

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

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### 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 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. 3, 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. 4 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. 4). 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. 3).

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. 6, 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. 7).

104 How much or whether growth increases at all depends on the non-linear effect of temperature  
105 on biological processes (Fig. 6). 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. 4). 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 (?). 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 (budset) 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 ??). Further, evergreen species are thought to grow more slowly and  
173 thus differences due to season length may be harder to detect (Waring & Franklin, 1979).

174 This division between evergreen and deciduous species hints at a larger suite of traits that predict  
175 growth by growing season length relationships among species. Species that budburst earlier and  
176 more readily produce additional leaves (e.g., leaf flushes after budset, and other characteristics  
177 more common to ‘indeterminate’ species, Kikuzawa, 1982; Lechowicz, 1984) may grow more with  
178 longer seasons (though potentially with a lag, see Box, Fig. 3) versus those that budburst later  
179 and flush new primary growth only once. Similarly, species adapted to cold, dry or high latitude  
180 conditions across their range may have different thresholds for when these external drivers limit  
181 or promote growth (e.g., some *Populus* and *Quercus* species, Soolanayakanahally *et al.*, 2013;  
182 McKown *et al.*, 2016; ?; de Sauvage *et al.*, 2022). Such differences could easily obscure any  
183 overall relationship between growth and growing season length. Supporting this possibility,  
184 current studies finding divergent results (Fig. ??, Fig. 5) span a wide range of species (we found  
185 57 species from 26 genera across 36 papers). While this diversity may appear to make identifying  
186 a common relationship between growth and growing season length more difficult, it may instead

<sup>187</sup> offer the path to an improved framework.

## <sup>188</sup> **Building a new framework for growth × season length relationships**

<sup>189</sup> Useful models of tree growth for climate change forecasting have to include a diversity of different  
<sup>190</sup> species, while overcoming the challenges of uneven sampling across species and their contrasting  
<sup>191</sup> responses. Leveraging the diversity of responses observed across species is possible by integrat-  
<sup>192</sup> ing ecological advances in how species traits and evolutionary history shape species responses  
<sup>193</sup> to climate change (Cornwell & Nakagawa, 2017). In particular, advances in phylogenetic com-  
<sup>194</sup> parative methods (Webb *et al.*, 2002) have moved research away from treating species identity  
<sup>195</sup> as a simple grouping factor where each species is unique (e.g., *Fagus sylvatica* is different from  
<sup>196</sup> *Quercus robur* and *Pinus sylvestris*) or fits into a limited set of groups (e.g., deciduous versus  
<sup>197</sup> evergreen) and towards species as suites of correlated observations, separated by their evolu-  
<sup>198</sup> tionary distance (*Fagus sylvatica* is much more closely related to *Quercus robur* compared to  
<sup>199</sup> *Pinus sylvestris*). New models built from these advances can fit data from all species at once  
<sup>200</sup> and layer in species-level information. Traits can capture differences in growth strategies while  
<sup>201</sup> phylogeny can capture additional species differences, which likely capture unmeasured ‘latent’  
<sup>202</sup> traits (Pearse *et al.*, 2019; Morales-Castilla *et al.*, 2024).

<sup>203</sup> In step with these advances, trait ecology has documented leaf and wood economic spectra that  
<sup>204</sup> suggest major traits to include in these models (with related databases of these traits often  
<sup>205</sup> available, Chave *et al.*, 2009; Diaz *et al.*, 2016). These ‘economics’ define a common trade-off  
<sup>206</sup> along an acquisitive to conservative axis, where some species grow rapidly and more flexibly to  
<sup>207</sup> take advantage of resources, but are less defended against herbivores and compete poorly at low  
<sup>208</sup> resource levels, whereas other species compete well at low resource levels, but at the expense of  
<sup>209</sup> growing slower (Grime, 1977; Chave *et al.*, 2009; Diaz *et al.*, 2016). While these traits likely miss  
<sup>210</sup> critical components for understanding how growing season length shapes growth, such as when  
<sup>211</sup> different species invest in shoot and leaf versus wood growth, they provide a baseline from which  
<sup>212</sup> to build, and a powerful approach to combine data usefully across species. This approach has  
<sup>213</sup> already been used to identify that early-leafout species often show faster-growing more acquisitive  
<sup>214</sup> strategies compared to later-leafout species (Cleland & Wolkovich, 2024)—differences that may  
<sup>215</sup> also impact how they respond to longer seasons.

