

1 Thesis Proposal

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4 **1 Introduction**

5 **1.1 Climate change impacts on tree phenology**

6 Research from the past decades has shown convincing evidence that human activity is increasingly affecting
7 many worldwide environmental processes (Ceballos *et al.*, 2017; Intergovernmental Panel On Climate
8 Change (Ipcc), 2023; Laurance, 2007; Parmesan & Yohe, 2003). This can be through land use change and
9 destruction, pollution, invasive species, resource overexploitation and climate change (Driscoll *et al.*, 2018;
10 Parmesan *et al.*, 1999; Wu, 2013). That alone raises major concern, and actions have been deployed to
11 mitigate these impacts, with varying success (e.g. (Campbell *et al.*, 2014)). Even though immediate actions
12 can have positive impacts and potentially reduce some threats to biodiversity, reversing 150 years of human-
13 induced greenhouse gas emissions is harder. These emissions have affected Earth's climate and are projected
14 to keep changing it for many centuries (Intergovernmental Panel On Climate Change (Ipcc), 2023). While
15 there is a scientific consensus that observed climate change is human-caused (Change, 2014; Lynas *et al.*,
16 2021; Oreskes, 2004), the magnitude and the extent of the consequences that a warming climate will have
17 on biological processes are still debatable (Huey *et al.*, 2012). Historically, the first case of attribution of a
18 biological change to climate change was on poleward shifts of European butterflies in Europe in response to
19 regional warming (Parmesan *et al.*, 1999).

20 **1.1.2. Trends of spring and autumn phenological events and their drivers**

21 The most frequently observed biological impact of climate change over the past decades is major changes in
22 spring and autumn phenology—the timing of recurring life history events (Parmesan & Yohe, 2003; Cleland
23 *et al.*, 2007; Lieth *et al.*, 1974; Woolway *et al.*, 2021; Menzel *et al.*, 2006). Understanding the consequences
24 of these shifts on ecosystems requires understanding how much the growing season has changed (Duputié
25 *et al.*, 2015). Spring phenological events (e.g. budburst and leafout) have been advancing from 0.5 (Wolfe
26 *et al.*, 2005) to 4.2 days/decade (Chmielewski & Rötzer, 2001; Fu *et al.*, 2014) and are mainly driven by
27 temperature (Chuine, 2010; Cleland *et al.*, 2007; Peñuelas & Filella, 2001). In contrast, autumn phenology
28 (e.g. budset and leaf senescence) is delayed, though to a much lesser extent than spring (Gallinat *et al.*,
29 2015; Jeong & Medvigh, 2014). The drivers regulating autumn phenology are far less understood than
30 those of spring for many reasons. First, autumn phenology has attracted much less attention compared to
31 spring (Piao *et al.*, 2019). Second, the data is often much noisier, since meteorological conditions in the
32 fall can drastically influence phenological phenomena. To illustrate this, trees going through leaf senescence
33 are subjected to a gradual leaf abscission that follows nutrient reabsorption, and the leaves within the same
34 individual might be at different senescence stages, but a strong wind spell may trigger leaf drop for all leaves,
35 thus affecting the temporal resolution of these data (Wu *et al.*, 2024). However, there is a general belief
36 that autumn phenophases are driven by shortening photoperiod and colder temperatures (Cooke *et al.*, 2012;
37 Flynn & Volkovich, 2018; Körner & Basler, 2010; Delpierre *et al.*, 2016). Different hypotheses are proposed
38 to explain delayed autumn phenophases. First, warmer autumn temperatures may extend the activity of
39 photosynthetic enzymes, which could be maintained at a higher level. Thus, the degradation rate of chloro-
40 phyll would decrease and the timing of senescence would be delayed (Yan *et al.*, 2021). Second, summer
41 droughts could make trees pause their activity schedule and delay senescence to increase carbon assimilation
42 (Dox *et al.*, 2022). Third, there could be an antagonistic effect of warming and brightening—caused by
43 reductions in atmospheric pollution and cloud cover (Sanchez-Lorenzo *et al.*, 2015)—on leaf senescence (Wu

45 *et al.*, 2021). Brightening accelerates the leaf senescence processes and reduces the temperature sensitivity
46 during that period, counteracting the expected warming-induced delays in leaf senescence (Wu *et al.*, 2021).
47 The photo-protection and sink limitation hypotheses provide plausible explanations for the negative effect of
48 radiation on leaf senescence and the declining effect of temperature sensitivity of leaf senescence in response
49 to brightening (Wu *et al.*, 2021; Zani *et al.*, 2020).

50

51 **1.1.3. Misleading evidence of declining sensitivity to warming**

52 While we have convincing proof that spring events advanced in the past decades, there is evidence that
53 this might decelerate because of declining sensitivity to warming (Fu *et al.*, 2015; Meng *et al.*, 2020). The
54 proposed mechanism is through the action of warmer winters on tree dormancy. In the fall, trees in boreal
55 and temperate forests slowly enter dormancy, which is initiated with budset. During this phase, cold hardi-
56 ness increases, which prepares the tree for the upcoming cold temperatures and prevents tissue damage.
57 Then, the tree enters dormancy, during which a certain duration of cold temperatures (chilling)—with some
58 interaction with photoperiod for some species—is necessary for the trees to be ready to accumulate forcing
59 (Vitasse *et al.*, 2014). In the late winter and early spring, they go through two forms of deacclimation before
60 budburst (Vitasse *et al.*, 2014). When deacclimation is reached, a certain amount of heat (forcing) is required
61 to initiate budburst (Fu *et al.*, 2015). The argument of declining sensitivity appears here: heat requirement
62 is met sooner in warm springs, but it's also negatively correlated with chilling (Fu *et al.*, 2015, 2013; Laube
63 *et al.*, 2014). However, it is this interaction between chilling and forcing requirements that determines the
64 timing of leaf unfolding. In other words, a decrease in chilling accumulation is proposed to explain the ob-
65 served weaker spring temperature sensitivities, where spring forcing loses its relative importance (Fu *et al.*,
66 2015; Meng *et al.*, 2020; Wolkovich *et al.*, 2021). However, a meta-analysis compiling 72 studies of 203 species
67 suggests that declining sensitivities observed in Europe may be a statistical artifact of how these responses
68 are calculated, thus casting doubt on this proposed trend (Ettinger *et al.*, 2020). This statistical artifact is
69 explained to be caused by using linear models for calculating non-linear processes (Wolkovich *et al.*, 2021).

70

71 **1.1.4. Mechanisms that could limit growth despite having a longer growing season**

72 Plants' seasonal activity has internal and external controls, both determined by environmental conditions
73 (Wolkovich *et al.*, 2025). Internal controls operate via autonomous clocks, activating genes and releasing
74 hormones which often rely on chilling and/or photoperiod (Körner *et al.*, 2023). The external controls, often
75 referred to as forcing, act directly on the developmental rate, meristem activity, tissue differentiation and
76 metabolism (Körner *et al.*, 2023). Understanding how these controls operate is critical to our comprehen-
77 sion of plants' capacity to adjust their activity schedule in response to changing conditions (Chuine & Régnière,
78 2017). In light of this, I hypothesize two possible drivers that could explain why a longer growing season
79 might not lead to increased growth: external (environmental) (Kolář *et al.*, 2016) and internal (Zohner *et al.*,
80 2023) constraints to growth (Wolkovich *et al.*, 2025).

81

82 **1.1.4.1. External constraints**

83 The complex nature of climate change makes predicting the external limits to growth hard to quantify at
84 the individual level, as these drivers affect communities as a whole. However, drought, spring frost and
85 heat waves are commonly mentioned as the main extreme events that could limit tree growth under climate
86 change (Tyree & Zimmermann, 2002; Choat *et al.*, 2018; Li *et al.*, 2023; Trenberth *et al.*, 2014; Change,
87 2014; Chiang *et al.*, 2021; Polgar & Primack, 2011; Reinmann *et al.*, 2023). Their definitions, respective
88 mechanisms, global trend of occurrence, consequences and differences among species are described in Tables
89 3.1. (Spring frosts), 3.2. (Droughts) and 3.3. (Heat waves).

90

91 **1.1.4.2. Internal constraints**

92 As for the internal constraints to growth, recent hypotheses propose that broadleaf deciduous tree species
93 may be sink-saturated, such that longer growing seasons with more carbon fixation do not necessarily increase
94 growth (Dow *et al.*, 2022). This one pathway is directly linked to the internal controls of plant growth, which
95 are under strong genetic control. In addition to height and radial growth varying across species, these growth
96 responses also vary by site (Silvestro *et al.*, 2023a; Aitken & Bemmels, 2016). Populations from higher alti-
97 tude or latitude grow less under the same conditions than individuals from lower altitude or latitude (Way &
98 Montgomery, 2015). This is further supported by phenological studies showing that growth cessation arrives

99 earlier from populations of higher latitude, demonstrating local adaptation to potentially avoid fall frost,
100 before nutrient uptake has finished (Aitken & Bemmels, 2016; Vitasse, 2013; Way & Montgomery, 2015).
101 These trees rely on photoperiod cues for setting buds (stopping height growth) (Way & Montgomery, 2015;
102 Soolanayakanahally *et al.*, 2013).

