flowers) in the preceding year. This means neither can
166 rapidly change their investment in leaf area in response to an earlier spring, but both can have
167 multiple flushes of leaves (Day & Greenwood, 2011; Soolanayakanahally *et al.*, 2013). Wood
168 growth in evergreen species is generally thought to come from current season photosynthate,
169 while deciduous species may more often use stored carbon resources (Gordon & Larson, 1968;
170 Monson *et al.*, 2018). These differences would suggest season length by growth relationships
171 may be most apparent via lagged effects in deciduous species, but this is rarely studied (and not
172 clearly supported to date Coulthard *et al.*, 2020; Klesse *et al.*, 2023). Further, evergreen species
173 are thought to grow more slowly and thus differences due to season length may be harder to
174 detect (Waring & Franklin, 1979).

175 This division between evergreen and deciduous species hints at a larger suite of traits that predict
176 growth by growing season length relationships among species. Species that budburst earlier and
177 more readily produce additional leaves (e.g., leaf flushes after budset, and other characteristics
178 more common to ‘indeterminate’ species, Kikuzawa, 1982; Lechowicz, 1984) may grow more with
179 longer seasons (though potentially with a lag, see Box, Fig.) versus those that budburst later
180 and flush new primary growth only once. Similarly, species adapted to cold, dry or high latitude
181 conditions across their range may have different thresholds for when these external drivers limit
182 or promote growth (e.g., some *Populus* and *Quercus* species, Soolanayakanahally *et al.*, 2013;
183 McKown *et al.*, 2016; Delpierre *et al.*, 2017; de Sauvage *et al.*, 2022). Such differences could
184 easily obscure any overall relationship between growth and growing season length. Supporting
185 this possibility, current studies finding divergent results (Fig. ??, Fig. 4) span a wide range of
186 species (we found 57 species from 26 genera across 36 papers). While this diversity may appear

¹⁸⁷ to make identifying a common relationship between growth and growing season length more
¹⁸⁸ difficult, it may instead offer the path to an improved framework.

¹⁸⁹ **Building a new framework for growth × season length relationships**

¹⁹⁰ Useful models of tree growth for climate change forecasting have to include a diversity of different
¹⁹¹ species, while overcoming the challenges of uneven sampling across species and their contrasting
¹⁹² responses. Leveraging the diversity of responses observed across species is possible by integrat-
¹⁹³ ing ecological advances in how species traits and evolutionary history shape species responses
¹⁹⁴ to climate change (Cornwell & Nakagawa, 2017). In particular, advances in phylogenetic com-
¹⁹⁵ parative methods (Webb *et al.*, 2002) have moved research away from treating species identity
¹⁹⁶ as a simple grouping factor where each species is unique (e.g., *Fagus sylvatica* is different from
¹⁹⁷ *Quercus robur* and *Pinus sylvestris*) or fits into a limited set of groups (e.g., deciduous versus
¹⁹⁸ evergreen) and towards species as suites of correlated observations, separated by their evolu-
¹⁹⁹ tionary distance (*Fagus sylvatica* is much more closely related to *Quercus robur* compared to
²⁰⁰ *Pinus sylvestris*). New models built from these advances can fit data from all species at once
²⁰¹ and layer in species-level information. Traits can capture differences in growth strategies while
²⁰² phylogeny can capture additional species differences, which likely capture unmeasured ‘latent’
²⁰³ traits (Pearse *et al.*, 2019; Morales-Castilla *et al.*, 2024).

²⁰⁴ In step with these advances, trait ecology has documented leaf and wood economic spectra that
²⁰⁵ suggest major traits to include in these models (with related databases of these traits often
²⁰⁶ available, Chave *et al.*, 2009; Diaz *et al.*, 2016). These ‘economics’ define a common trade-off
²⁰⁷ along an acquisitive to conservative axis, where some species grow rapidly and more flexibly to
²⁰⁸ take advantage of resources, but are less defended against herbivores and compete poorly at low
²⁰⁹ resource levels, whereas other species compete well at low resource levels, but at the expense of
²¹⁰ growing slower (Grime, 1977; Chave *et al.*, 2009; Diaz *et al.*, 2016). While these traits likely miss
²¹¹ critical components for understanding how growing season length shapes growth, such as when
²¹² different species invest in shoot and leaf versus wood growth, they provide a baseline from which
²¹³ to build, and a powerful approach to combine data usefully across species. This approach has
²¹⁴ already been used to identify that early-leafout species often show faster-growing more acquisitive
²¹⁵ strategies compared to later-leafout species (Cleland & Wolkovich, 2024)—differences that may
²¹⁶ also impact how they respond to longer seasons.

²¹⁷ In addition to naturally organizing species differences, a trait-based phylogenetic comparative
²¹⁸ approach can help build a more testable and predictable framework. Because this approach can
²¹⁹ flexibly fit evolutionary history and traits together, it allows clades or species groupings that
²²⁰ respond similarly to emerge from the data and models (Davies *et al.*, 2019), versus being a priori
²²¹ grouped or defined. Similarly traits that co-vary with different responses can be more quickly
²²² identified (e.g., Willis *et al.*, 2008; Davies *et al.*, 2019, see Fig. 7). Both of these benefits could
²²³ help identify which species or traits to focus additional studies on to gain the most insights, while

similarly suggesting areas that should be less studied (e.g., traits that may be too confounded with evolutionary history, Cornwell *et al.*, 2014; Westoby *et al.*, 2023) or outlier species that may not represent most species (Morales-Castilla *et al.*, 2024). This approach may thus redefine debates over which metrics of growth or growing season length are relevant into debates over which metrics are most relevant for which clades and/or traits.

Importantly, trait-mediated phylogenetic models aid the search a universal model that can be useful for global forecasts of how growing season length influences growth. By effectively assuming one model, which is then shaped by evolutionary history and trait differences to produce the divergent responses observed across species today, this approach yields an overall estimated growth response alongside a response for each species, which can then be variously combined to scale up. For example, species-level estimates combined with data on species abundance across forests (e.g. Forest Service - United States Department of Agriculture; Fischer *et al.*, 2019) could predict larger-scale metrics, such as satellite observations of phenology and productivity. This framework also provides an organizing method to re-approach the fundamental question of how external and internal drivers shape growth responses to longer seasons, and a way to tackle what we are argue the three most critical questions in this area.

What is the scale of variation in growing season length x growth relationships across space and time?

The idea that growing season length influences plant growth is fundamental to plant biology, but we found it is rarely tested in ways relevant to the current debate (see ‘Growth × elevation relationships’ in Supplement), providing a major gap that limits progress. While multiple papers report a lack of relationship between growth and growing season length (Figs. 1, 3), we have no fundamental understanding of what the effect size of this relationship should be, and thus no way to know if we have sufficient power in current studies to detect it.

Identifying the macro-scale pattern of how growth and growing season length relate should be a primary goal, and one that seems broadly tractable. Tree ring studies designed to leverage latitudinal and elevational gradients in climate could quickly provide the raw data. Research will then need to develop models that tease out the effects of warmer temperatures across the season—likely affecting important biological rates (Figs. 5- 6)—versus longer seasons. Disentangling these may require focused efforts to understand xylogenesis across species and climates, but doing so across major climatic gradients could make differences more obvious. Wood growth provides an obvious and tractable baseline from which to set expectations of how much growth can vary across space, and links to existing major datasets (Fig. 8). Research will also then need to integrate beyond wood growth, including methods to better characterize changes across the leaf, shoot and wood architecture of different species (e.g., Puletti *et al.*, 2020; Sillett *et al.*, 2024) and also extending to the complexity of roots (McKown *et al.*, 2016; Radville *et al.*, 2016). These data can provide a baseline to compare to the scale of shifts over time, which studies

261 of growth \times growing season length to date have focused on (Fig. 3), since the same tree rings
262 measured for understanding spatial variation will also capture inter-annual variation.