<sup>216</sup> In addition to naturally organizing species differences, a trait-based phylogenetic comparative  
<sup>217</sup> approach can help build a more testable and predictable framework. Because this approach can  
<sup>218</sup> flexibly fit evolutionary history and traits together, it allows clades or species groupings that  
<sup>219</sup> respond similarly to emerge from the data and models (Davies *et al.*, 2019), versus being a priori  
<sup>220</sup> grouped or defined. Similarly traits that co-vary with different responses can be more quickly  
<sup>221</sup> identified (e.g., Willis *et al.*, 2008; Davies *et al.*, 2019, see Fig. 8). Both of these benefits could  
<sup>222</sup> help identify which species or traits to focus additional studies on to gain the most insights, while  
<sup>223</sup> 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, 4), 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. 6- 7)—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. 9). 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 of growth × growing season length to date have focused on (Fig. 4), since the same tree rings

261 measured for understanding spatial variation will also capture inter-annual variation.

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

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

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

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

287 The complexity of climate change and plant growth in response to longer, warmer seasons  
288 makes experiments vital to building useful mechanistic models for forecasting. Observational  
289 data—used mainly to date to tackle this question (Figs. 4, ??)—generally confounds multiple  
290 external drivers, including season length, temperature and precipitation regimes (Ren *et al.*,  
291 2019; Canadell *et al.*, 2021; Camarero *et al.*, 2022), making it impossible to tease out actual  
292 drivers behind observed trends. Experiments, in contrast, can provide more robust tests. While  
293 juvenile stages of trees are often more flexible than their adult forms, they still usually provide  
294 predictable inference in differences across species and populations, and so should be integrated  
295 far more into studies of how season length affects growth. Using saplings and controlled en-  
296 vironments could quickly test how much growth can shift with longer seasons—providing a  
297 potentially standardized way to compare constraints across species and populations—and then

layer on shifts in external drivers.

In particular, mechanistic models will need to tease out changes in season length from warming that affects rates; a challenge best addressed by new experiments that decouple these two factors. Such experiments could start on juvenile trees to help inform the underlying model, select representative species to focus on, and develop predictions for large-scale studies. Experiments could also inform a better model of lag effects across species, with small-scale studies sampling saplings multiple years after manipulations (versus the common practice of destructive sampling at the end of the treatment growing season) and large-scale studies following existing efforts to test for ecological ‘memory’ (e.g. Flinker *et al.*, 2021; Schweiger *et al.*, 2022; Chin *et al.*). These efforts should help bridge across the contrasting timescales of current physiological and dendrochronological studies of growing season length: 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.

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

*Conclusions:* Anthropogenic climate change has often been described as an unfortunate and unplanned experiment. Like many experiments, it has highlighted important biology we do not know well. 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 across species. A mechanistic understanding of how these drivers integrate over species diverse growth strategies and the imprints of evolutionary history to affect growth today is possible, but will require new approaches. Starting now to leverage data across species to inform and design new large-scale studies and experiments be critical for accurate models of future forest and related carbon dynamics, with implications for projections of carbon sequestration and carbon markets.

