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Thesis Proposal

2

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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). Though some immediate actions can be deployed to mitigate these impacts
11 (e.g. (Campbell *et al.*, 2014)), reversing 150 years of human-induced greenhouse gas emissions is harder.
12 These emissions have affected Earth's climate and are projected to keep changing it for many centuries (Intergovernmental Panel On Climate Change (Ipcc), 2023). While there is a scientific consensus that observed
13 climate change is human-caused (Change, 2014; Lynas *et al.*, 2021; Oreskes, 2004), the magnitude and the
14 extent of the consequences that a warming climate will have on biological processes are still debatable (Huey
15 *et al.*, 2012).

17

18 1.1.1. Trends of spring and autumn phenological events and their drivers

19

20 *1.1.1.1. Changes in phenology:* The most frequently observed biological impact of climate change over
21 the past decades is major changes in spring and autumn phenology —the timing of recurring life history
22 events (Parmesan & Yohe, 2003; Cleland *et al.*, 2007; Lieth *et al.*, 1974; Woolway *et al.*, 2021; Menzel *et al.*,
23 2006). Together, shifts in spring and autumn phenology modify when the growing season starts and when
24 it ends. Understanding the consequences of changing growing season length on ecosystems requires under-
25 standing how much, and why it has changed (Duputié *et al.*, 2015).

26

27 *1.1.1.2. Drivers of spring phenology:* Spring phenological events (e.g. budburst and leafout) have been
28 advancing from 0.5 (Wolfe *et al.*, 2005) to 4.2 days/decade (Chmielewski & Rötzer, 2001; Fu *et al.*, 2014)
29 and are mainly driven by temperature (Chuine, 2010; Cleland *et al.*, 2007; Peñuelas & Filella, 2001). In the
30 winter, when trees are still in dormancy, they accumulate cold temperatures (chilling) for which a certain
31 amount is required to be ready to accumulate heat (forcing) (Vitasse *et al.*, 2014). Then, in the spring,
32 a certain amount of forcing triggers budburst (Fu *et al.*, 2015). Heat requirement is met sooner in warm
33 springs, thus explaining the advancement of spring events and earlier onset of growing season over the last
34 decades (Fu *et al.*, 2015, 2013; Laube *et al.*, 2014).

35

36 *1.1.1.3. Drivers of autumn phenology:* In contrast, autumn phenology (e.g. budset and leaf senescence)
37 is delayed, though to a much lesser extent than spring (Gallinat *et al.*, 2015; Jeong & Medvigy, 2014), and
38 its drivers are also far less understood than those of spring. These ambiguities are caused by the lesser atten-
39 tion payed to autumn phenology (Piao *et al.*, 2019) and because the data is often noisier (Wu *et al.*, 2024).
40 However, there is a general belief that autumn phenophases are driven by shortening photoperiod and colder
41 temperatures (Cooke *et al.*, 2012; Flynn & Wolkovich, 2018; Körner & Basler, 2010; Delpierre *et al.*, 2016).
42 Several hypotheses can explain delayed autumn phenophases. First, warmer autumn temperatures may ex-
43 tend the activity of photosynthetic enzymes which causes decreases the degradation rate of chlorophyll, thus
44 delaying the timing of leaf senescence (Yan *et al.*, 2021). Second, summer droughts could pause the activity

45 schedule of trees and delay senescence to increase carbon assimilation (Dox *et al.*, 2022). Third, there could
46 be an antagonistic effect of warming and brightening—caused by reductions in atmospheric pollution and
47 cloud cover (Sanchez-Lorenzo *et al.*, 2015)—on leaf senescence (Wu *et al.*, 2021). Brightening accelerates
48 the leaf senescence processes and reduces the temperature sensitivity during that period, counteracting the
49 expected warming-induced delays in leaf senescence (Wu *et al.*, 2021).