263 **How prevalent are internal constraints across species and populations?**

264 New evidence suggests inter-annual variation in growth may be limited because of internal con-
265 straints that prevent plants from fully using longer seasons (Zohner *et al.*, 2023). If true, this
266 would have major ramifications for how much we expect growth to shift with warming. All
267 plants are limited by internal constraints and how quickly they can build new tissues (Marchand
268 *et al.*, 2021; Luo *et al.*, 2024), but selection towards different growth strategies (e.g., acquisitive
269 versus conservative) should drive variation in these constraints across species. Selection should
270 also drive local adaptation in these constraints at the population-level (McKown *et al.*, 2016;
271 Soolanayakanahally *et al.*, 2013), by favoring individuals that match to local environmental
272 optima (Colautti *et al.*, 2010; McKown *et al.*, 2014). This appears to be the case for budset—
273 which indicates the end of height growth, though we currently have data on only a few species
274 (Aitken & Bemmels, 2016; Zeng & Wolkovich, 2024). Further, new studies could rapidly test for
275 constraints across species and populations, to work towards a predictive framework using phy-
276 logeny and traits to predict these constraints. This approach has already yielded useful insights
277 in spring phenology, highlighting which environmental factors consistently drive budburst across
278 species while also showing widely-cited results may not extend beyond one well-studied species
279 (Morales-Castilla *et al.*, 2024).

280 **How do external drivers and internal constraints act together?**

281 The external and internal factors that affect how longer seasons impact growth are inherently
282 interconnected (Nobel *et al.*, 1983). While research often acknowledges this, modeling these
283 together will require both experiments and observational studies, ideally designed to integrate
284 into trait-mediated phylogenetic models. Studies across space could provide some inference
285 by studying how growing seasons measured by vegetative versus wood phenology vary—and
286 attributing variation through models that nest species within populations and include traits
287 while also testing for how climate drives growth.

288 The complexity of climate change and plant growth in response to longer, warmer seasons
289 makes experiments vital to building useful mechanistic models for forecasting. Observational
290 data—used mainly to date to tackle this question (Figs. 3, ??)—generally confounds multiple
291 external drivers, including season length, temperature and precipitation regimes (Ren *et al.*,
292 2019; Canadell *et al.*, 2021; Camarero *et al.*, 2022), making it impossible to tease out actual
293 drivers behind observed trends. Experiments, in contrast, can provide more robust tests. While
294 juvenile stages of trees are often more flexible than their adult forms, they still usually provide
295 predictable inference in differences across species and populations, and so should be integrated
296 far more into studies of how season length affects growth. Using saplings and controlled en-
297 vironments could quickly test how much growth can shift with longer seasons—providing a

298 potentially standardized way to compare constraints across species and populations—and then
299 layer on shifts in external drivers.

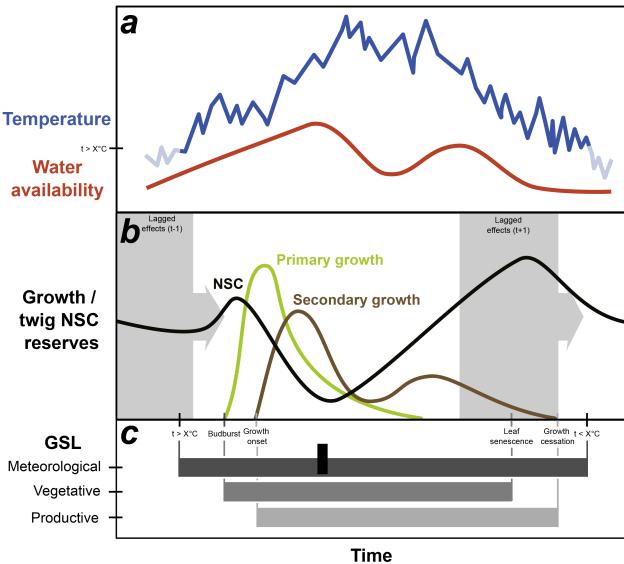
300 In particular, mechanistic models will need to tease out changes in season length from warming
301 that affects rates; a challenge best addressed by new experiments that decouple these two factors.
302 Such experiments could start on juvenile trees to help inform the underlying model, select
303 representative species to focus on, and develop predictions for large-scale studies. Experiments
304 could also inform a better model of lag effects across species, with small-scale studies sampling
305 saplings multiple years after manipulations (versus the common practice of destructive sampling
306 at the end of the treatment growing season) and large-scale studies following existing efforts to
307 test for ecological ‘memory’ (e.g. Flinker *et al.*, 2021; Schweiger *et al.*, 2022; Chin *et al.*, 2025).
308 These efforts should help bridge across the contrasting timescales of current physiological and
309 dendrochronological studies of growing season length: we found most physiological studies of
310 growth × growing season length relationships studied 1-2 years of dynamics, usually of juvenile
311 trees, while tree ring studies focused on synthesizing across decades of adult tree growth.

312 Expanding studies across more species will be critical for useful models that can forecast at
313 relevant scales and to help design large-scale experiments. While experimenting on adult trees
314 is difficult, previous challenges in climate change research have led to large-scale experiments
315 to understand other complex drivers (e.g. SPRUCE, DroughtNet, Pfynwald, Norby & Zak,
316 2011; Hanson *et al.*, 2017; Smith *et al.*, 2016). We expect similar experiments will be critical
317 here. Preparing for these large experiments using trait-mediated phylogenetic models to under-
318 stand responses across species, however, could advance new experiments well beyond past efforts
319 (Morales-Castilla *et al.*, 2024). By informing which species or clades to study, new experiments
320 could span enough phylogenetic and trait diversity to forecast to species beyond the experiment
321 and maximize the information gained (Cadotte *et al.*, 2017).

322 *Conclusions:* Anthropogenic climate change has often been described as an unfortunate and
323 unplanned experiment. Like many experiments, it has highlighted important biology we do not
324 know well. Understanding when, how and why longer seasons lead to increased tree growth
325 requires an interdisciplinary reckoning with how temperature, time and a suite of external and
326 internal drivers affect plant growth across species. A mechanistic understanding of how these
327 drivers integrate over species diverse growth strategies and the imprints of evolutionary history
328 to affect growth today is possible, but will require new approaches. Starting now to leverage
329 data across species to inform and design new large-scale studies and experiments be critical for
330 accurate models of future forest and related carbon dynamics, with implications for projections
331 of carbon sequestration and carbon markets.

332 *Acknowledgements:* B. Wuu for extracting growth × elevation data; R. Zäch for logistical sup-
333 port; N. Pederson for discussion, J. Davies and three reviewers for comments that improved the
334 manuscript.

Box. Growth, growing season length and the challenge of standardized metrics



335

336 A major challenge in determining how growth responds to longer growing seasons is the com-
 337 plexity of each, which means that neither can have one simple definition. Here we show the
 338 simplified climate of one year (a), which drives variation (b) in primary growth (root, shoot and
 339 leaf elongation) and secondary growth (radial wood growth), both of which often depend on
 340 growth from previous seasons. Each of these types of growth could define the growing season
 341 length (GSL, c) but similarly it can be defined meteorologically (e.g., days above 5°C with some
 342 level of soil moisture) or by large-scale measures of plant productivity (Körner *et al.*, 2023).

343 Of studies in our literature review, the largest proportion used metrics related to secondary
 344 growth, quantifying growth by measuring radial growth (e.g., through increment cores or den-
 345 drometers, $n = 28$), but a number also looked at metrics related to primary growth, including C
 346 assimilation (e.g. net ecosystem productivity or gross primary productivity, $n = 20$). A smaller
 347 number used metrics that reflect combined primary and secondary growth, including biomass,
 348 height, or number of stems ($n = 9$), and root:shoot ratio ($n = 1$). Some studies used modeled
 349 estimates of photosynthesis (e.g., Smith *et al.* (2014) relied on daily photosynthesis estimates
 350 derived from the LPJ-GUESS photosynthesis model, while Chen *et al.* (2000) estimated photo-
 351 syntheze using the Integrated Terrestrial Ecosystem C-budget model, InTEC). Others measured
 352 photosynthesis at the leaf level, through flux towers, or used greenness metrics (NDVI).

353 For growing season length, the largest number of studies used vegetative (e.g., budburst to leaf
 354 senescence in our figure above, 26 studies) or wood phenology 11 studies) as their definition,
 355 while a smaller number used a meteorological definitions or fixed dates (7 studies). We found 14
 356 that did not directly measure GSL (e.g., Zhu *et al.*, 2021; Dow *et al.*, 2022; Zohner *et al.*, 2023).

357 Further, these definitions of GSL are simplified and could not be easily aligned, as we found 14
358 different metrics of start of season, 16 metrics of end of season (25 metrics of growing season
359 length. See also ‘The challenge of metrics: Measuring growth and growing season length’ in the
360 Supplement.