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583 2 Figures

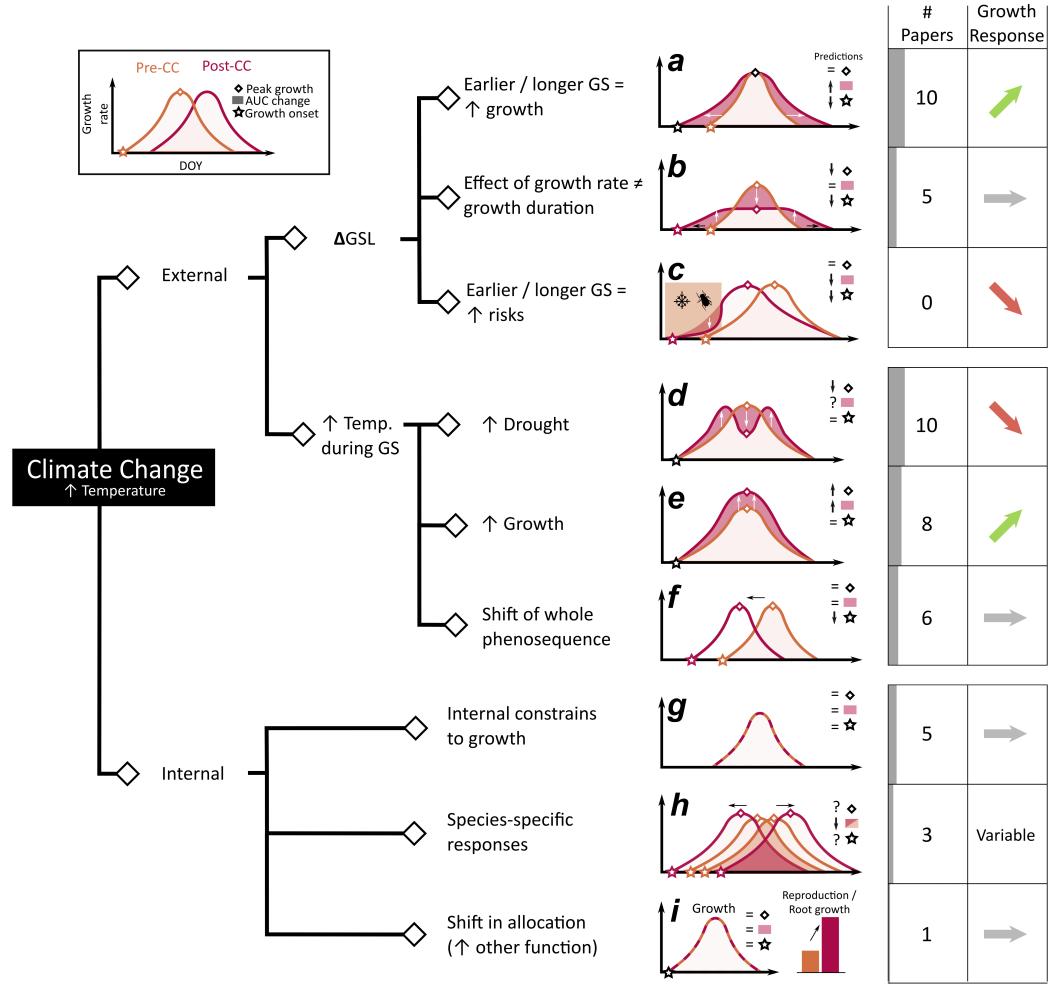


Figure 1: Climate change may alter growing season (GS) length, which can then affect growth through diverse pathways. We review hypotheses for these pathways showing the number of papers (from a review of papers studying growth  $\times$  growing season length) that mentioned each hypothesis (width of 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.

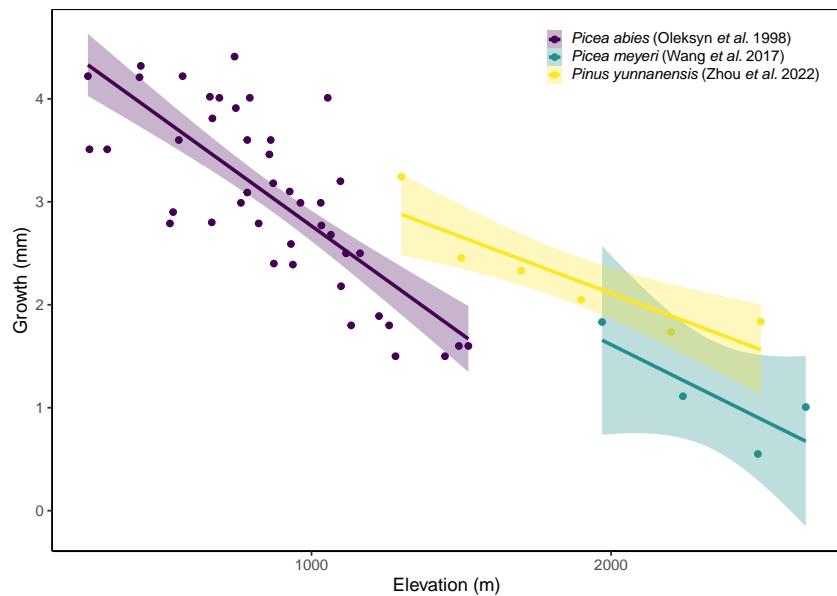


Figure 2: Growth  $\times$  elevation relationships from the literature with simple linear regression fits shown with 89% confidence intervals. Oleksyn *et al.* (1998) measured growth (mm) as diameter at breast height increments, while the other studies (Wang *et al.*, 2017; Zhou *et al.*, 2022) measured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