103
104 Growth seasonality has huge consequences on annual growth, but this seasonality is also closely tied to
105 the environmental conditions experienced by an individual. For instance, warming spring temperatures seem
106 to positively affect growth, but recent evidence suggests a shift in this net positive effect near the summer
107 solstice. Indeed Zohner *et al.* (2023) found that warmer temperatures before the solstice advanced the onset
108 of senescence, but it slowed the progression of leaf colouring when temperatures post-solstice were warmer.
109 This further reinforces the importance of understanding how the timing of warmer conditions affects tree
110 species.

111
112 **1.1.5. How these shifts translate into effects on trees/forests is not clear - Pros and cons of**
113 **early/late start/end of season**

114 Shifts in spring and autumn phenology support a long-lasting and intuitive assumption that earlier spring
115 and delayed autumn events lead to longer seasons—and thus increased growth (Keenan *et al.*, 2014; Stridbeck
116 *et al.*, 2022). However, research from the past three years has cast doubt on this hypothesis (Dow *et al.*,
117 2022; Green & Keenan, 2022; Silvestro *et al.*, 2023b). For instance, (Dow *et al.*, 2022) showed that despite an
118 earlier growth onset, neither growth rate nor overall annual increment was increased by longer seasons. This
119 could substantially affect carbon-cycle model projections and thus feedbacks to future climate (Richardson
120 *et al.*, 2013; Swidrak *et al.*, 2013). Starting to grow earlier and stopping later both have pros and cons
121 (Figure 1).

122 Understanding these findings requires answering why trees do not grow more despite longer growing sea-
123 sons. While carbon allocation to above-ground biomass is one of the largest carbon sinks, how this carbon is
124 allocated into wood is poorly understood. Indeed, the linear relationship assumption between wood growth
125 and carbon assimilation is not well supported mechanistically and represents an important limitation of
126 vegetation models (Cabon *et al.*, 2022). Net primary production represents the difference between photosyn-
127 thesis and plant respiration, but this commonly used metric completely omits the representation of growth
128 processes. This is perhaps because of a long-lasting paradigm of source-limited photosynthesis. This has
129 now been debunked with carbon fertilization experiments, supporting evidence that direct environmental
130 constraints on growth may be stronger than those on photosynthesis (Friend *et al.*, 2019; Parent *et al.*,
131 2010). This opens up a new—poorly tested—temperature sensitivity relationship between cambial activity
132 and photosynthesis. Growing evidence suggests that cambial activity may be more sensitive than photo-
133 synthesis to a range of environmental conditions, such as water and nutrient availability, and temperature
134 (Cabon *et al.*, 2022, 2020; Muller *et al.*, 2011; Peters *et al.*, 2021). This demonstrates that carbon projection
135 models that heavily rely on vegetation alone may mislead the amount of carbon sequestered in our forests.

136
137 **1.1.6. Growing season shifts and consequences on forest ecosystems and services**

138 Spring and fall phenological events are shifting with debatable consequences on tree growth. The sensitivity
139 of cambial activity to water, temperature and nutrients has the potential to have far-reaching consequences
140 given the hard-to-predict nature of future climate change, where any of these variables could vary from low to
141 high amplitude (Almagro *et al.*, 2025; Cabon *et al.*, 2022). This expected asymmetry of future environmental
142 changes makes understanding the internal and external limits to growth critical. Especially, the capacity
143 to tease apart different biomes—as for example boreal vs tropical forests are expected to react differently
144 (REF)—is critical and empirical data coming from experiments, but also from observations are paramount
145 to predict the changes of forest carbon offset from human GHG emissions (Wolkovich *et al.*, 2025).

146 **1.2 Nature of the problem, and how to address it**

147 **1.2.1. Past phenological trends can help (or not) predict future phenological changes**

148 Observed phenological trends in the last decades cannot be used directly to extrapolate future phenological
149 changes because: (1) the mechanisms guiding them aren't clear, and (2) phenological responses of trees
150 to warming are very likely to be non-linear (Ettinger *et al.*, 2020; Fu *et al.*, 2013). Indeed, accurate pre-

151 ditions require an in-depth, accurate mechanistic understanding of phenophases and their sensitivities to
152 environmental drivers, especially to temperature and photoperiod (Fu *et al.*, 2013). Therefore, the very
153 foundation of the assumption that longer seasons increase growth may shift with future climate change. The
154 well-observed advance in spring phenology may decelerate, and delayed fall phenology may shift towards
155 earlier leaf senescence (through summer drought-induced growth cessation).

156

157 **1.2.2. The assumption that longer seasons lead to increased growth is called into question**

158 Recent work shows an absence of increased growth despite apparent better environmental conditions, thus
159 casting doubt on a simple and intuitive positive relationship between growing season length and growth. This
160 paradox further emphasizes the need to better understand the drivers regulating growth across biomes, but
161 also how these drivers vary across the species within these biomes. Phenology varies greatly across species
162 (e.g. closely related species tend to budburst at similar times under similar conditions) (Wolkovich *et al.*,
163 2014), but so does the relationship between growth and season length, which may explain the wide variation
164 of this relationship within communities (Buckley & Kingsolver, 2012). This highlights another weakness of
165 current carbon sequestration models that pool species together, which likely overpass important nuances in
166 the growth responses that could be explained by species differences. This may mislead the future of forest
167 carbon source-sink ratios (Green & Keenan, 2022; Cabon *et al.*, 2022). To better understand how different
168 species respond to warming, different strategies can be used.

169

170 First, experiments are paramount to robustly tease apart the external vs internal drivers (e.g. warmer
171 springs from severe drought later in the season—a common co-occurring reality in natural environments)
172 (Morin *et al.*, 2010; Primack *et al.*, 2015). However, experiments are most often performed on juvenile trees,
173 which are critical for their role in forest regeneration projections, but their responses can hardly be translated
174 to mature trees, which hold the overwhelming carbon biomass proportion of forests (Augspurger & Bartlett,
175 2003; Silvestro *et al.*, 2023b; Vitasse, 2013).

176

177 SLeaf phenology through ground-based observations can provide valuable insights into the growth onset
178 and end of trees that are not suitable for experimental trials, since cambial and leaf phenology are closely
179 linked to the other. It is to say that knowing when leaves elongate and colour can guide when trees start
180 and stop growing—fundamental metrics to determine the growing season length. Ground observations have
181 the advantage of providing accurate data on phenological events for specific sites and species. Recently, the
182 widespread use of smartphones has opened a whole new world of possible phenological monitoring through
183 citizen scientists' records of data over much larger areas and for a wider range of species (Dickinson *et al.*,
184 2012; Hufkens *et al.*, 2019; Piao *et al.*, 2019). While there are drawbacks to these observations (e.g. non-
185 standard protocols, highly uneven spatiotemporal distribution of these observations), these methods have a
186 huge potential to diversify the phenology data.

187

188 **1.2.3. Goals of my thesis**

189 Using citizen science data, a common garden study and a large-scale experiment, I aim to better understand
190 how different tree species, at different lifespan stages, vary in their growth responses to different season
191 length.

192

1.3 Complexity of measuring growth and defining growing season length

193

1.3.1. What is a growing season?

194 To understand how trees respond to growing season conditions, it is important to clarify what a growing
195 season and growth are.

196 First, a problem that arises when one tries to quantify how shifting growing seasons affect growth comes from
197 the definition of the growing season itself. Recently, Körner *et al.* (2023) proposed four definitions addressing
198 this issue: (1) true growing season, based on measurable growth; (2) phenological season, based on visible
199 phenological markers; (3) the productive season, based on primary production and (4) meteorological season,
200 based on environmental conditions.

201 Here, I will focus on how definition (2), incorporating (4) affects definition (1) as the data collected
202 for this thesis can't address (3). I will use definition (2) to infer a "window of opportunity" during which

203 meteorological conditions will be used to calculate growing degree days (GDD). I am using the meteorological
204 season within a constrained window, instead of simply using it irrespective of phenology because of the illusion
205 that an absolute increase in GDD over the last decades—irrespective of the timing of phenophases—also
206 increases growth. Springs are warmer, falls are also sometimes warmer, and summers are warmer, which
207 together increase the number of GDD, which may appear to be a reliable proxy for better environmental
208 conditions. However, models that accumulate GDD before and/or after trees grow could mislead about how
209 this variable drives growth.