361 **1 References**

362

- 363 Aitken, S.N. & Bemmels, J.B. (2016) Time to get moving: assisted gene flow of forest trees.
364 *Evol Appl* **9**, 271–90.
- 365 Ávila-Lovera, E., Winter, K. & Goldsmith, G.R. (2023) Evidence for phylogenetic signal and
366 correlated evolution in plant–water relation traits. *New Phytologist* **237**, 392–407.
- 367 Berdanier, A.B. & Klein, J.A. (2011) Growing season length and soil moisture interactively
368 constrain high elevation aboveground net primary production. *Ecosystems* **14**, 963–974.
- 369 Cabon, A., Kannenberg, S.A., Arain, A., Babst, F., Baldocchi, D., Belmecheri, S., Delpierre,
370 N., Guerrieri, R., Maxwell, J.T., McKenzie, S. *et al.* (2022) Cross-biome synthesis of source
371 versus sink limits to tree growth. *Science* **376**, 758–761.
- 372 Cadotte, M.W., Davies, T.J. & Peres-Neto, P.R. (2017) Why phylogenies do not always predict
373 ecological differences. *Ecological Monographs* **87**, 535–551.
- 374 Camarero, J.J., Campelo, F., Colangelo, M., Valeriano, C., Knorre, A., Solé, G. & Rubio-
375 Cuadrado, Á. (2022) Decoupled leaf-wood phenology in two pine species from contrasting
376 climates: Longer growing seasons do not mean more radial growth. *Agricultural and Forest
377 Meteorology* **327**, 109223.
- 378 Canadell, J., Monteiro, P., Costa, M., Cotrim da Cunha, L., Cox, P., Eliseev, A., Henson, S.,
379 Ishii, M., Jaccard, S., Koven, C., Lohila, A., Patra, P., Piao, S., Rogelj, J., Syampungani, S.,
380 Zaehle, S. & Zickfeld, K. (2021) *Climate Change 2021: The Physical Science Basis. Contribution
381 of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on
382 Climate Change*. Cambridge University Press, New York, NY.
- 383 Chamberlain, C.J., Cook, B.I., Morales-Castilla, I. & Wolkovich, E.M. (2021) Climate change
384 reshapes the drivers of false spring risk across european trees. *New Phytologist* **229**, 323–334.
- 385 Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a
386 worldwide wood economics spectrum. *Ecology Letters* **12**, 351–366.
- 387 Chen, W., Black, T., Yang, P., Barr, A., Neumann, H., Nesic, Z., Blanken, P., Novak, M., Eley,
388 J., Ketler, R. *et al.* (1999) Effects of climatic variability on the annual carbon sequestration
389 by a boreal aspen forest. *Global Change Biology* **5**, 41–53.
- 390 Chen, W., Chen, J., Liu, J. & Cihlar, J. (2000) Approaches for reducing uncertainties in regional
391 forest carbon balance. *Global Biogeochemical Cycles* **14**, 827–838.

- 392 Chin, A.R., Gessler, A., Laín, O., Østerlund, I., Schaub, M., Théroux-Rancourt, G., Voggendorf,
393 K. & Lambers, J.H.R. (2025) The memory of past water abundance shapes trees 7 years later.
394 *American Journal of Botany* p. e16452.
- 395 Cleland, E.E., Allen, J.M., Crimmins, T.M., Dunne, J.A., Pau, S., Travers, S.E., Zavaleta, E.S.
396 & Wolkovich, E.M. (2012) Phenological tracking enables positive species responses to climate
397 change. *Ecology* **93**, 1765–1771.
- 398 Cleland, E.E. & Wolkovich, E. (2024) Effects of phenology on plant community assembly and
399 structure. *Annual Review of Ecology, Evolution, and Systematics* **55**, 471–492.
- 400 Colautti, R.I., Eckert, C.G. & Barrett, S.C.H. (2010) Evolutionary constraints on adaptive
401 evolution during range expansion in an invasive plant. *Proceedings of the Royal Society B-
402 Biological Sciences* **277**, 1799–1806, colautti, Robert I. Eckert, Christopher G. Barrett, Spencer
403 C. H.
- 404 Cornwell, W. & Nakagawa, S. (2017) Phylogenetic comparative methods. *Current Biology* **27**,
405 R333–R336.
- 406 Cornwell, W.K., Westoby, M., Falster, D.S., FitzJohn, R.G., O'Meara, B.C., Pennell, M.W.,
407 McGlinn, D.J., Eastman, J.M., Moles, A.T., Reich, P.B. *et al.* (2014) Functional distinctiveness
408 of major plant lineages. *Journal of Ecology* **102**, 345–356.
- 409 Cosgrove, D.J. (2005) Growth of the plant cell wall. *Nature reviews molecular cell biology* **6**,
410 850–861.
- 411 Cosgrove, D.J. (2023) Structure and growth of plant cell walls. *Nature Reviews Molecular Cell
412 Biology* pp. 1–19.
- 413 Coulthard, B.L., George, S.S. & Meko, D.M. (2020) The limits of freely-available tree-ring
414 chronologies. *Quaternary Science Reviews* **234**, 106264.
- 415 Cuapio-Hernández, L., Reyes-Ortiz, J.L., De La Rosa, A.B., Pavón, N.P., López-Herrera, M.,
416 Villanueva-Díaz, J. & Sánchez-González, A. (2022) Is there a response pattern between radial
417 growth of trees and elevation gradient? *Tree-Ring Research* .
- 418 Cuny, H.E., Rathgeber, C.B., Lebourgeois, F., Fortin, M. & Fournier, M. (2012) Life strategies
419 in intra-annual dynamics of wood formation: example of three conifer species in a temperate
420 forest in north-east france. *Tree physiology* **32**, 612–625.
- 421 Davies, T.J., Regetz, J., Wolkovich, E.M. & McGill, B.J. (2019) Phylogenetically weighted
422 regression: A method for modelling non-stationarity on evolutionary trees. *Global ecology and
423 biogeography* **28**, 275–285.
- 424 Day, M.E. & Greenwood, M.S. (2011) Regulation of ontogeny in temperate conifers. *Size-and
425 age-related changes in tree structure and function*, pp. 91–119, Springer.

- 426 de Sauvage, J.C., Vitasse, Y., Meier, M., Delzon, S. & Bigler, C. (2022) Temperature rather
427 than individual growing period length determines radial growth of sessile oak in the pyrenees.
428 *Agricultural and Forest Meteorology* **317**, 108885.
- 429 Delpierre, N., Guillemot, J., Dufrêne, E., Cecchini, S. & Nicolas, M. (2017) Tree phenological
430 ranks repeat from year to year and correlate with growth in temperate deciduous forests.
431 *Agricultural and Forest Meteorology* **234**, 1–10.
- 432 Diaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M.,
433 Wirth, C., Prentice, I.C., Garnier, E., Bonisch, G., Westoby, M., Poorter, H., Reich, P.B.,
434 Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Wright, S.J., Sheremet'ev,
435 S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves,
436 F., Joswig, J.S., Gunther, A., Falcuk, V., Ruger, N., Mahecha, M.D. & Gorne, L.D. (2016)
437 The global spectrum of plant form and function. *Nature* **529**, 167–U73.
- 438 Dow, C., Kim, A.Y., D'Orangeville, L., Gonzalez-Akre, E.B., Helcoski, R., Herrmann, V., Harley,
439 G.L., Maxwell, J.T., McGregor, I.R., McShea, W.J. *et al.* (2022) Warm springs alter timing
440 but not total growth of temperate deciduous trees. *Nature* **608**, 552–557.
- 441 Etzold, S., Sterck, F., Bose, A.K., Braun, S., Buchmann, N., Eugster, W., Gessler, A., Kahmen,
442 A., Peters, R.L., Vitasse, Y. *et al.* (2022) Number of growth days and not length of the growth
443 period determines radial stem growth of temperate trees. *Ecology Letters* **25**, 427–439.
- 444 Finzi, A.C., Giasson, M.A., Plotkin, A.A.B., Aber, J.D., Boose, E.R., Davidson, E.A., Dietze,
445 M.C., Ellison, A.M., Frey, S.D., Goldman, E., Keenan, T.F., Melillo, J.M., Munger, J.W.,
446 Nadelhoffer, K.J., Ollinger, V. S., Orwig, D.A., Pederson, N., Richardson, A.D., Savage, K.,
447 Tang, J., Thompson, J.R., Williams, C.A., Wofsy, S.C., Zhou, Z. & Foster, D.R. (2020) Carbon
448 budget of the harvard forest long-term ecological research site: pattern, process, and response
449 to global change. *Ecological Monographs* **90**.
- 450 Fischer, C., Traub, B. *et al.* (2019) *Swiss National Forest Inventory-methods and models of the*
451 *fourth assessment*. Springer.
- 452 Flinker, R.H., Cardenas, M.B., Caldwell, T.G., Flerchinger, G.N., Roy, R. & Reich, P.B. (2021)
453 Promise and pitfalls of modeling grassland soil moisture in a free-air co2 enrichment experi-
454 ment (biocon) using the shaw model. *Pedosphere* **31**, 783–795.
- 455 Forest Service - United States Department of Agriculture (????) Forest Inventory and Analysis
456 (FIA) database.
- 457 Frank, D., Fang, K. & Fonti, P. (2022) Dendrochronology: Fundamentals and innovations. *Stable*
458 *Isotopes in Tree Rings: Inferring Physiological, Climatic and Environmental Responses*, pp.
459 21–59, Springer International Publishing Cham.