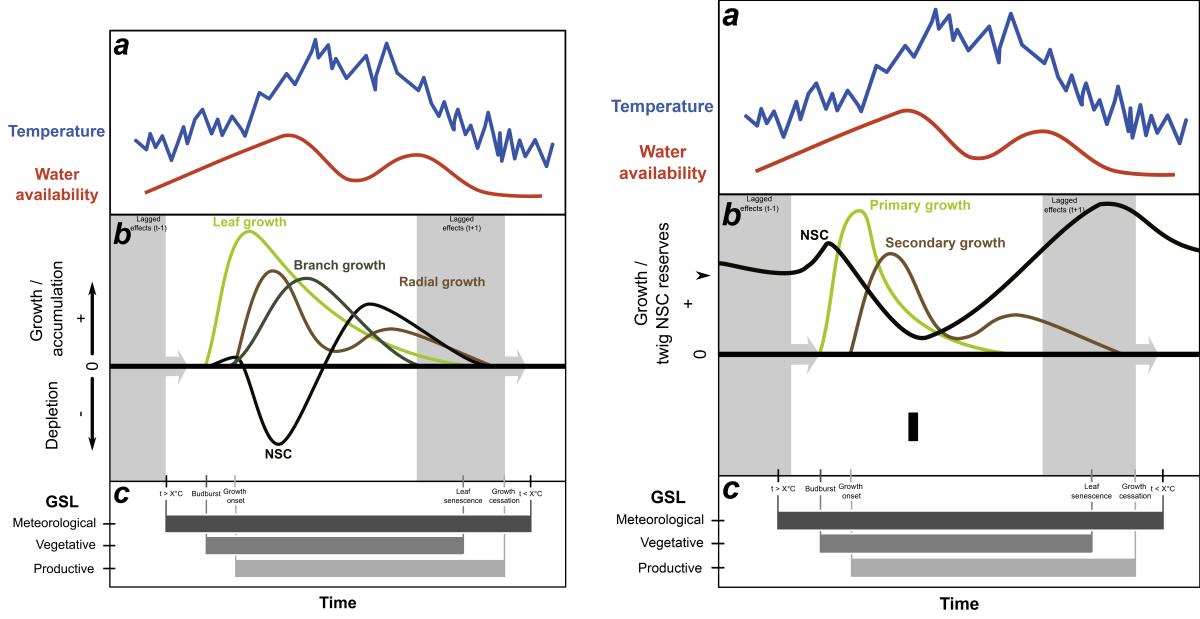


Figure 3: A major challenge in determining how growth responds to longer growing seasons is the complexity of each. Here we show the simplified climate of one year (a), which drives variation (b) in primary growth (root, shoot and leaf elongation) and secondary growth (radial wood growth), both of which often depend on growth from previous seasons. Each of these types of growth could define the growing season length (GSL, c) but similarly it can be defined meteorologically (e.g., days above  $5^{\circ}\text{C}$  with some level of soil moisture) or by large-scale measures of plant productivity (Körner *et al.*, 2023). See also ‘The challenge of metrics: Measuring growth and growing season length’ in the Supplement. [TWO versions of figure shown here currently—please comment if you have a strong preference.]