50

51 **1.1.2. How these shifts translate into effects on trees/forests is not clear - Pros and cons of** 52 **early/late start/end of season**

53 Shifts in spring and autumn phenology support a long-lasting and intuitive assumption that earlier spring
54 and delayed autumn events lead to longer seasons—and thus increased growth (Keenan *et al.*, 2014; Stridbeck
55 *et al.*, 2022). However, research from the past three years has cast doubt on this hypothesis (Dow *et al.*,
56 2022; Green & Keenan, 2022; Silvestro *et al.*, 2023b). For instance, (Dow *et al.*, 2022) showed that despite an
57 earlier growth onset, longer seasons did not increase the growth rate nor overall annual increment. This could
58 substantially affect carbon-cycle model projections and thus feedbacks to future climate (Richardson *et al.*,
59 2013; Swidrak *et al.*, 2013). Starting to grow earlier and stopping later both have different consequences
60 (Figure 1).

61 Understanding these findings requires answering why trees do not grow more despite longer growing
62 seasons. While carbon allocation to above-ground biomass is one of the largest carbon sinks, how this car-
63 bon is allocated into wood is poorly understood. Indeed, the linear relationship assumption between wood
64 growth and carbon assimilation is not well supported mechanistically and represents an important limita-
65 tion of vegetation models (Cabon *et al.*, 2022). Net primary production represents the difference between
66 photosynthesis and plant respiration, but this commonly used metric completely omits the representation
67 of growth processes. This is perhaps because of a long-lasting paradigm of source-limited photosynthesis.
68 Whether photosynthesis limits growth dependsThis has now been debunked with carbon fertilization exper-
69 iments, supporting evidence that direct environmental constraints on growth may be stronger than those on
70 photosynthesis (Friend *et al.*, 2019; Parent *et al.*, 2010). This opens up a new—poorly tested—temperature
71 sensitivity relationship between cambial activity and photosynthesis. Growing evidence suggests that cam-
72 bial activity may be more sensitive than photosynthesis to a range of environmental conditions, such as
73 water and nutrient availability, and temperature (Cabon *et al.*, 2022, 2020; Muller *et al.*, 2011; Peters *et al.*,
74 2021). This demonstrates that carbon projection models that heavily rely on vegetation alone may mislead
75 the amount of carbon sequestered in our forests.

76

77 **1.1.3. Growing season shifts and consequences on forest ecosystems and services**

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

86

1.2 Nature of the problem, and how to address it

87

88 **1.2.1. Past phenological trends can help (or not) predict future phenological changes**

89 We cannot directly use observed phenological trends in the last decades to extrapolate future phenological
90 changes because: (1) the mechanisms guiding them aren't clear, and (2) phenological responses of trees
91 to warming are very likely to be non-linear (Ettinger *et al.*, 2020; Fu *et al.*, 2013). Indeed, accurate pre-
92 dictions require an in-depth, accurate mechanistic understanding of phenophases and their sensitivities to
93 environmental drivers, especially to temperature and photoperiod (Fu *et al.*, 2013). Therefore, the very
94 foundation of the assumption that longer seasons increase growth may shift with future climate change. The
95 well-observed advance in spring phenology may decelerate, and delayed fall phenology may shift towards
earlier leaf senescence (through summer drought-induced growth cessation).

97 **1.2.2. The assumption that longer seasons lead to increased growth is called into question**

98 *1.2.2.1. Absence of growth despite better conditions and strategies that can be used* Recent work shows
99 an absence of increased growth despite apparent better environmental conditions, thus casting doubt on a
100 simple and intuitive positive relationship between growing season length and growth. This paradox further
101 emphasizes the need to better understand the drivers regulating growth across biomes, but also how these
102 drivers vary across the species within these biomes. Phenology varies greatly across species (e.g. closely
103 related species tend to budburst at similar times under similar conditions) (Wolkovich *et al.*, 2014), but
104 so does the relationship between growth and season length, which may explain the wide variation of this
105 relationship within communities (Buckley & Kingsolver, 2012). This highlights another weakness of current
106 carbon sequestration models that pool species together, likely overpassing important nuances in the growth
107 responses that could be explained by species differences. Excluding species differences in models may mislead
108 the future of forest carbon source-sink ratios (Green & Keenan, 2022; Cabon *et al.*, 2022; Wolkovich *et al.*,
109 2025). Different strategies can help in understanding how different species respond to warming.