210 Models using degree-days are still widely used even if they have been employed for decades in agriculture
211 (e.g. (Gilmore & Rogers, 1958; Mcmaster, 1997)). These rely on developmental patterns that are based
212 on temperature dependence to estimate a particular ecological process, in my case, tree-ring width. These
213 models describe a particular response variable as a composite of time and temperature as opposed to time
214 alone. This is a partimonious method that requires three variables: daily minimum and maximum temper-
215 atures and the base temperature at which the process of interest cannot occur (cambial activation in this
216 case) (Mcmaster, 1997; Moore & Remais, 2014). However, this simplicity comes with a drawback of over-
217 simplifying potentially complex developmental processes in response to varying environmental conditions
218 within a season (Bonhomme, 2000).

219

220 *What is growth?*

221 Wood formation (xylogenesis) is the major biological process by which carbon is allocated and long-term
222 stored in woody plants. Radial growth is determined by the production of xylem and phloem cells that begins
223 with cambial activation and cell production by cambial initials, followed by cell differentiation through the
224 following events: (1) Cell enlargement (2) Secondary-wall formation and lignification and (3) programmed
225 cell death (Etzold *et al.*, 2022; Silvestro *et al.*, 2025). The rate and duration of these phases lead to irre-
226 versible radial growth increments usually represented through tree rings. In these, secondary xylem cells
227 account disproportionately to the number of cells produced because they divide more than phloem cells
228 (Plomion *et al.*, 2001; Rathgeber *et al.*, 2016).

229

230 **1.3.2. Traditional diameter measurements miss the resolution of annual growth increment**

231 Foresters have measured tree diameter and height for decades to infer allometries that could give them a
232 good estimate of how much wood they could harvest in a forest (e.g. (Meyer, 1940; Saunders & Wagner,
233 2008)). The widely used method in forestry is to measure diameter at breast height at punctual time
234 intervals (Yuancai & Parresol, 2001). However, these measurements don't provide short-term indicators of
235 growth—especially if taken at multiple-year intervals. Therefore, extreme events affecting growth are likely
236 to be missed. In addition, many forest inventories only report diameter measurements and exclude height,
237 because of logistical constraints ((Saunders & Wagner, 2008)), which reduces biomass estimation quality.
238 This growth data lacks the temporal resolution necessary to properly infer a relationship between growth
239 and environmental conditions.

240

241 Alongside the diameter-height allometric relationship, dendrochronology and its related fields also have
242 long-standing traditions in forestry and silviculture. Indeed, tree-ring research was developed in the early
243 1900s to perform archeological dating and climate reconstruction (Douglass, 1928; Pearl *et al.*, 2020). Since
244 then, different dendrochronology methods have been developed for different purposes, such as the calibration
245 of the terrestrial radiocarbon curve (Helama, 2023; Reimer *et al.*, 2020) and modelling Earth's past climate
246 and ecological change (Pearl *et al.*, 2020). More recently, dendroecology—applications of dendrochronologi-
247 cal techniques to problems in ecology (Fritts & Swetnam, 1989)—emerged to answer ecological problems as
248 well as to hindcast (e.g. (Bergeron *et al.*, 2004)) and forecast ecological processes both at the regional (Gazol
249 *et al.*, 2018) and global scale (Manzanedo & Pederson, 2019; Büntgen *et al.*, 2018). Now, these methods
250 can be used to understand more precise growth patterns and their relationship with different environmental
251 factors.

252

253 **1.3.3. Growth increment needs to incorporate wood density in order to evaluate how much** 254 **structural carbohydrates were stored within a single year.**

255 While tree-ring width is a reliable proxy to how much trees grow in each year, at relatively low cost and
256 time, the inclusion of wood density in the analysis may provide additional information. For example, Čufar

257 *et al.* (2008) showed that intra- and inter-annual density variations in beech provided more information and
258 at a higher temporal resolution than tree-ring widths alone.

259 In addition to densitometry, an increasing number of studies are going beyond traditional ring width by
260 performing analysis using wood anatomy data. For instance, low-cost techniques (e.g. "blue intensity" proxy
261 for latewood density (Babst *et al.*, 2016; Campbell *et al.*, 2007) and high resolution imaging (Griffin *et al.*,
262 2021; Levanič, 2007; Von Arx & Carrer, 2014)) give rise to a whole new world of possibilities regarding the
263 microscopic components of wood anatomical features. Micro-anatomical analyses within tree rings could be
264 applied to a wide range of applications (Pearl *et al.*, 2020). The character of annual rings, cell structure,
265 timing of growth and markers for trauma can assist in answering a variety of ecological and physiological
266 questions previously unanswered with ring width or density alone, such as how growth is affected by growing
267 season length under anthropogenic forcing.

268 **1.3.4. Asynchrony between primary and secondary growth (internal growth control?)**

269 I argue that internal growth control in trees may shape their growth responses to growing season length, and
270 these can be split into two categories: primary and secondary growth synchronicity and growth determinancy.

271 Primary (shoot elongation) and secondary (xylem and phloem formation) growth both contribute to how
272 much carbon is stored in plant tissue, but how much they differ in their responses to environmental drivers
273 is poorly understood. After a dormancy period, trees will start growing, both vertically (primary) and
274 horizontally (secondary), but there is high variation among species as to when each growth starts, for how
275 long it lasts and when it stops. For instance, ring-porous species initiate primary growth early in the season,
276 sometimes even before budburst (e.g. oaks) (Stridbeck *et al.*, 2022), whereas xylogenesis in diffuse-porous
277 species is usually more synchronized with budburst. These two examples highlight how more complicated
278 it might be to infer general conclusions as to how growing season shifts may also shift growth, where some
279 species may extend their primary growth, but restrict their secondary growth and vice versa.

280 In addition to differences in primary and secondary growth synchronicity, the role of internal growth
281 control—often overlooked—may misshape our understanding of growth responses to growing season length
282 (Baumgarten *et al.*, 2025). In perennial plants, two dichotomous growth strategies are commonly mentioned:
283 determinate and indeterminate growth, though it appears that species exist along a gradient of these (Baum-
284 garten *et al.*, 2025). Indeterminate growth is usually associated with short-lived and fast growth species,
285 where these life-history strategies may give them a competing advantage as tissue growth can be produced
286 quickly in response to changing environmental conditions, but this comes with a higher risk of late spring
287 and early fall frost as well as late droughts (Baumgarten *et al.*, 2025; Brienen *et al.*, 2020). At the opposite
288 side of the spectrum, determinate species are usually long-lived and slow-growing and are mainly constrained
289 by conditions during bud formation; this may increase bud survival at the detriment of opportunistic growth
290 in face of better-than-expected conditions (Baumgarten *et al.*, 2025).

291 Thus, primary versus secondary growth allocation, coupled with growth determinancy, are variables often
292 overlooked, but which greatly vary across species and that are likely to affect how trees respond to shifting
293 season length.

294 **1.3.5. Getting growth temporal resolution is labor-intensive and expensive (e.g. dendrometer costs)**

295 To know when trees start and stop growing within a single growing season (data not extractable through
296 tree rings), there are two methods, one being labour-intensive (1) and the other being expensive (2).

297 1. Trehor is a tool that allows recurrent sampling of mature trees where a 2mm microcore is extracted
298 from the tree at different moments during the growing season. By sampling multiple times a single tree,
299 growth temporality can be inferred by counting the ring cell increment between each sample. While this
300 non-destructive tool can be extremely valuable, getting a large sample size can hardly be feasible (Rossi *et al.*,
301 2006).

302 2. Dendrometers allow for monitoring stem radius variation, measuring irreversible secondary growth, but
303 also stem water fluctuations and thermal expansion, often leading to biased estimates of growth increment
304 temporality (Camarero *et al.*, 2010).

308 **1.4 Objectives**

309 My objectives for Fuelinex are to assess tree species' potential to prolong or stretch their activity schedule by
310 artificially manipulating growing season length and analyze how this translates (or not) into growth, during
311 the current year (2024) and in the following year (2025). I will also conduct a secondary experiment to
312 examine whether trees can absorb nutrients late in the season and if that translates into growth during the
313 following season. For the CookieSpotters projects, I will investigate how the timing of phenological events
314 affects growth across years for juvenile and mature trees, using observational phenology data and tree ring.

315 Together, my two chapters will allow me to address the paradox of the absence of increased growth
316 despite longer growing seasons.

317 **1.5 Research questions**

318 *necessary after the objectives? It feels redundant...*

319 Fuelinex: How do extended growing seasons affect tree growth across different species, both immediately
320 (in the same year as the extended season) and in subsequent years? CookieSpotters: How does phenology
321 regulate tree growth in urban ecosystems?