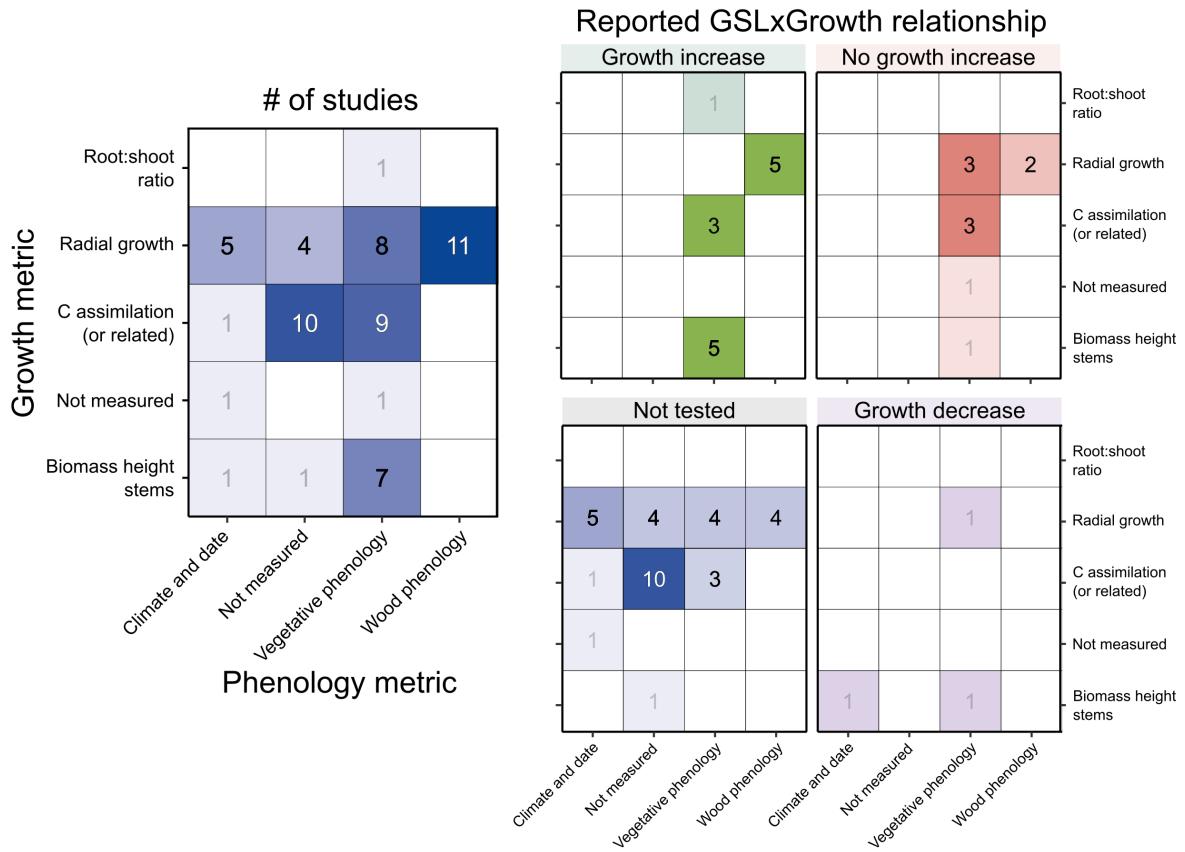


Figure 4: A review of growth  $\times$  growing season length relationship studies spanned a diversity of methods, but there was no coherency in which methods did or did not find a positive relationship. A number of studies tested relationships possibly related to growth  $\times$  growing season length (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.