110
111 *1.2.2.2. Experiments:* First, experiments are paramount to robustly tease apart the external vs internal
112 drivers (e.g. warmer springs from severe drought later in the season—a common co-occurring reality in natu-
113 ral environments) (Morin *et al.*, 2010; Primack *et al.*, 2015). However, experiments are most often performed
114 on juvenile trees, which are critical for their role in forest regeneration projections, but their responses hardly
115 translate to mature trees, which hold the overwhelming carbon biomass proportion of forests (Augspurger
116 & Bartlett, 2003; Silvestro *et al.*, 2023b; Vitasse, 2013).

117
118 *1.2.2.3. Ground based observations:* Second, leaf phenology through ground-based observations can pro-
119 vide valuable insights into the growth temporality of trees that are not suitable for experimental trials. Since
120 cambial and leaf phenology are closely linked to the other, having the more accessible leaf phenology data
121 can act as a reliable proxy for the onset and end of tree growth. It is to say that knowing when leaves
122 elongate and colour can guide when trees start and stop growing—fundamental metrics to determine the
123 growing season length. Ground observations have the advantage of providing accurate data on phenological
124 events for specific sites and species. Recently, the widespread use of smartphones has opened a whole new
125 world of possible phenological monitoring through citizen scientists' records of data over much larger areas
126 and for a wider range of species (Dickinson *et al.*, 2012; Hufkens *et al.*, 2019; Piao *et al.*, 2019). While there
127 are drawbacks to these observations (e.g. non-standard protocols, highly uneven spatiotemporal distribution
128 of these observations), these methods have a huge potential to diversify the phenology data.

129
130 **1.2.3. Goals of my thesis**
131 Using citizen science data, a common garden study and a large-scale experiment, I aim to better understand
132 how different tree species, at different lifespan stages, vary in their growth responses to different season
133 length. Answering these patterns requires specifying the definitions of growth and the growing season.

134 **1.3 Complexity of measuring growth and defining growing season length**

135 To understand how trees respond to growing season conditions, it is important to clarify what is a growing
136 season and growth.

137 *1.3.1.1. What is a growing season?*

138
139 The definition of the growing season itself is not a well-defined concept and an array of definitions are
140 used differently accross studies. Recently, Körner *et al.* (2023) proposed four definitions addressing this issue:
141 (1) true growing season, based on measurable growth; (2) phenological season, based on visible phenological
142 markers; (3) the productive season, based on primary production and (4) meteorological season, based on
143 environmental conditions.

144 Here, I will focus on how definition (2), incorporating (4), affects definition (1) as the data collected
145 for this thesis can't address (3). I will use definition (2) to infer a "window of opportunity", to calculate
146 growing degree days (GDD)—a measure of heat accumulation—using meteorological conditions. I am using
147 the meteorological season within a constrained window, instead of simply using it irrespective of phenology
148 because of the illusion that an absolute increase in GDD over the last decades—is irrespective of the timing of

149 phenophases—also increases growth. Springs are warmer, falls are also sometimes warmer, and summers are
150 warmer, which together increase the number of GDD, which may appear to be a reliable proxy for better
151 environmental conditions. However, models that accumulate GDD before and/or after trees grow could
152 mislead about how this variable drives growth.

153 *1.3.1.2. What is growth?*

154 Wood formation (xylogenesis) consists of allocating carbon for long-term storage in woody plants. Xylogen-
155 esis starts with cambial activation and cell production which produces xylem and phloem cells (Etzold *et al.*,
156 2022; Silvestro *et al.*, 2025). The rate and duration of these phases lead to irreversible radial growth incre-
157 ments usually represented through tree rings. In these, secondary xylem cells account disproportionately to
158 the number of cells produced because they divide more than phloem cells (Plomion *et al.*, 2001; Rathgeber
159 *et al.*, 2016).