322

323 **3.1. Spring frosts**

Definition:	Late spring frosts are below-freezing temperatures in late spring (Zohner <i>et al.</i> , 2020)
Mechanisms	Early warm spells → early leaf out → hard frost (<-2Celsius) → tissue death = loss of photosynthetic capacity (Polgar & Primack, 2011); Response: second cohort of leaves are more efficient and mitigate carbon sequestration loss (Reinmann <i>et al.</i> , 2023)
Global trend of occurrence	Most vulnerable regions are the ones with no past risk of occurrence (); ↑ in Europe and East Asia, but ↓ North America; Global trend is controversial (Reinmann <i>et al.</i> , 2023)
Consequences (Individual and Ecosystem level consequences)	Loss of vegetative tissue = ↓ photosynthesis = ↓ and remobilization of NSC to repair damaged tissues = ↓ secondary growth (Meyer <i>et al.</i> , 2024); Loss of reproductive tissue (higher flower mortality) (Sgubin <i>et al.</i> , 2018); Costs for orchards and stuff (Reinmann <i>et al.</i> , 2023)
Differences across species/provenance	

325

3.2. Drought

	<p>Definition: "Drought is a prolonged absence or marked deficiency of precipitation that results in water shortage or a period of abnormally dry weather sufficiently prolonged for the lack of precipitation to cause a serious hydrological imbalance (Trenberth <i>et al.</i>, 2014; Intergovernmental panel on climate change, 2007).</p>
	<p>Mechanisms</p> <ul style="list-style-type: none"> — Hot temperature + low precipitation (aka global-change-type drought (Tyree & Zimmermann, 2002)) = ↑ evapotranspiration → less water in soil → cavitation → embolism → hydraulic failure (Tyree & Zimmermann, 2002) = tissue death (Choat <i>et al.</i>, 2018); — Earlier spring phenology = longer GS → increases vegetative growth → increases evapotranspiration → increases drawdown of soil moisture = progressive water stress (Li <i>et al.</i>, 2023) — Long-term vs short-term stomatal responses and consequences on tissue death (Choat <i>et al.</i>, 2018); — Recovery and its determinants (Choat <i>et al.</i>, 2018; Li <i>et al.</i>, 2023)
326	<p>Global trend of occurrence</p> <ul style="list-style-type: none"> — ↑ precipitation anomalies since 1990 (Trenberth <i>et al.</i>, 2014); — Models often exclude PDO/ENSO which limit the capacity to attribute increasing droughts to CC (Trenberth <i>et al.</i>, 2014); — Weak evidence of detection and attribution of changes in meteorological drought since the mid-20th century (Change, 2014); — Using a spacial, model-based perspective, anthropogenic forcing increased the frequency, duration and intensity of SPI-based droughts for North America (Hidalgo <i>et al.</i>, 2009), Europe and the Mediterranean (Spinoni <i>et al.</i>, 2018), (Kurnik <i>et al.</i>, 2011) and E Asia (Chiang <i>et al.</i>, 2021; Marvel <i>et al.</i>, 2019; Spinoni <i>et al.</i>, 2014)
	<p>Consequences (Individual and Ecosystem level consequences)</p> <ul style="list-style-type: none"> — Recurring droughts may limit trees' ability to recover from other types of stress. — Tree mortality (e.g. Texas and California extreme droughts are estimated to have killed 300 and 102 million trees (Li <i>et al.</i>, 2023))
327	<p>Differences across species/provenance</p>

328

3.3. Heat waves

Definition:	Heat wave is a period of excessively hot weather (5 or more consecutive days of prolonged heat in which the daily maximum temperature is higher than the average maximum temperature by 5 °C), which may be accompanied by high humidity (Marx <i>et al.</i> , 2021).
Mechanisms	<p>↑ atmospheric CO₂ = ↑ temperature → ↑ heat waves... More specifically: A mechanism for the increase occurrence of heat waves is a weakening of the polar jet stream (important weather factor for middle latitude regions of North America, Europe and Asia) caused by global warming which increases the occurrence of stationary weather, resulting in heavy rain falls or heat waves (Marx <i>et al.</i>, 2021). Extreme heat → growth either through (1) Directly via cell processes disruption or (2) indirectly via effects of rising leaf-to-air vapor deficit (VPD) (Gagne <i>et al.</i>, 2020).</p> <p>Increased temperature leads to reduced photosynthesis which can be attributed to: 1. Damage to photosynthetic machinery 2. Inactivation of RUBISCO 3. Reduction to RuBP regeneration 4. Membrane stability 5. Increased mitochondrial respiration and photorespiration (Hauck <i>et al.</i>, 2025)</p>
329 Global trend of occurrence	Heat waves have increased (Gagne <i>et al.</i> , 2020; Meehl & Tebaldi, 2004; Teskey <i>et al.</i> , 2015) and are expected to increase under future climate change (Dosio <i>et al.</i> , 2018; Change, 2014; Teskey <i>et al.</i> , 2015). Summertime extreme temperatures associated with prolonged heat waves, lasting for several weeks, now impact approximately 10% of land surfaces, up from only 1% in the 1960s. (Teskey <i>et al.</i> , 2015). The more intense and more frequently occurring heat waves cannot be explained solely by natural climate variations and without human-made climate change (Marx <i>et al.</i> , 2021).
Consequences (Individual and Ecosystem level consequences)	- Reduced photosynthesis - Increased mortality - Photosynthetic tissue loss (Gagne <i>et al.</i> , 2020).
Differences across species/provenance	Some species have thermal photosynthetic/respiratory acclimation while others don't. Growth and survival will change depending on species to thermally acclimate to both photosynthesis and respiration - This is explained by growth strategies of gymnosperms vs angiosperms (which are usually better)

330 References

- 331 Aitken, S.N. & Bemmels, J.B. (2016). Time to get moving: assisted gene flow of forest trees. *Evolutionary Applications*, 9, 271–290.
- 332
- 333 Almagro, D., Martin-Benito, D., Rossi, S., Conde, M., Fernández-de-Uña, L. & Gea-Izquierdo, G. (2025). Long-Term Cambial Phenology Reveals Diverging Growth Responses of Two Tree Species in a Mixed Forest Under Climate Change. *Global Change Biology*, 31, e70503.
- 334
- 335
- 336 Augspurger, C.K. & Bartlett, E.A. (2003). Differences in leaf phenology between juvenile and adult trees in a temperate deciduous forest. *Tree Physiology*, 23, 517–525.
- 337
- 338 Babst, F., Wright, W.E., Szejner, P., Wells, L., Belmecheri, S. & Monson, R.K. (2016). Blue intensity parameters derived from Ponderosa pine tree rings characterize intra-annual density fluctuations and reveal seasonally divergent water limitations. *Trees*, 30, 1403–1415.
- 339
- 340
- 341 Baumgarten, F., Aitken, S., Vitasse, Y., Guy, R.D. & Wolkovich, E. (2025). Invest now, get paid later? Limits and opportunities of woody plants to time growth in a future climate. *In review*.
- 342
- 343 Bergeron, Y., Gauthier, S., Flannigan, M. & Kafka, V. (2004). Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. *Ecology*, 85, 1916–1932.
- 344
- 345 Bonhomme, R. (2000). Bases and limits to using ‘degree.day’ units. *European Journal of Agronomy*, 13, 1–10.
- 346