- 460 Friedlingstein, P., O'sullivan, M., Jones, M.W., Andrew, R.M., Gregor, L., Hauck, J., Le Quéré,
461 C., Luijkx, I.T., Olsen, A., Peters, G.P. *et al.* (2022) Global carbon budget 2022. *Earth System
462 Science Data Discussions* **2022**, 1–159.
- 463 Gantois, J. (2022) New tree-level temperature response curves document sensitivity of tree
464 growth to high temperatures across a us-wide climatic gradient. *Global Change Biology* **28**,
465 6002–6020.
- 466 Gordon, J.C. & Larson, P.R. (1968) Seasonal course of photosynthesis, respiration, and distri-
467 bution of 14c in young pinus resinosa trees as related to wood formation. *Plant Physiology* **43**,
468 1617–1624.
- 469 Green, J.K. & Keenan, T.F. (2022) The limits of forest carbon sequestration. *Science* **376**,
470 692–693.
- 471 Grime, J.P. (1977) Evidence for existence of 3 primary strategies in plants and its relevance to
472 ecological and evolutionary theory. *American Naturalist* **111**, 1169–1194.
- 473 Hacket-Pain, A., Friend, A., Lageard, J. & Thomas, P. (2016a) Tree rings and masting: con-
474 sidering reproductive phenomena when interpreting tree rings? *Tree Rings in Archaeology,
475 Climatology and Ecology* **14**, 78–85.
- 476 Hacket-Pain, A.J., Cavin, L., Friend, A.D. & Jump, A. (2016b) Consistent limitation of growth
477 by high temperature and low precipitation from range core to southern edge of european beech
478 indicates widespread vulnerability to changing climate. *European Journal of Forest Research*
479 **135**, 897–909.
- 480 Hanson, P.J., Riggs, J.S., Nettles, W.R., Phillips, J.R., Krassovski, M.B., Hook, L.A., Gu, L.,
481 Richardson, A.D., Aubrecht, D.M., Ricciuto, D.M. *et al.* (2017) Attaining whole-ecosystem
482 warming using air and deep-soil heating methods with an elevated co 2 atmosphere. *Bioge-
483osciences* **14**, 861–883.
- 484 Hilty, J., Muller, B., Pantin, F. & Leuzinger, S. (2021) Plant growth: The what, the how, and
485 the why. *New Phytologist* **232**, 25–41.
- 486 Howe, G.T., Aitken, S.N., Neale, D.B., Jermstad, K.D., Wheeler, N.C. & Chen, T.H. (2003)
487 From genotype to phenotype: unraveling the complexities of cold adaptation in forest trees.
488 *Canadian Journal of Botany* **81**, 1247–1266.
- 489 Ito, G., Romanou, A., Kiang, N.Y., Faluvegi, G., Aleinov, I., Ruedy, R., Russell, G., Lerner,
490 P., Kelley, M. & Lo, K. (2020) Global carbon cycle and climate feedbacks in the nasa giss
491 modele2. 1. *Journal of Advances in Modeling Earth Systems* **12**, e2019MS002030.
- 492 Journé, V., Szymkowiak, J., Foest, J., Hacket-Pain, A., Kelly, D. & Bogdziewicz, M. (2024) Sum-
493 mer solstice orchestrates the subcontinental-scale synchrony of mast seeding. *Nature Plants*
494 **10**, 367–373.

- 495 Keenan, T.F., Gray, J., Friedl, M.A., Toomey, M., Bohrer, G., Hollinger, D.Y., Munger, J.W.,
496 O'Keefe, J., Schmid, H.P., Wing, I.S. *et al.* (2014) Net carbon uptake has increased through
497 warming-induced changes in temperate forest phenology. *Nature Climate Change* **4**, 598–604.
- 498 Kikuzawa, K. (1982) Leaf survival and evolution in betulaceae. *Annals of Botany* **50**, 345–353.
- 499 King, G.M., Gugerli, F., Fonti, P. & Frank, D.C. (2013) Tree growth response along an eleva-
500 tional gradient: climate or genetics? *Oecologia* **173**, 1587–1600.
- 501 Klesse, S., Babst, F., Evans, M.E., Hurley, A., Pappas, C. & Peters, R.L. (2023) Legacy effects
502 in radial tree growth are rarely significant after accounting for biological memory. *Journal of*
503 *Ecology* **111**, 1188–1202.
- 504 Kolář, T., Giaglio, K., Trnka, M., Bednářová, E., Vavrčík, H. & Rybníček, M. (2016) Response of
505 the leaf phenology and tree-ring width of european beech to climate variability. *Silva Fennica*
506 **50**.
- 507 Körner, C., Möhl, P. & Hiltbrunner, E. (2023) Four ways to define the growing season. *Ecology*
508 *Letters* .
- 509 Kramer, P. (2012) *Physiology of woody plants*. Elsevier, New York.
- 510 La Porta, N., Capretti, P., Thomsen, I., Kasanen, R., Hietala, A. & Von Weissenberg, K. (2008)
511 Forest pathogens with higher damage potential due to climate change in europe. *Canadian*
512 *Journal of Plant Pathology* **30**, 177–195.
- 513 Lange, H., Økland, B. & Krokene, P. (2006) Thresholds in the life cycle of the spruce bark beetle
514 under climate change. *Interjournal for Complex Systems* **1648**, 1–10.
- 515 Larcher, W. (1980) *Plant Physiological Ecology*. Springer-Verlag.
- 516 Lechowicz, M.J. (1984) Why do temperate deciduous trees leaf out at different times - adaptation
517 and ecology of forest communities. *American Naturalist* **124**, 821–842.
- 518 Leuning, R. (2002) Temperature dependence of two parameters in a photosynthesis model. *Plant,*
519 *Cell & Environment* **25**, 1205–1210.
- 520 Luo, Y., Zohner, C., Crowther, T.W., Feng, J., Hoch, G., Li, P., Richardson, A.D., Vitasse, Y. &
521 Gessler, A. (2024) Internal physiological drivers of leaf development in trees: Understanding
522 the relationship between non-structural carbohydrates and leaf phenology. *Functional Ecology*
523 .
- 524 Marchand, L.J., Dox, I., Gričar, J., Prislan, P., Van den Bulcke, J., Fonti, P. & Campioli, M.
525 (2021) Timing of spring xylogenesis in temperate deciduous tree species relates to tree growth
526 characteristics and previous autumn phenology. *Tree Physiology* **41**, 1161–1170.