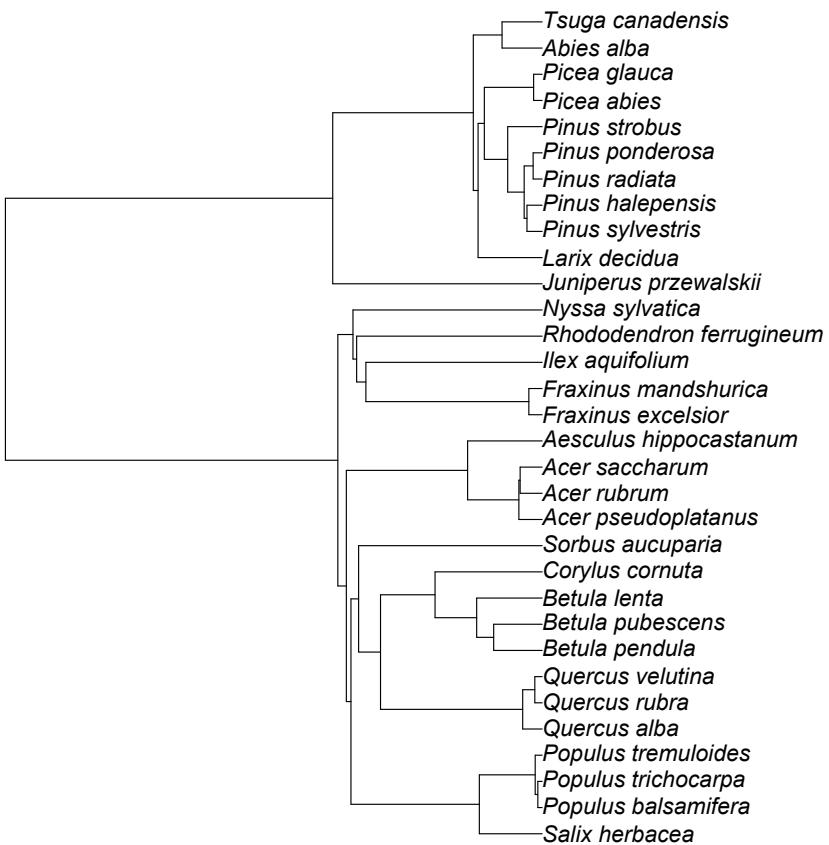


Figure 5: We could switch Fig. ?? from Supp to main text and plot on phylogeny ... I just had time to plot the phylogeny quickly so did not layer on yes/no or find the missing species, like *Fagus*.

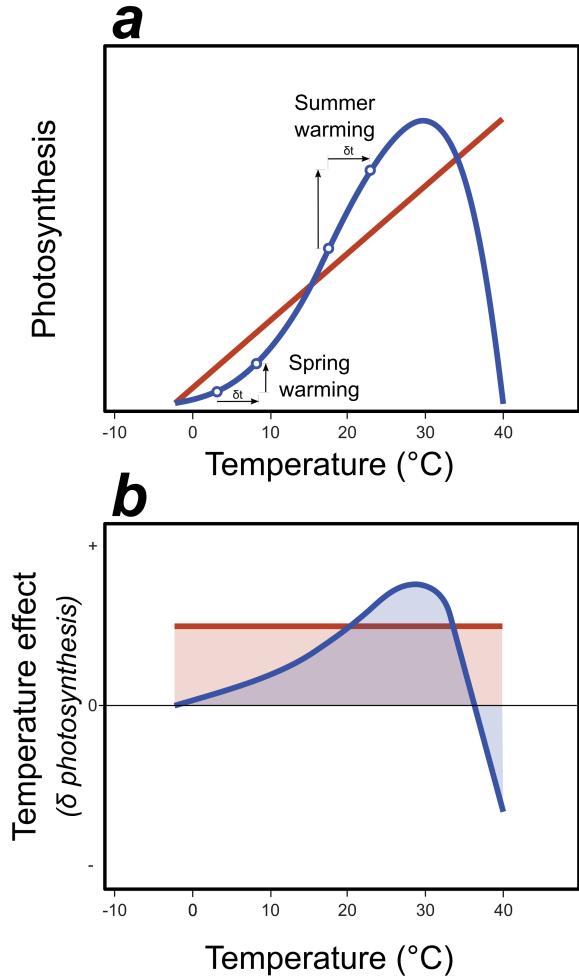


Figure 6: (a) Growth responses to temperature depends on a suite of complex factors and is often represented as net photosynthesis, which has a non-linear response to temperature (blue curve, adapted from meta-analysis of Rezende & Bozinovic, 2019), though it is often modeled as linear (red). (b) This 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.

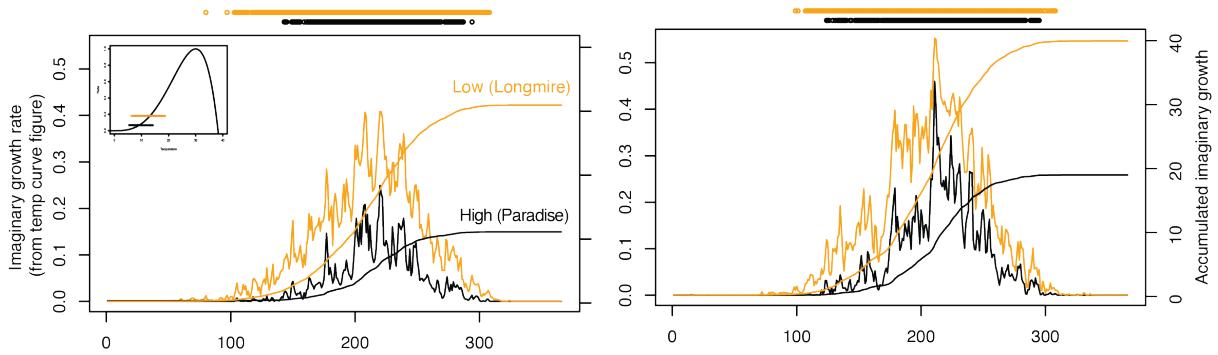


Figure 7: (DRAFT of potential new figure): Testing how growth varies across larger spatial gradients of growing season length could help establish a baseline expectation of the scale of temporal—especially inter-annual variation—and force a greater reckoning with drivers that shift alongside growing 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  $5^{\circ}\text{C}$  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?]