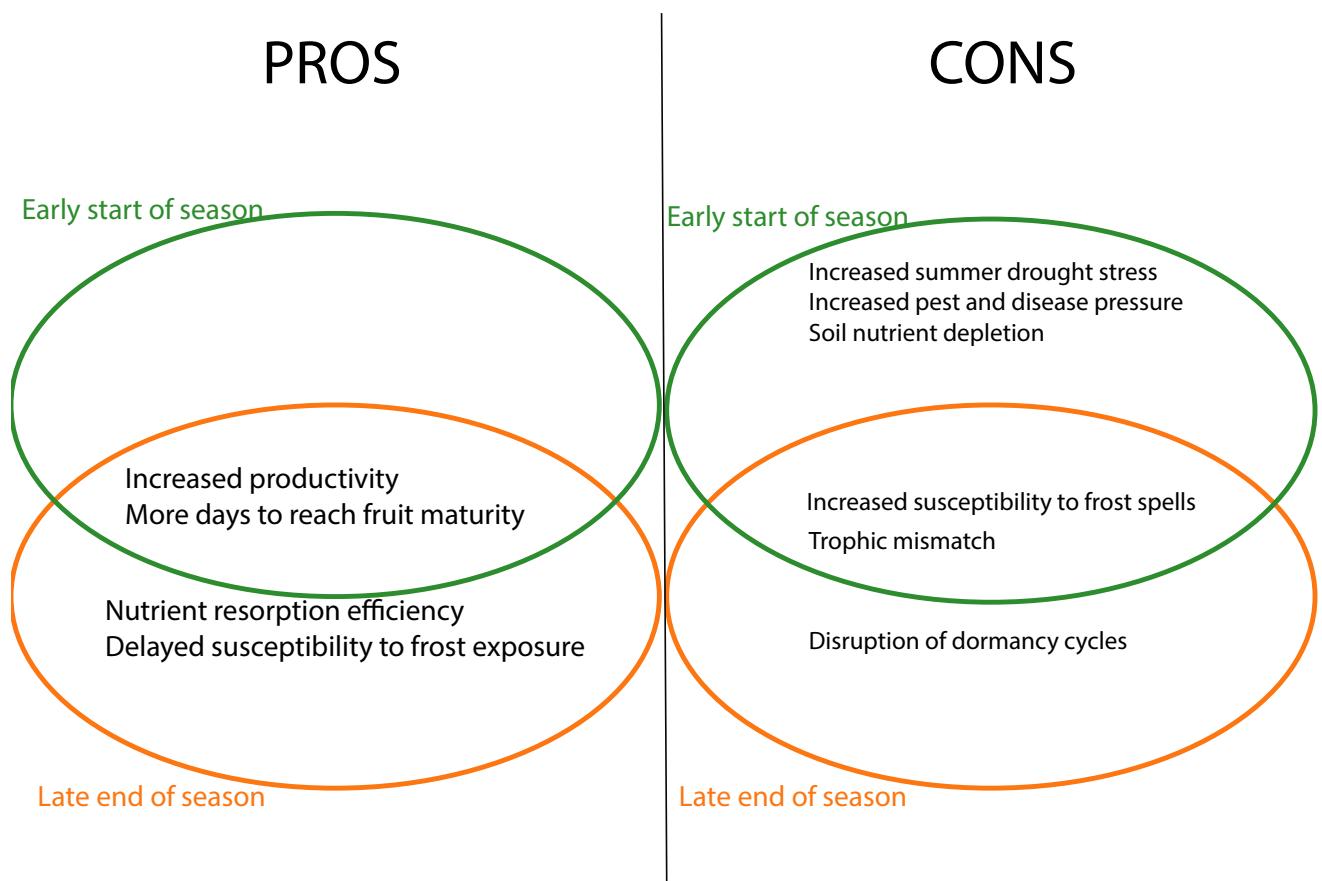


Figure 1: Pros and cons of early start and late end of growing season.

- 347 Brienen, R.J.W., Caldwell, L., Duchesne, L., Voelker, S., Barichivich, J., Baliva, M., Ceccantini, G., Di Fil-
348 ippo, A., Helama, S., Locosselli, G.M., Lopez, L., Piovesan, G., Schöngart, J., Villalba, R. & Gloor, E.
349 (2020). Forest carbon sink neutralized by pervasive growth-lifespan trade-offs. *Nature Communications*,
350 11, 4241.
- 351 Buckley, L.B. & Kingsolver, J.G. (2012). Functional and Phylogenetic Approaches to Forecasting Species'
352 Responses to Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, 43, 205–226.
- 353 Büntgen, U., Wacker, L., Galván, J.D., Arnold, S., Arseneault, D., Baillie, M., Beer, J., Bernabei, M.,
354 Bleicher, N., Boswijk, G., Bräuning, A., Carrer, M., Ljungqvist, F.C., Cherubini, P., Christl, M., Christie,
355 D.A., Clark, P.W., Cook, E.R., Esper, J., Fowler, A.M., Gennaretti, F., Grießinger, J., Grissino-Mayer,
356 H., Grudd, H., Gunnarson, B.E., Hantemirov, R., Herzig, F., Hessl, A., Heussner, K.U., Jull, A.J.T.,
357 Kukarskikh, V., Kirdyanov, A., Krusic, P.J., Kyncl, T., Lara, A., LeQuesne, C., Linderholm, H.W., Loader,
358 N.J., Luckman, B., Miyake, F., Myglan, V.S., Nicolussi, K., Oppenheimer, C., Palmer, J., Panyushkina, I.,
359 Pederson, N., Rybníček, M., Schweingruber, F.H., Seim, A., Sigl, M., Churakova, O., Speer, J.H., Synal,
360 H.A., Tegel, W., Treydte, K., Villalba, R., Wiles, G., Wilson, R., Winship, L.J., Wunder, J., Yang, B. &
361 Young, G.H.F. (2018). Tree rings reveal globally coherent signature of cosmogenic radiocarbon events in
362 774 and 993 CE. *Nature Communications*, 9, 3605.
- 363 Cabon, A., Fernández-de-Uña, L., Gea-Izquierdo, G., Meinzer, F.C., Woodruff, D.R., Martínez-Vilalta, J. &
364 De Cáceres, M. (2020). Water potential control of turgor-driven tracheid enlargement in Scots pine at its
365 xeric distribution edge. *New Phytologist*, 225, 209–221.
- 366 Cabon, A., Kannenberg, S.A., Arain, A., Babst, F., Baldocchi, D., Belmecheri, S., Delpierre, N., Guerrieri,
367 R., Maxwell, J.T., McKenzie, S., Meinzer, F.C., Moore, D.J.P., Pappas, C., Rocha, A.V., Szejner, P.,
368 Ueyama, M., Ulrich, D., Vincke, C., Voelker, S.L., Wei, J., Woodruff, D. & Anderegg, W.R.L. (2022).
369 Cross-biome synthesis of source versus sink limits to tree growth. *Science*, 376, 758–761.
- 370 Camarero, J.J., Olano, J.M. & Parras, A. (2010). Plastic bimodal xylogenesis in conifers from continental
371 Mediterranean climates. *New Phytologist*, 185, 471–480.
- 372 Campbell, L.M., Hagerman, S. & Gray, N.J. (2014). Producing Targets for Conservation: Science and Politics
373 at the Tenth Conference of the Parties to the Convention on Biological Diversity. *Global Environmental
374 Politics*, 14, 41–63.
- 375 Campbell, R., McCarroll, D., Loader, N.J., Grudd, H., Robertson, I. & Jalkanen, R. (2007). Blue intensity
376 in *Pinus sylvestris* tree-rings: developing a new palaeoclimate proxy. *The Holocene*, 17, 821–828.
- 377 Ceballos, G., Ehrlich, P.R. & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction
378 signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*,
379 114.
- 380 Change, I.P.O.C. (2014). Detection and Attribution of Climate Change: from Global to Regional. In:
381 *Climate Change 2013 – The Physical Science Basis*. Cambridge University Press, pp. 867–952. 1st edn.
- 382 Chiang, F., Mazdiyasni, O. & AghaKouchak, A. (2021). Evidence of anthropogenic impacts on global drought
383 frequency, duration, and intensity. *Nature Communications*, 12, 2754.
- 384 Chmielewski, F.M. & Rötzer, T. (2001). Response of tree phenology to climate change across Europe.
385 *Agricultural and Forest Meteorology*, 108, 101–112.
- 386 Choat, B., Brodribb, T.J., Brodersen, C.R., Duursma, R.A., López, R. & Medlyn, B.E. (2018). Triggers of
387 tree mortality under drought. *Nature*, 558, 531–539.
- 388 Chuine, I. (2010). Why does phenology drive species distribution? *Philosophical Transactions of the Royal
389 Society B: Biological Sciences*, 365, 3149–3160.
- 390 Chuine, I. & Régnière, J. (2017). Process-Based Models of Phenology for Plants and Animals. *Annual
391 Review of Ecology, Evolution, and Systematics*, 48, 159–182.