- 527 Martinez-Meier, A., Sanchez, L., Pastorino, M., Gallo, L. & Rozenberg, P. (2008) What is hot
528 in tree rings? the wood density of surviving douglas-firs to the 2003 drought and heat wave.
529 *Forest Ecology and Management* **256**, 837–843.
- 530 McKown, A.D., Guy, R.D., Klapste, J., Geraldès, A., Friedmann, M., Cronk, Q.C.B., El-
531 Kassaby, Y.A., Mansfield, S.D. & Douglas, C.J. (2014) Geographical and environmental gra-
532 dients shape phenotypic trait variation and genetic structure in *populus trichocarpa*. *New*
533 *Phytologist* **201**, 1263–1276, mCKown, Athena D. Guy, Robert D. Klapste, Jaroslav Geraldès,
534 Armando Friedmann, Michael Cronk, Quentin C. B. El-Kassaby, Yousry A. Mansfield, Shawn
535 D. Douglas, Carl J.
- 536 McKown, A.D., Guy, R.D. & Quamme, L.K. (2016) Impacts of bud set and lammas phenology on
537 root: shoot biomass partitioning and carbon gain physiology in poplar. *Trees* **30**, 2131–2141.
- 538 Michelot, A., Simard, S., Rathgeber, C., Dufrêne, E. & Damesin, C. (2012) Comparing the
539 intra-annual wood formation of three European species (*Fagus sylvatica*, *Quercus petraea* and
540 *Pinus sylvestris*) as related to leaf phenology and non-structural carbohydrate dynamics. *Tree*
541 *physiology* **32**, 1033–1045.
- 542 Mitton, J.B. & Ferrenberg, S.M. (2012) Mountain pine beetle develops an unprecedented summer
543 generation in response to climate warming. *The American Naturalist* **179**, E163–E171.
- 544 Monson, R.K., Szejner, P., Belmecheri, S., Morino, K.A. & Wright, W.E. (2018) Finding the
545 seasons in tree ring stable isotope ratios. *American journal of botany* **105**, 819–821.
- 546 Morales-Castilla, I., Davies, T., Legault, G., Buonaiuto, D., Chamberlain, C.J., Ettinger, A.K.,
547 Garner, M., Jones, F.A., Loughnan, D., Pearse, W.D. *et al.* (2024) Phylogenetic estimates of
548 species-level phenology improve ecological forecasting. *Nature Climate Change* pp. 1–7.
- 549 Myneni, R.B., Keeling, C., Tucker, C.J., Asrar, G. & Nemani, R.R. (1997) Increased plant
550 growth in the northern high latitudes from 1981 to 1991. *Nature* **386**, 698–702.
- 551 Nobel, P.S. *et al.* (1983) *Biophysical plant physiology and ecology*. WH Freeman and company.
- 552 Norby, R.J. & Zak, D.R. (2011) Ecological lessons from free-air co₂ enrichment (face) experi-
553 ments. *Annual review of ecology, evolution, and systematics* **42**, 181–203.
- 554 Oleksyn, J., Modrzynski, J., Tjoelker, M., Z. ytkowiak, R., Reich, P.B. & Karolewski, P. (1998)
555 Growth and physiology of *picea abies* populations from elevational transects: common garden
556 evidence for altitudinal ecotypes and cold adaptation. *Functional Ecology* **12**, 573–590.
- 557 Pearse, W.D., Legendre, P., Peres-Neto, P.R. & Davies, T.J. (2019) The interaction of phylogeny
558 and community structure: Linking the community composition and trait evolution of clades.
559 *Global Ecology and Biogeography* **28**, 1499–1511.

- 560 Peters, R.L., Steppe, K., Cuny, H.E., De Pauw, D.J., Frank, D.C., Schaub, M., Rathgeber, C.B.,
561 Cabon, A. & Fonti, P. (2021) Turgor—a limiting factor for radial growth in mature conifers
562 along an elevational gradient. *New Phytologist* **229**, 213–229.
- 563 Puletti, N., Grotti, M., Ferrara, C. & Chianucci, F. (2020) Lidar-based estimates of aboveground
564 biomass through ground, aerial, and satellite observation: a case study in a mediterranean
565 forest. *Journal of Applied Remote Sensing* **14**, 044501–044501.
- 566 Radville, L., McCormack, M.L., Post, E. & Eissenstat, D.M. (2016) Root phenology in a chang-
567 ing climate. *Journal of Experimental Botany* **67**, 3617–3628.
- 568 Ren, P., Ziaoc, E., Rossi, S., Biondi, F., Prislan, P. & Liang, E. (2019) Growth rate rather than
569 growing season length determines wood biomass in dry environments. *Agricultural and Forest
570 Meteorology* **271**, 46–53.
- 571 Rezende, E.L. & Bozinovic, F. (2019) Thermal performance across levels of biological organiza-
572 tion. *Philosophical Transactions of the Royal Society B* **374**, 20180549.
- 573 Schaber, J. & Badeck, F.W. (2002) Evaluation of methods for the combination of phenological
574 time series and outlier detection. *Tree Physiology* **22**, 973–982.
- 575 Schweiger, A., Awdamet, F.T., Drenckhan, W. & Berauer, B.J. (2022) Transgenerational effects
576 of elevated co 2: Downregulation of photosynthetic efficiency and stomatal sensitivity to
577 drought .
- 578 Senf, C., Seidl, R. & Hostert, P. (2017) Remote sensing of forest insect disturbances: Current
579 state and future directions. *International journal of applied earth observation and geoinfor-
580 mation* **60**, 49–60.
- 581 Sillett, S.C., Graham, M.E., Montague, J.P., Antoine, M.E. & Koch, G.W. (2024) Ground-based
582 calibration for remote sensing of biomass in the tallest forests. *Forest Ecology and Management*
583 **561**, 121879.
- 584 Silvestro, R., Zeng, Q., Buttò, V., Sylvain, J.D., Drolet, G., Mencuccini, M., Thiffault, N.,
585 Yuan, S. & Rossi, S. (2023) A longer wood growing season does not lead to higher carbon
586 sequestration. *Scientific reports* **13**, 4059.
- 587 Smith, B., Wårlind, D., Arneth, A., Hickler, T., Leadley, P., Siltberg, J. & Zaehle, S. (2014) Im-
588 plications of incorporating n cycling and n limitations on primary production in an individual-
589 based dynamic vegetation model. *Biogeosciences* **11**, 2027–2054.
- 590 Smith, M.D., Wilcox, K., Sala, O., Phillips, R., Luo, Y., Knapp, A. & Lemoine, N.P. (2016)
591 Drought-net: A global network merging observations, experiments, and modeling to forecast
592 terrestrial ecosystem sensitivity to drought. *AGU Fall Meeting Abstracts*, vol. 2016, pp. B11J–
593 06.

- 594 Soolanayakanahally, R.Y., Guy, R.D., Silim, S.N. & Song, M. (2013) Timing of photoperiodic
595 competency causes phenological mismatch in balsam poplar (*populus balsamifera* l.). *Plant,*
596 *cell & environment* **36**, 116–127.
- 597 Sturrock, R., Frankel, S., Brown, A., Hennon, P., Kliejunas, J., Lewis, K., Worrall, J. & Woods,
598 A. (2011) Climate change and forest diseases. *Plant pathology* **60**, 133–149.
- 599 Thomas, S.C. (2011) Age-related changes in tree growth and functional biology: The role
600 of reproduction. *Size- and Age-Related Changes in Tree Structure and Function* (eds. F.C.
601 MEINZER, B. Lachenbruch & T.E. Dawson), chap. 2, pp. 33–64, Springer.
- 602 Wang, M., Jiang, Y., Zhang, W., Dong, M., Kang, M. & Xu, H. (2017) Climatic response of
603 tracheid features of *picea meyeri* along altitude gradient of luyashan mountains of north china.
604 *Polish Journal of Ecology* **65**, 345–358.
- 605 Waring, R.H. & Franklin, J.F. (1979) Evergreen coniferous forests of the pacific northwest:
606 Massive long-lived conifers dominating these forests are adapted to a winter-wet, summer-dry
607 environment. *Science* **204**, 1380–1386.
- 608 Webb, C.O., Ackerly, D.D., McPeek, M. & Donoghue, M.J. (2002) Phylogenies and community
609 ecology. *Annual Review of Ecology and Systematics* **33**, 475–505.
- 610 Went, F.W. (1957) The experimental control of plant growth. *The experimental control of plant*
611 *growth*. **17**.
- 612 Westoby, M., Yates, L., Holland, B. & Halliwell, B. (2023) Phylogenetically conservative trait
613 correlation: quantification and interpretation. *Journal of Ecology* **111**, 2105–2117.
- 614 Willis, C.G., Ruhfel, B., Primack, R.B., Miller-Rushing, A.J. & Davis, C.C. (2008) Phylogenetic
615 patterns of species loss in thoreau's woods are driven by climate change. *Proceedings of the*
616 *National Academy of Sciences* **105**, 17029–17033.
- 617 Zeng, Z.A. & Wolkovich, E.M. (2024) Weak evidence of provenance effects in spring phenology
618 across europe and north america. *New Phytologist* .
- 619 Zhou, Y., Yi, Y., Liu, H., Song, J., Jia, W. & Zhang, S. (2022) Altitudinal trends in climate
620 change result in radial growth variation of *pinus yunnanensis* at an arid-hot valley of southwest
621 china. *Dendrochronologia* **71**, 125914.
- 622 Zhu, L., Liu, S., Arzac, A., Cooper, D.J., Jin, Y., Yuan, D., Zhu, Y., Zhang, X., Li, Z., Zhang, Y.,
623 et al. (2021) Different response of earlywood vessel features of *fraxinus mandshurica* to rapid
624 warming in warm-dry and cold-wet areas. *Agricultural and Forest Meteorology* **307**, 108523.
- 625 Zohner, C.M., Mirzagholi, L., Renner, S.S., Mo, L., Rebindaine, D., Bucher, R., Palouš, D.,
626 Vitasse, Y., Fu, Y.H., Stocker, B.D. et al. (2023) Effect of climate warming on the timing of
627 autumn leaf senescence reverses after the summer solstice. *Science* **381**, eadf5098.