160 **1.3.2. Traditional diameter measurements miss the resolution of annual growth increment**

161 Foresters have measured tree diameter and height for decades, but these measurements are not suitable for
162 interpreting a relationship between growth and environmental conditions. Diameter and height are used infer
163 allometries that could give in how much wood could be harvested in a forest (e.g. (Meyer, 1940; Saunders
164 & Wagner, 2008)). The widely used method in forestry is to measure diameter at breast height at punctual
165 time intervals (Yuancai & Parresol, 2001). However, these measurements don't provide short-term indicators
166 of growth, and are likely to miss extreme events affecting growth. In addition, many forest inventories only
167 report diameter measurements and exclude height, because of logistical constraints ((Saunders & Wagner,
168 2008)), which reduces biomass estimation quality. This growth data lacks the temporal resolution necessary
169 to properly infer a relationship between growth and environmental conditions.

170 **1.3.3. Dendroecology to analyses growth responses to changing growing season length**

171 Alongside the diameter-height allometric relationship, dendroecology—applications of dendrochronological
172 techniques to problems in ecology (Fritts & Swetnam, 1989)—emerged to answer ecological problems as well
173 as to hindcast (e.g. (Bergeron *et al.*, 2004)) and forecast ecological processes both at the regional (Gazol
174 *et al.*, 2018) and global scale (Manzanedo & Pederson, 2019; Büntgen *et al.*, 2018). Now, these methods
175 can be used to understand more precise growth patterns and their relationship with different environmen-
176 tal factors. This is why I will use tree ring width as a reliable proxy for how much trees grew in any given year.

177 **1.3.4. Asynchrony between primary and secondary growth (internal growth control)?**

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

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

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

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

206

207 1.4 Objectives

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

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

216 1.5 Research questions

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

220

221 2 Methodology

222 2.1 Coringtreespotters

223 2.1. Studies locations **Common garden** In 2014-2015, we collected seeds from four field sites in northeastern
224 North America spanning approximately a 3.5° latitudinal gradient. The four field sites included Harvard
225 Forest (42.55°N, 72.20°W), the White Mountains (44.11°N, 71.40°W), Second College Grant, (44.79°N,
226 71.15°W), and St. Hippolyte, QC, CAN (45.98°N, 74.01°W). We transported all seeds back to the Weld
227 Hill Research Building at the Arnold Arboretum in Boston Massachusetts (42.30°N, 71.13°W) where we
228 germinated seeds following standard germination protocols, and grew them to seedling stages in the research
229 greenhouse. In the spring of 2017 we out-planted seedlings to establish the garden. Plots were regularly
230 weeded and watered throughout the duration of the study and were pruned in the fall of 2020.

231 In the spring of 2023, we collected 1 tree core on some trees and cross-sections for other trees. Both the
232 cores and cross-sections were left to dry at ambient temperature for three months.

233 **2.1. Coringtreespotters** The citizen science programs, the Treespotters was started in 2015 and aimed
234 to train citizen scientist for accurate and rigorous phenological monitoring. From 2015 to 2024, hundreds of
235 citizen scientists monitored * trees of * species regularly from the early phenostage in the spring until leaf
236 colouring in the fall. The BBCH scale was used (check if that's true).

237 From 20 to 22 April 2025, we collected a 2.5-mm diameter core, 15-cm length at 1.3 meter above
238 ground from 50 trees of the 11 species (Table XX) that were previously monitored for phenology, using
239 an increment borer (Mora Borer, Haglöfs Sweden, Bromma, Stockholm, Sweden). The cores were collected
240 perpendicularly to the slope and at 180 degrees from each other. We cleaned the increment borer with alcohol
241 (70% ethanol?) and the inside with a brush before collecting each core. We stored the cores in paper straws
242 that were previously labelled and punched to help drying. They were stored at ambient temperature for
243 three months.