- 392 Cleland, E., Chuine, I., Menzel, A., Mooney, H. & Schwartz, M. (2007). Shifting plant phenology in response
393 to global change. *Trends in Ecology & Evolution*, 22, 357–365.
- 394 Cooke, J.E.K., Eriksson, M.E. & Junntila, O. (2012). The dynamic nature of bud dormancy in trees:
395 environmental control and molecular mechanisms. *Plant, Cell & Environment*, 35, 1707–1728.
- 396 Delpierre, N., Vitasse, Y., Chuine, I., Guillemot, J., Bazot, S., Rutishauser, T. & Rathgeber, C.B.K. (2016).
397 Temperate and boreal forest tree phenology: from organ-scale processes to terrestrial ecosystem models.
398 *Annals of Forest Science*, 73, 5–25.
- 399 Dickinson, J.L., Shirk, J., Bonter, D., Bonney, R., Crain, R.L., Martin, J., Phillips, T. & Purcell, K. (2012).
400 The current state of citizen science as a tool for ecological research and public engagement. *Frontiers in
401 Ecology and the Environment*, 10, 291–297.
- 402 Dosio, A., Mentaschi, L., Fischer, E.M. & Wyser, K. (2018). Extreme heat waves under 1.5 °C and 2 °C
403 global warming. *Environmental Research Letters*, 13, 054006.
- 404 Douglass, A. (1928). Climate and trees. *Nature Magazine*, 12, 51–53.
- 405 Dow, C., Kim, A.Y., D'Orangeville, L., Gonzalez-Akre, E.B., Helcoski, R., Herrmann, V., Harley, G.L.,
406 Maxwell, J.T., McGregor, I.R., McShea, W.J., McMahon, S.M., Pederson, N., Tepley, A.J. & Anderson-
407 Teixeira, K.J. (2022). Warm springs alter timing but not total growth of temperate deciduous trees.
408 *Nature*, 608, 552–557.
- 409 Dox, I., Skrøppa, T., Decoster, M., Prislan, P., Gascó, A., Gričar, J., Lange, H. & Campioli, M. (2022).
410 Severe drought can delay autumn senescence of silver birch in the current year but advance it in the next
411 year. *Agricultural and Forest Meteorology*, 316, 108879.
- 412 Driscoll, D.A., Bland, L.M., Bryan, B.A., Newsome, T.M., Nicholson, E., Ritchie, E.G. & Doherty, T.S.
413 (2018). A biodiversity-crisis hierarchy to evaluate and refine conservation indicators. *Nature Ecology &
414 Evolution*, 2, 775–781.
- 415 Duputié, A., Rutschmann, A., Ronce, O. & Chuine, I. (2015). Phenological plasticity will not help all species
416 adapt to climate change. *Global Change Biology*, 21, 3062–3073.
- 417 Ettinger, A.K., Chamberlain, C.J., Morales-Castilla, I., Buonaiuto, D.M., Flynn, D.F.B., Savas, T., Samaha,
418 J.A. & Wolkovich, E.M. (2020). Winter temperatures predominate in spring phenological responses to
419 warming. *Nature Climate Change*, 10, 1137–1142.
- 420 Etzold, S., Sterck, F., Bose, A.K., Braun, S., Buchmann, N., Eugster, W., Gessler, A., Kahmen, A., Peters,
421 R.L., Vitasse, Y., Walther, L., Ziemińska, K. & Zweifel, R. (2022). Number of growth days and not length
422 of the growth period determines radial stem growth of temperate trees. *Ecology Letters*, 25, 427–439.
- 423 Flynn, D.F.B. & Wolkovich, E.M. (2018). Temperature and photoperiod drive spring phenology across all
424 species in a temperate forest community. *New Phytologist*, 219, 1353–1362.
- 425 Friend, A.D., Eckes-Shephard, A.H., Fonti, P., Rademacher, T.T., Rathgeber, C.B.K., Richardson, A.D. &
426 Turton, R.H. (2019). On the need to consider wood formation processes in global vegetation models and
427 a suggested approach. *Annals of Forest Science*, 76, 49.
- 428 Fritts, H. & Swetnam, T. (1989). Dendroecology: A Tool for Evaluating Variations in Past and Present
429 Forest Environments. In: *Advances in Ecological Research*. Elsevier, vol. 19, pp. 111–188.
- 430 Fu, Y.H., Campioli, M., Deckmyn, G. & Janssens, I.A. (2013). Sensitivity of leaf unfolding to experimental
431 warming in three temperate tree species. *Agricultural and Forest Meteorology*, 181, 125–132.
- 432 Fu, Y.H., Piao, S., Op De Beeck, M., Cong, N., Zhao, H., Zhang, Y., Menzel, A. & Janssens, I.A. (2014).
433 Recent spring phenology shifts in western Central Europe based on multiscale observations. *Global Ecology
434 and Biogeography*, 23, 1255–1263.

- 435 Fu, Y.H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., Ciais, P., Huang, M., Menzel, A., Peñuelas,
 436 J., Song, Y., Vitassee, Y., Zeng, Z. & Janssens, I.A. (2015). Declining global warming effects on the
 437 phenology of spring leaf unfolding. *Nature*, 526, 104–107. Publisher: Nature Publishing Group.
- 438 Gagne, M.A., Smith, D.D. & McCulloh, K.A. (2020). Limited physiological acclimation to recurrent heat-
 439 waves in two boreal tree species. *Tree Physiology*, 40, 1680–1696.
- 440 Gallinat, A.S., Primack, R.B. & Wagner, D.L. (2015). Autumn, the neglected season in climate change
 441 research. *Trends in Ecology & Evolution*, 30, 169–176.
- 442 Gazol, A., Camarero, J.J., Vicente-Serrano, S.M., Sánchez-Salguero, R., Gutiérrez, E., De Luis, M.,
 443 Sangüesa-Barreda, G., Novak, K., Rozas, V., Tíscar, P.A., Linares, J.C., Martín-Hernández, N., Martínez
 444 Del Castillo, E., Ribas, M., García-González, I., Silla, F., Camisón, A., Génova, M., Olano, J.M., Longares,
 445 L.A., Hevia, A., Tomás-Burguera, M. & Galván, J.D. (2018). Forest resilience to drought varies across
 446 biomes. *Global Change Biology*, 24, 2143–2158.
- 447 Gilmore, E.C. & Rogers, J.S. (1958). Heat Units as a Method of Measuring Maturity in Corn. *Agronomy
 448 Journal*, 50, 611–615.
- 449 Green, J.K. & Keenan, T.F. (2022). The limits of forest carbon sequestration. *Science*, 376, 692–693.
- 450 Griffin, D., Porter, S.T., Trumper, M.L., Carlson, K.E., Crawford, D.J., Schwalen, D. & McFadden, C.H.
 451 (2021). Gigapixel Macro Photography of Tree Rings. *Tree-Ring Research*, 77.
- 452 Hauck, M., Schneider, T., Bahlinger, S., Fischbach, J., Oswald, G., Csapek, G. & Dulamsuren, C. (2025).
 453 Heat tolerance of temperate tree species from Central Europe. *Forest Ecology and Management*, 580,
 454 122541.
- 455 Helama, S. (2023). Distinguishing Type I and II errors in statistical tree-ring dating. *Quaternary Geochronol-
 456 ogy*, 78, 101470.
- 457 Hidalgo, H.G., Das, T., Dettinger, M.D., Cayan, D.R., Pierce, D.W., Barnett, T.P., Bala, G., Mirin, A.,
 458 Wood, A.W., Bonfils, C., Santer, B.D. & Nozawa, T. (2009). Detection and Attribution of Streamflow
 459 Timing Changes to Climate Change in the Western United States. *Journal of Climate*, 22, 3838–3855.
- 460 Huey, R.B., Kearney, M.R., Krockenberger, A., Holtum, J.A.M., Jess, M. & Williams, S.E. (2012). Predicting
 461 organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philosophical
 462 Transactions of the Royal Society B: Biological Sciences*, 367, 1665–1679.
- 463 Hufkens, K., Melaas, E.K., Mann, M.L., Foster, T., Ceballos, F., Robles, M. & Kramer, B. (2019). Monitoring
 464 crop phenology using a smartphone based near-surface remote sensing approach. *Agricultural and Forest
 465 Meteorology*, 265, 327–337.
- 466 Intergovernmental panel on climate change (ed.) (2007). *Climate change 2007: the physical science basis*.
 467 Cambridge university press, Cambridge.
- 468 Intergovernmental Panel On Climate Change (Ipcc) (2023). *Climate Change 2022 – Impacts, Adaptation and
 469 Vulnerability: Working Group II Contribution to the Sixth Assessment Report of the Intergovernmental
 470 Panel on Climate Change*. 1st edn. Cambridge University Press.
- 471 Jeong, S. & Medvigy, D. (2014). Macroscale prediction of autumn leaf coloration throughout the continental
 472 United States. *Global Ecology and Biogeography*, 23, 1245–1254.
- 473 Keenan, T.F., Gray, J., Friedl, M.A., Toomey, M., Bohrer, G., Hollinger, D.Y., Munger, J.W., O'Keefe, J.,
 474 Schmid, H.P., Wing, I.S., Yang, B. & Richardson, A.D. (2014). Net carbon uptake has increased through
 475 warming-induced changes in temperate forest phenology. *Nature Climate Change*, 4, 598–604.
- 476 Kolář, T., Giagli, K., Trnka, M., Bednářová, E., Vavrčík, H. & Rybníček, M. (2016). Response of the leaf
 477 phenology and tree-ring width of European beech to climate variability. *Silva Fennica*, 50.