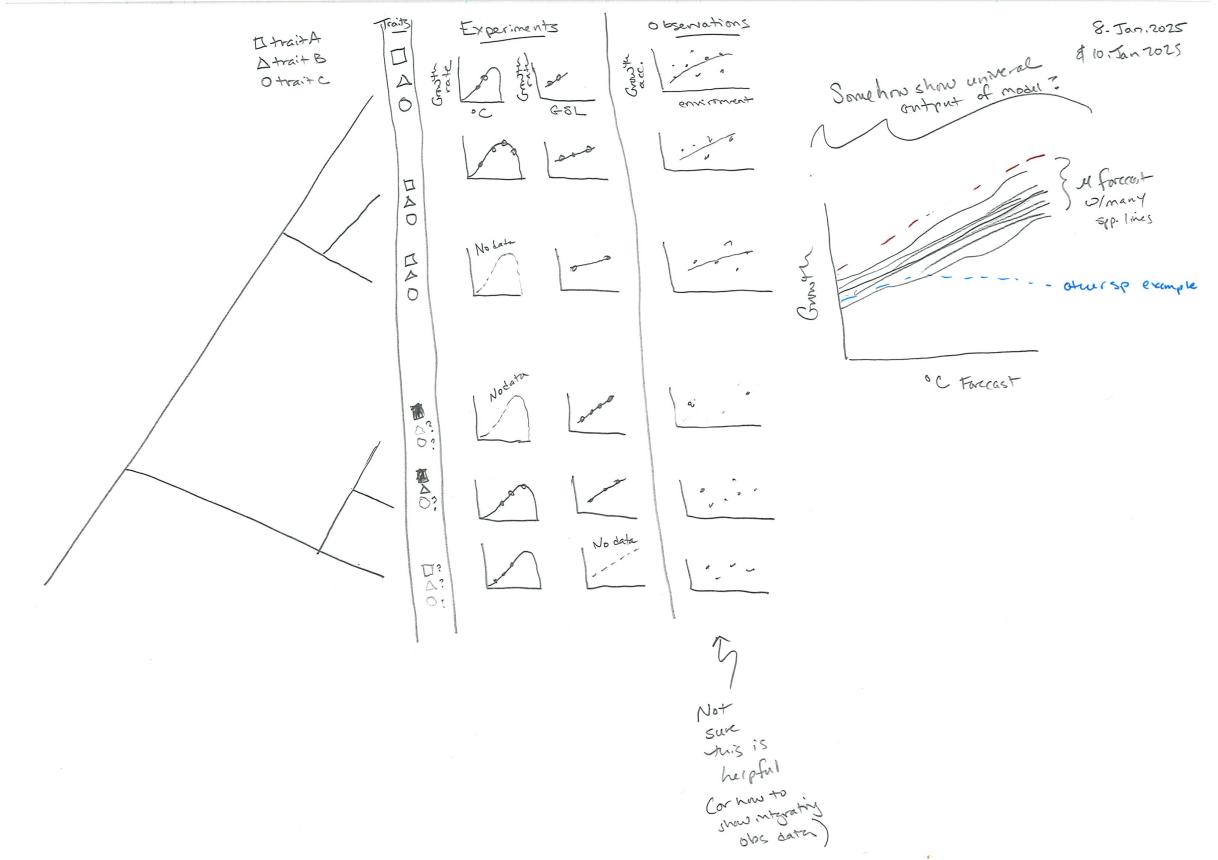


Figure 8: (DRAFT of potential new figure): A trait-based phylogenetic model provides a way to naturally organize species (and, not shown, population) responses to predict how they will respond to longer seasons. This approach leverages species shared evolutionary history (shown at left via a phylogenetic tree) to produce a universal model across species while also predicting how each species should uniquely respond while handling unevenness in sampling and missing data (the ‘no data’ curves represent that the model will predict a curve for each species, informed to various degrees—with the degree determined by the model—by the traits and phylogeny). 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 – ACTUALLY, I do not sow this, but could).