628 2 Figures

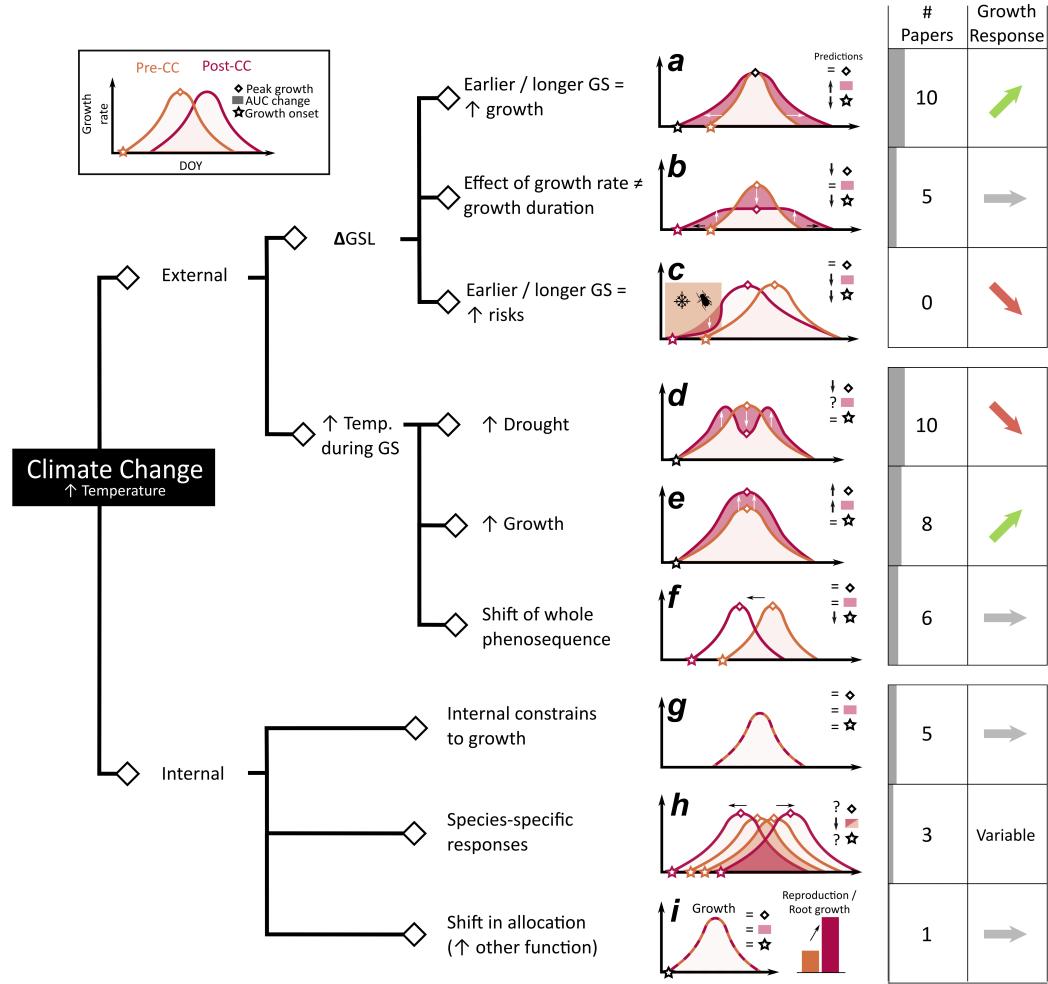


Figure 1: Climate change may alter growing season (GS) length, which can then affect growth through diverse pathways. We review hypotheses for these pathways showing the number of papers (from a review of papers studying growth \times growing season length) that mentioned each hypothesis (width of the shaded areas of left column is proportional to the number of papers with the number also given, right column shows the expected growth response for each hypothesis). We group hypotheses as focused on mechanisms moderated by the environment (“external”) versus those focused on internal physiological constraints, which span both source (photosynthesis-limited) and sink limitation, and could act together. For more details, see Supplement.

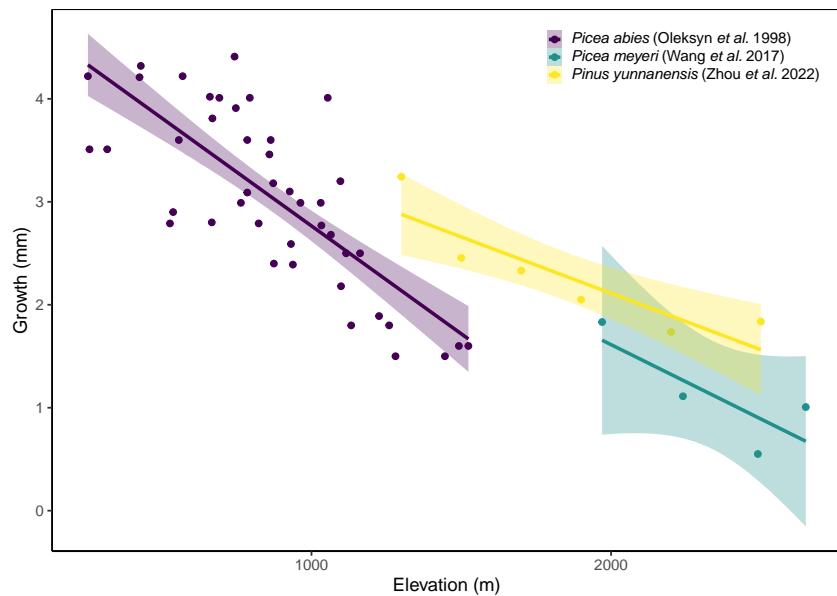


Figure 2: Growth \times elevation relationships from the literature with simple linear regression fits shown with 89% confidence intervals. Oleksyn *et al.* (1998) measured growth (mm) as diameter at breast height increments, while the other studies (Wang *et al.*, 2017; Zhou *et al.*, 2022) measured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