- 478 Kurnik, B., Barbosa, P. & Vogt, J. (2011). Testing two different precipitation datasets to compute the
479 standardized precipitation index over the Horn of Africa. *International Journal of Remote Sensing*, 32,
480 5947–5964.
- 481 Körner, C. & Basler, D. (2010). Phenology Under Global Warming. *Science*, 327, 1461–1462. Publisher:
482 American Association for the Advancement of Science.
- 483 Körner, C., Möhl, P. & Hiltbrunner, E. (2023). Four ways to define the growing season. *Ecology Letters*, 26,
484 1277–1292.
- 485 Laube, J., Sparks, T.H., Estrella, N., Höfler, J., Ankerst, D.P. & Menzel, A. (2014). Chilling outweighs
486 photoperiod in preventing precocious spring development. *Global Change Biology*, 20, 170–182.
- 487 Laurance, W.F. (2007). Have we overstated the tropical biodiversity crisis? *Trends in Ecology & Evolution*,
488 22, 65–70.
- 489 Levanič, T. (2007). Atrics – A New System for Image Acquisition in Dendrochronology. *Tree-Ring Research*,
490 63, 117–122.
- 491 Li, Y., Zhang, W., Schwalm, C.R., Gentine, P., Smith, W.K., Ciais, P., Kimball, J.S., Gazol, A., Kannenberg,
492 S.A., Chen, A., Piao, S., Liu, H., Chen, D. & Wu, X. (2023). Widespread spring phenology effects on
493 drought recovery of Northern Hemisphere ecosystems. *Nature Climate Change*, 13, 182–188.
- 494 Lieth, H., Jacobs, J., Lange, O.L., Olson, J.S. & Wieser, W. (eds.) (1974). *Phenology and Seasonality
495 Modeling*. vol. 8 of *Ecological Studies*. Springer Berlin Heidelberg, Berlin, Heidelberg.
- 496 Lynas, M., Houlton, B.Z. & Perry, S. (2021). Greater than 99% consensus on human caused climate change
497 in the peer-reviewed scientific literature. *Environmental Research Letters*, 16, 114005.
- 498 Manzanedo, R.D. & Pederson, N. (2019). Towards a More Ecological Dendroecology. *Tree-Ring Research*,
499 75, 152.
- 500 Marvel, K., Cook, B.I., Bonfils, C.J.W., Durack, P.J., Smerdon, J.E. & Williams, A.P. (2019). Twentieth-
501 century hydroclimate changes consistent with human influence. *Nature*, 569, 59–65.
- 502 Marx, W., Haunschild, R. & Bornmann, L. (2021). Heat waves: a hot topic in climate change research.
503 *Theoretical and Applied Climatology*, 146, 781–800.
- 504 McMaster, G. (1997). Growing degree-days: one equation, two interpretations. *Agricultural and Forest
505 Meteorology*, 87, 291–300.
- 506 Meehl, G.A. & Tebaldi, C. (2004). More Intense, More Frequent, and Longer Lasting Heat Waves in the
507 21st Century. *Science*, 305, 994–997.
- 508 Meng, L., Mao, J., Zhou, Y., Richardson, A.D., Lee, X., Thornton, P.E., Ricciuto, D.M., Li, X., Dai, Y., Shi,
509 X. & Jia, G. (2020). Urban warming advances spring phenology but reduces the response of phenology
510 to temperature in the conterminous United States. *Proceedings of the National Academy of Sciences*, 117,
511 4228–4233.
- 512 Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská,
513 O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Defila, C., Donnelly, A., Filella, Y., Jatczak,
514 K., Mestre, A., Peñuelas, J., Pirinen, P., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wiel-
515 golaski, F., Zach, S. & Zust, A. (2006). European phenological response to climate change matches the
516 warming pattern. *Global Change Biology*, 12, 1969–1976.
- 517 Meyer, B.F., Buras, A., Gregor, K., Layritz, L.S., Principe, A., Kreyling, J., Rammig, A. & Zang, C.S.
518 (2024). Frost matters: incorporating late-spring frost into a dynamic vegetation model regulates regional
519 productivity dynamics in European beech forests. *Biogeosciences*, 21, 1355–1370.
- 520 Meyer, H.A. (1940). A Mathematical Expression for Height Curves. *Journal of Forestry*, 38, 415–420.

- 521 Moore, J.L. & Remais, J.V. (2014). Developmental Models for Estimating Ecological Responses to Environmental Variability: Structural, Parametric, and Experimental Issues. *Acta Biotheoretica*, 62, 69–90.
- 523 Morin, X., Roy, J., Sonié, L. & Chuine, I. (2010). Changes in leaf phenology of three European oak species in response to experimental climate change. *New Phytologist*, 186, 900–910.
- 525 Muller, B., Pantin, F., Génard, M., Turc, O., Freixes, S., Piques, M. & Gibon, Y. (2011). Water deficits uncouple growth from photosynthesis, increase C content, and modify the relationships between C and growth in sink organs. *Journal of Experimental Botany*, 62, 1715–1729.
- 528 Oreskes, N. (2004). The Scientific Consensus on Climate Change. *Science*, 306, 1686–1686.
- 529 Parent, B., Turc, O., Gibon, Y., Stitt, M. & Tardieu, F. (2010). Modelling temperature-compensated physiological rates, based on the co-ordination of responses to temperature of developmental processes. *Journal of Experimental Botany*, 61, 2057–2069.
- 532 Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A. & Warren, M. (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, 399, 579–583.
- 535 Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42.
- 537 Pearl, J.K., Keck, J.R., Tintor, W., Siekacz, L., Herrick, H.M., Meko, M.D. & Pearson, C.L. (2020). New frontiers in tree-ring research. *The Holocene*, 30, 923–941.
- 539 Peters, R.L., Steppe, K., Cuny, H.E., De Pauw, D.J., Frank, D.C., Schaub, M., Rathgeber, C.B., Cabon, A. & Fonti, P. (2021). Turgor – a limiting factor for radial growth in mature conifers along an elevational gradient. *New Phytologist*, 229, 213–229.
- 542 Peñuelas, J. & Filella, I. (2001). Responses to a Warming World. *Science*, 294, 793–795. Publisher: American Association for the Advancement of Science.
- 544 Piao, S., Liu, Q., Chen, A., Janssens, I.A., Fu, Y., Dai, J., Liu, L., Lian, X., Shen, M. & Zhu, X. (2019). Plant phenology and global climate change: Current progresses and challenges. *Global Change Biology*, 25, 1922–1940.
- 547 Plomion, C., Leprovost, G. & Stokes, A. (2001). Wood Formation in Trees. *Plant Physiology*, 127, 1513–1523.
- 548 Polgar, C.A. & Primack, R.B. (2011). Leaf-out phenology of temperate woody plants: from trees to ecosystems. *New Phytologist*, 191, 926–941.
- 550 Primack, R.B., Laube, J., Gallinat, A.S. & Menzel, A. (2015). From observations to experiments in phenology research: investigating climate change impacts on trees and shrubs using dormant twigs. *Annals of Botany*, 116, 889–897.
- 553 Rathgeber, C.B.K., Cuny, H.E. & Fonti, P. (2016). Biological Basis of Tree-Ring Formation: A Crash Course. *Frontiers in Plant Science*, 7.
- 555 Reimer, P.J., Austin, W.E.N., Bard, E., Bayliss, A., Blackwell, P.G., Bronk Ramsey, C., Butzin, M., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Hajdas, I., Heaton, T.J., Hogg, A.G., Hughen, K.A., Kromer, B., Manning, S.W., Muscheler, R., Palmer, J.G., Pearson, C., Van Der Plicht, J., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Turney, C.S.M., Wacker, L., Adolphi, F., Büntgen, U., Capano, M., Fahrni, S.M., Fogtmann-Schulz, A., Friedrich, R., Köhler, P., Kudsk, S., Miyake, F., Olsen, J., Reinig, F., Sakamoto, M., Sookdeo, A. & Talamo, S. (2020). The IntCal20 Northern Hemisphere Radiocarbon Age Calibration Curve (0–55 cal kBP). *Radiocarbon*, 62, 725–757.
- 562 Reinmann, A.B., Bowers, J.T., Kaur, P. & Kohler, C. (2023). Compensatory responses of leaf physiology reduce effects of spring frost defoliation on temperate forest tree carbon uptake. *Frontiers in Forests and Global Change*, 6, 988233.