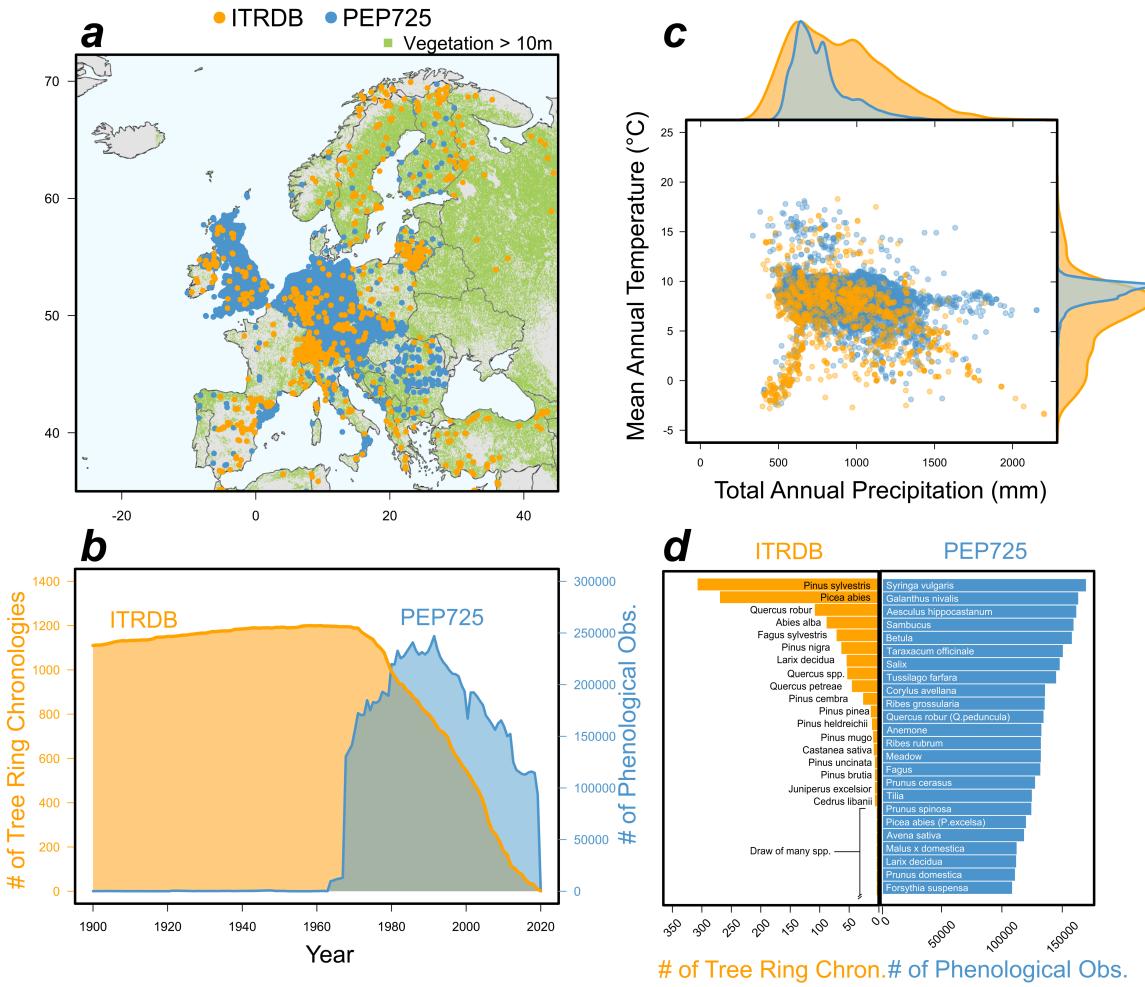


Figure 9: Data overlap between the two major databases of growth (International Tree Ring Data Bank, ITRDB, orange) and plant phenology (Pan European Phenology Project, PEP725, blue). Both databases are compared in terms of their spatial distributions (a), temporal overlaps (b), coverage of environmental 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.