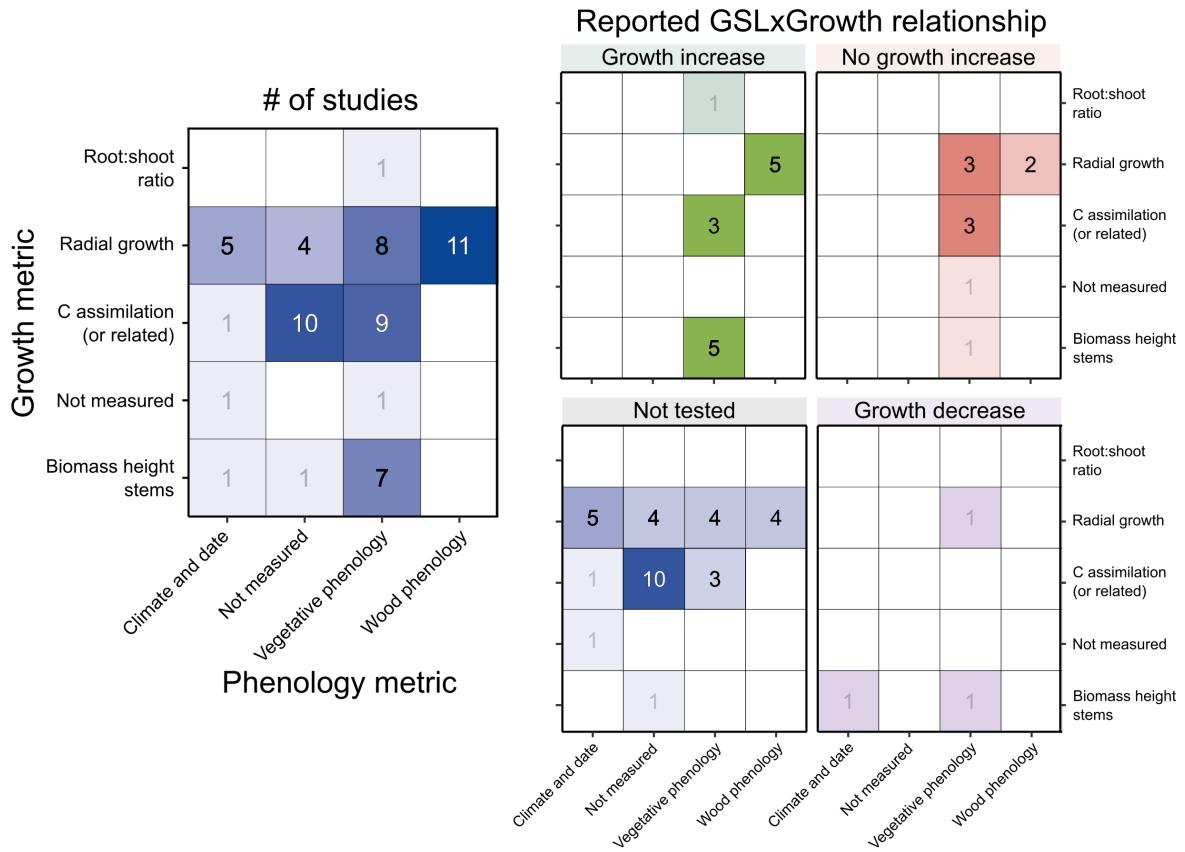


Figure 3: A review of growth \times growing season length relationship studies spanned a diversity of methods, but there was no coherency in which methods did or did not find a positive relationship. A number of studies tested relationships possibly related to growth \times growing season length (e.g.,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

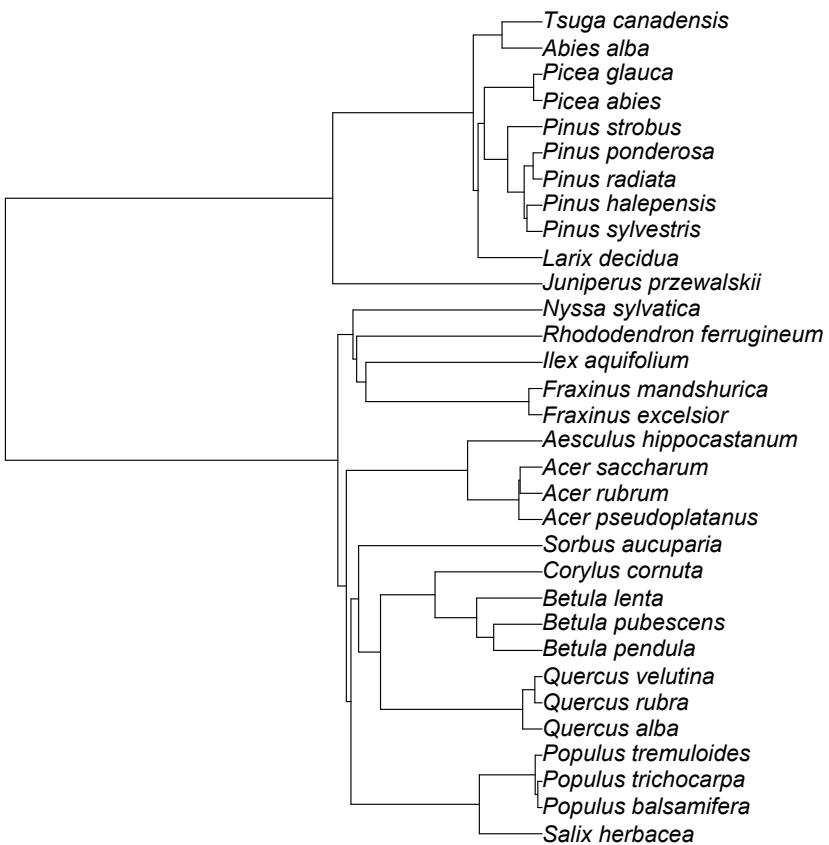


Figure 4: We could switch Fig. ?? from Supp to main text and plot on phylogeny ... I just had time to plot the phylogeny quickly so did not layer on yes/no or find the missing species, like *Fagus*.

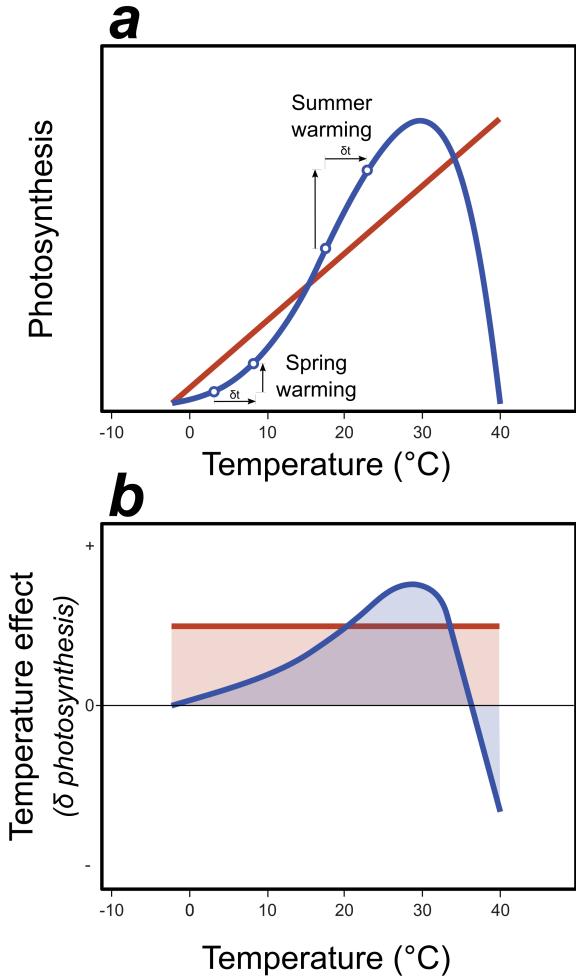


Figure 5: (a) Growth responses to temperature depends on a suite of complex factors and is often represented as net photosynthesis, which has a non-linear response to temperature (blue curve, adapted from meta-analysis of Rezende & Bozinovic, 2019), though it is often modeled as linear (red). (b) This non-linearity means that increases in lower temperatures—such as those in the spring when much of growing season extensions may happen—have lower absolute increases 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.

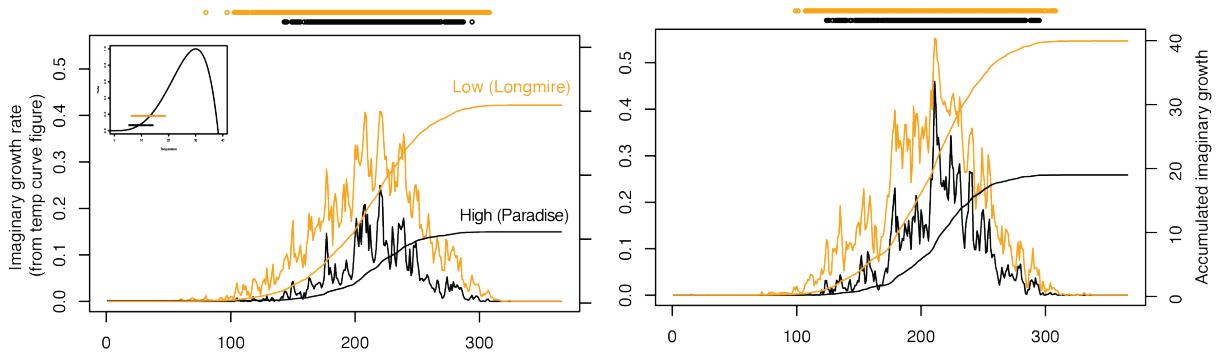


Figure 6: (DRAFT of potential new figure): Testing how growth varies across larger spatial gradients of growing season length could help establish a baseline expectation of the scale of temporal—especially inter-annual variation—and force a greater reckoning with drivers that shift alongside growing season length. This conceptual figure uses data from a cool-weather, temperate site at two elevations (Mount Rainier/Tahoma in USA) with show potential differences in growing season length (dots on top) and biological rates. Other gradients in warmer locations would show much higher rates, but also likely more days where rates are zero due to too high temperatures. Here we estimated growing season length as days above 5°C and used an idealized curve (inset) to calculate daily rates. Left shows based on climatic data from the 1980s, while the right is based on 2014-2023. [I could edit this to show TWO species that respond slightly differently to temperature, but then we need to drop one elevation or one time period. THOUGHTS?]