- 565 Richardson, A.D., Keenan, T.F., Migliavacca, M., Ryu, Y., Sonnentag, O. & Toomey, M. (2013). Climate
566 change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural*
567 and *Forest Meteorology*, 169, 156–173.
- 568 Rossi, S., Anfodillo, T. & Menardi, R. (2006). Trehpor: A New Tool for Sampling Microcores from tree
569 stems. *IAWA Journal*, 27, 89–97.
- 570 Sanchez-Lorenzo, A., Wild, M., Brunetti, M., Guijarro, J.A., Hakuba, M.Z., Calbó, J., Mystakidis, S. &
571 Bartok, B. (2015). Reassessment and update of long-term trends in downward surface shortwave radiation
572 over Europe (1939–2012). *Journal of Geophysical Research: Atmospheres*, 120, 9555–9569.
- 573 Saunders, M.R. & Wagner, R.G. (2008). Height-diameter models with random coefficients and site variables
574 for tree species of Central Maine. *Annals of Forest Science*, 65, 203–203.
- 575 Sgubin, G., Swingedouw, D., Dayon, G., García De Cortázar-Atauri, I., Ollat, N., Pagé, C. & Van Leeuwen,
576 C. (2018). The risk of tardive frost damage in French vineyards in a changing climate. *Agricultural and*
577 *Forest Meteorology*, 250–251, 226–242.
- 578 Silvestro, R., Deslauriers, A., Prislan, P., Rademacher, T., Rezaie, N., Richardson, A.D., Vitassee, Y. &
579 Rossi, S. (2025). From Roots to Leaves: Tree Growth Phenology in Forest Ecosystems. *Current Forestry*
580 *Reports*, 11, 12.
- 581 Silvestro, R., Mura, C., Alano Bonacini, D., De Lafontaine, G., Faubert, P., Mencuccini, M. & Rossi, S.
582 (2023a). Local adaptation shapes functional traits and resource allocation in black spruce. *Scientific*
583 *Reports*, 13, 21257.
- 584 Silvestro, R., Zeng, Q., Buttò, V., Sylvain, J.D., Drolet, G., Mencuccini, M., Thiffault, N., Yuan, S. & Rossi,
585 S. (2023b). A longer wood growing season does not lead to higher carbon sequestration. *Scientific Reports*,
586 13, 4059.
- 587 Soolanayakanahally, R.Y., Guy, R.D., Silim, S.N. & Song, M. (2013). Timing of photoperiodic competency
588 causes phenological mismatch in balsam poplar (*Populus balsamifera* L.). *Plant, Cell & Environment*, 36,
589 116–127.
- 590 Spinoni, J., Naumann, G., Carrao, H., Barbosa, P. & Vogt, J. (2014). World drought frequency, duration,
591 and severity for 1951–2010. *International Journal of Climatology*, 34, 2792–2804.
- 592 Spinoni, J., Vogt, J.V., Naumann, G., Barbosa, P. & Dosio, A. (2018). Will drought events become more
593 frequent and severe in Europe? *International Journal of Climatology*, 38, 1718–1736.
- 594 Stridbeck, P., Björklund, J., Fuentes, M., Gunnarson, B.E., Jönsson, A.M., Linderholm, H.W., Ljungqvist,
595 F.C., Olsson, C., Rayner, D., Rocha, E., Zhang, P. & Seftigen, K. (2022). Partly decoupled tree-ring
596 width and leaf phenology response to 20th century temperature change in Sweden. *Dendrochronologia*,
597 75, 125993.
- 598 Swidrak, I., Schuster, R. & Oberhuber, W. (2013). Comparing growth phenology of co-occurring deciduous
599 and evergreen conifers exposed to drought. *Flora: Morphology, Distribution, Functional Ecology of Plants*,
600 208, 609–617.
- 601 Teskey, R., Werten, T., Bauweraerts, I., Ameye, M., McGuire, M.A. & Steppe, K. (2015). Responses of tree
602 species to heat waves and extreme heat events. *Plant, Cell & Environment*, 38, 1699–1712.
- 603 Trenberth, K.E., Dai, A., Van Der Schrier, G., Jones, P.D., Barichivich, J., Briffa, K.R. & Sheffield, J.
604 (2014). Global warming and changes in drought. *Nature Climate Change*, 4, 17–22.
- 605 Tyree, M.T. & Zimmermann, M.H. (2002). *Xylem Structure and the Ascent of Sap*. Springer Series in Wood
606 Science. Springer Berlin Heidelberg, Berlin, Heidelberg.
- 607 Vitasse, Y. (2013). Ontogenetic changes rather than difference in temperature cause understory trees to leaf
608 out earlier. *New Phytologist*, 198, 149–155.

- 609 Vitasse, Y., eLenz, A. & eKoerner, C. (2014). The interaction between freezing tolerance and phenology in
610 temperate deciduous trees. *Frontiers in Plant Science*, 5. Publisher: Frontiers Media S.A.
- 611 Von Arx, G. & Carrer, M. (2014). ROXAS – A new tool to build centuries-long tracheid-lumen chronologies
612 in conifers. *Dendrochronologia*, 32, 290–293.
- 613 Way, D.A. & Montgomery, R.A. (2015). Photoperiod constraints on tree phenology, performance
614 and migration in a warming world. *Plant, Cell & Environment*, 38, 1725–1736. _eprint:
615 <https://onlinelibrary.wiley.com/doi/pdf/10.1111/pce.12431>.
- 616 Wolfe, D.W., Schwartz, M.D., Lakso, A.N., Otsuki, Y., Pool, R.M. & Shaulis, N.J. (2005). Climate change
617 and shifts in spring phenology of three horticultural woody perennials in northeastern USA. *International
618 Journal of Biometeorology*, 49, 303–309.
- 619 Wolkovich, E.M., Auerbach, J., Chamberlain, C.J., Buonaiuto, D.M., Ettinger, A.K., Morales-Castilla, I.
620 & Gelman, A. (2021). A simple explanation for declining temperature sensitivity with warming. *Global
621 Change Biology*, 27, 4947–4949.
- 622 Wolkovich, E.M., Cook, B.I. & Davies, T.J. (2014). Progress towards an interdisciplinary science of plant
623 phenology: building predictions across space, time and species diversity. *New Phytologist*, 201, 1156–1162.
624 _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/nph.12599>.
- 625 Wolkovich, E.M., Ettinger, A.K., Chin, A., Chamberlain, C.J., Baumgarten, F., Pradhan, K., Manzanedo,
626 R.D. & Lambers, J.H.R. (2025). Why longer seasons with climate change may not increase tree growth.
627 *In review*.
- 628 Woolway, R.I., Sharma, S., Weyhenmeyer, G.A., Debolskiy, A., Golub, M., Mercado-Bettín, D., Perroud,
629 M., Stepanenko, V., Tan, Z., Grant, L., Ladwig, R., Mesman, J., Moore, T.N., Shatwell, T., Vanderkelen,
630 I., Austin, J.A., DeGasperi, C.L., Dokulil, M., La Fuente, S., Mackay, E.B., Schladow, S.G., Watanabe,
631 S., Marcé, R., Pierson, D.C., Thiery, W. & Jennings, E. (2021). Phenological shifts in lake stratification
632 under climate change. *Nature Communications*, 12, 2318.
- 633 Wu, J. (2013). Key concepts and research topics in landscape ecology revisited: 30 years after the Allerton
634 Park workshop. *Landscape Ecology*, 28, 1–11.
- 635 Wu, X., Niu, C., Liu, X., Hu, T., Feng, Y., Zhao, Y., Liu, S., Liu, Z., Dai, G., Zhang, Y., Van Meerbeek, K.,
636 Wu, J., Liu, L., Guo, Q. & Su, Y. (2024). Canopy structure regulates autumn phenology by mediating
637 the microclimate in temperate forests. *Nature Climate Change*, 14, 1299–1305.
- 638 Wu, Z., Chen, S., De Boeck, H.J., Stenseth, N.C., Tang, J., Vitasse, Y., Wang, S., Zohner, C. & Fu, Y.H.
639 (2021). Atmospheric brightening counteracts warming-induced delays in autumn phenology of temperate
640 trees in Europe. *Global Ecology and Biogeography*, 30, 2477–2487.
- 641 Yan, T., Fu, Y.H., Campioli, M., Peñuelas, J. & Wang, X. (2021). Divergent responses of phenology and
642 growth to summer and autumnal warming. *Global Change Biology*, 27, null.
- 643 Yuancai, L. & Parresol, B.R. (2001). Remarks on Height-Diameter Modeling. Tech. Rep. SRS-RN-10, U.S.
644 Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.
- 645 Zani, D., Crowther, T.W., Mo, L., Renner, S.S. & Zohner, C.M. (2020). Increased growing-season productiv-
646 ity drives earlier autumn leaf senescence in temperate trees. *Science*, 370, 1066–1071. Publisher: American
647 Association for the Advancement of Science.
- 648 Zohner, C.M., Mirzagholi, L., Renner, S.S., Mo, L., Rebindaine, D., Bucher, R., Palouš, D., Vitasse, Y., Fu,
649 Y.H., Stocker, B.D. & Crowther, T.W. (2023). Effect of climate warming on the timing of autumn leaf
650 senescence reverses after the summer solstice. *Science*, 381.

- 651 Zohner, C.M., Mo, L., Renner, S.S., Svenning, J.C., Vitasse, Y., Benito, B.M., Ordonez, A., Baumgarten,
652 F., Bastin, J.F., Sebald, V., Reich, P.B., Liang, J., Nabuurs, G.J., de Miguel, S., Alberti, G., Antón-
653 Fernández, C., Balazy, R., Brändli, U.B., Chen, H.Y.H., Chisholm, C., Cienciala, E., Dayanandan, S.,
654 Fayle, T.M., Frizzera, L., Gianelle, D., Jagodzinski, A.M., Jaroszewicz, B., Jucker, T., Kepfer-Rojas, S.,
655 Khan, M.L., Kim, H.S., Korjus, H., Johannsen, V.K., Laarmann, D., Lang, M., Zawila-Niedzwiecki, T.,
656 Niklaus, P.A., Paquette, A., Pretzsch, H., Saikia, P., Schall, P., Šeben, V., Svoboda, M., Tikhonova, E.,
657 Viana, H., Zhang, C., Zhao, X. & Crowther, T.W. (2020). Late-spring frost risk between 1959 and 2017
658 decreased in North America but increased in Europe and Asia. *Proceedings of the National Academy of*
659 *Sciences*, 117, 12192–12200.
- 660 Čufar, K., Prislan, P., De Luis, M. & Gričar, J. (2008). Tree-ring variation, wood formation and phenology
661 of beech (*Fagus sylvatica*) from a representative site in Slovenia, SE Central Europe. *Trees*, 22, 749–758.