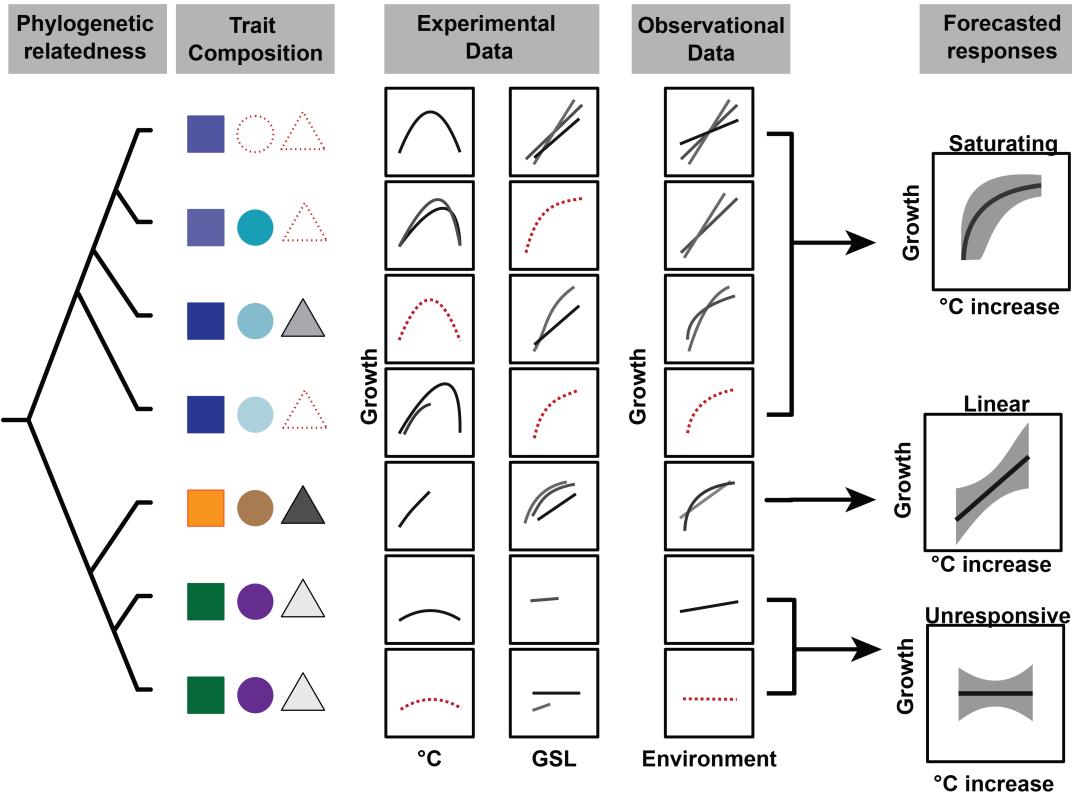


Figure 7: A trait-based phylogenetic model provides a way to naturally organize species (and, not shown, population) responses to predict how they respond to longer seasons. This approach estimates a universal model that is then shaped by species evolutionary history (shown at left via a phylogenetic tree) and traits to estimate how each species should uniquely respond. We argue this framework can organize and guide experiments that separate out changes in temperature from changes in growing season length ($^{\circ}\text{C}$ and GSL in see middle panels) to better integrate observational data and identify different responses by species that can help forecast (see ‘Building a new framework for growth \times season length relationships’ section for more details). In this example, we show how this approach can identify one clade (top) with a common response to longer seasons that also shares a suite of similar traits, and can identify a unique response in by one species in a clade where that species also has a unique trait compared to other species with the same common ancestor (lower clade). Estimating responses across species through a phylogenetic model has the additional benefit of robustly estimating responses given uneven sampling and missing data (the dashed red lines represent that the model will predict a response for each species, informed to various degrees—with the degree determined by the model—by the traits and phylogeny).

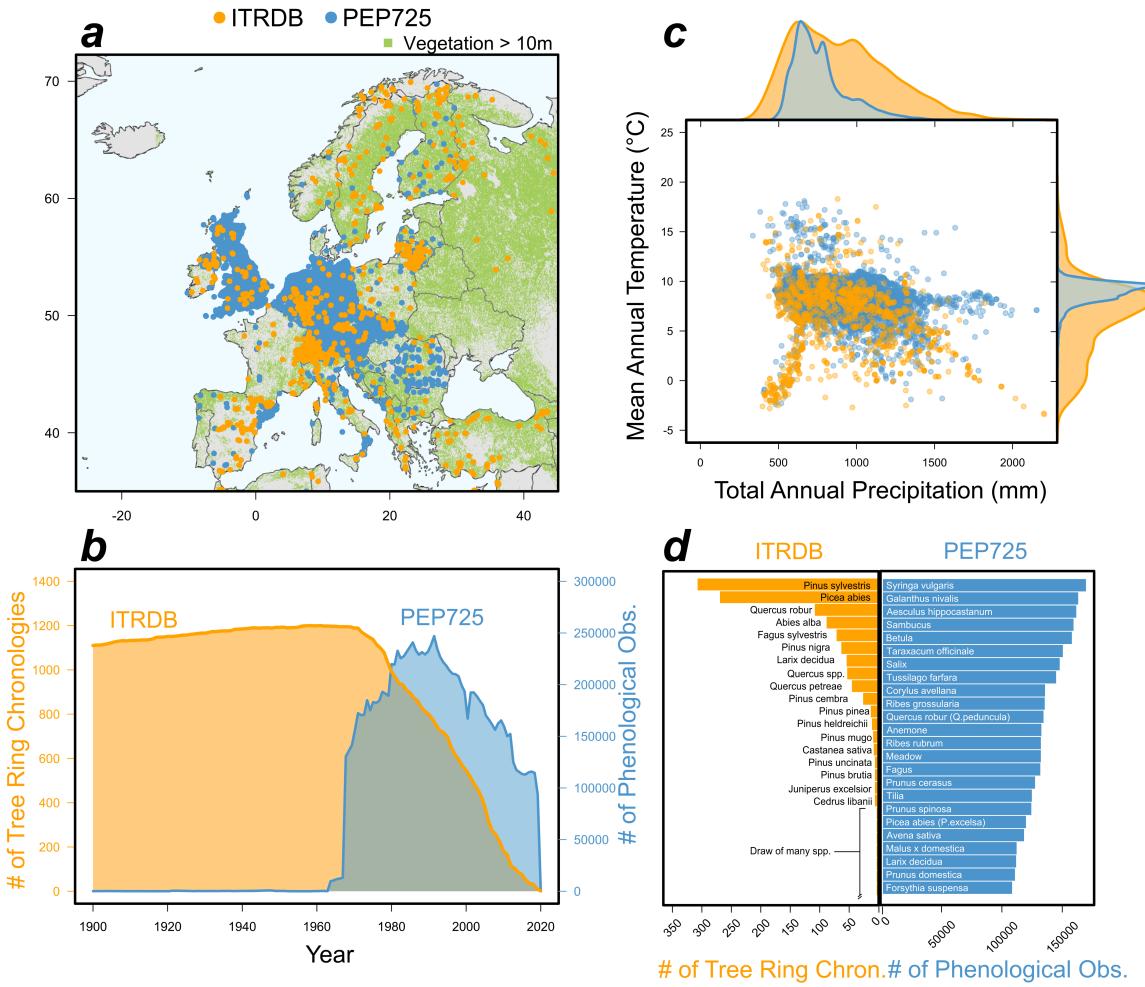


Figure 8: Data overlap between the two major databases of growth (International Tree Ring Data Bank, ITRDB, orange) and plant phenology (Pan European Phenology Project, PEP725, blue). Both databases are compared in terms of their spatial distributions (a), temporal overlaps (b), coverage of environmental 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.