244 **Sample processing, imaging and measuring** Then we mounted the cores on wooden mounts, and
245 sanded the cores and cross-sections using progressively fine grit (150, 300, 400, 600, 800, 1000). We scanned
246 the cores and cross-sections at a resolution of ***dpi using a homemade great scanner (Tina2026?). We
247 used the digitalized images to measure the tree ring widths with Fiji Image J. Then, we performed visual
248 crossdating using Dplr, but no statistical crossdating was performed because of the short chronologies that
249 limit the capacity for these analyses.

250 **3 Supplemental material**

251 **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	

253

3.2. Drought

254

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).
Mechanisms	<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)
Global trend of occurrence	<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)
Consequences (Individual and Ecosystem level consequences)	<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))
Differences across species/provenance	

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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>
257 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)

258 References

- 259 Aitken, S.N. & Bemmels, J.B. (2016). Time to get moving: assisted gene flow of forest trees. *Evolutionary Applications*, 9, 271–290.
- 260
- 261 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.
- 262
- 263
- 264 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.
- 265
- 266 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.
- 267
- 268
- 269 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*.
- 270
- 271 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.
- 272
- 273 Bonhomme, R. (2000). Bases and limits to using ‘degree.day’ units. *European Journal of Agronomy*, 13, 1–10.
- 274

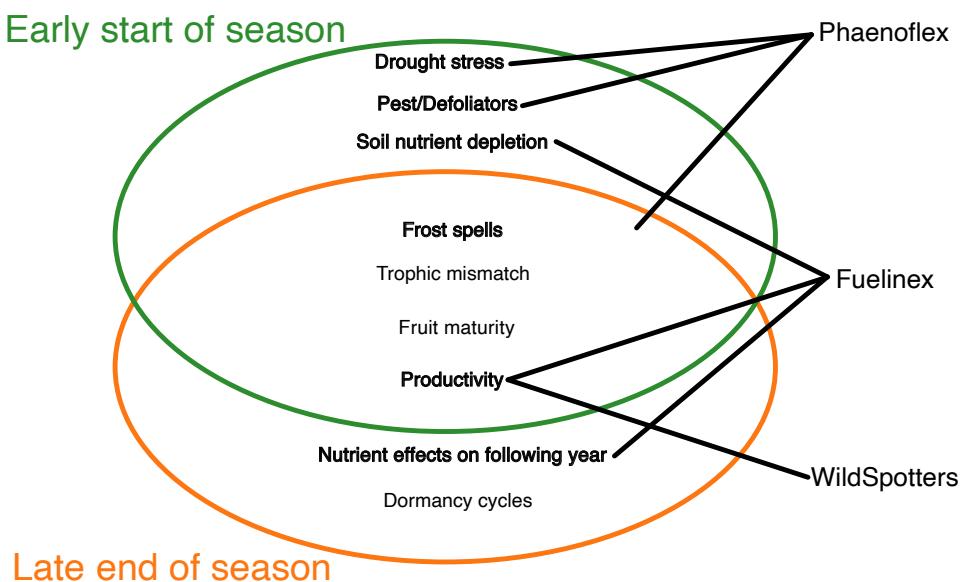


Figure 1: Pros and cons of early start and late end of growing season.

- 275 Brienen, R.J.W., Caldwell, L., Duchesne, L., Voelker, S., Barichivich, J., Baliva, M., Ceccantini, G., Di Fil-
276 ippo, A., Helama, S., Locosselli, G.M., Lopez, L., Piovesan, G., Schöngart, J., Villalba, R. & Gloor, E.
277 (2020). Forest carbon sink neutralized by pervasive growth-lifespan trade-offs. *Nature Communications*,
278 11, 4241.
- 279 Buckley, L.B. & Kingsolver, J.G. (2012). Functional and Phylogenetic Approaches to Forecasting Species'
280 Responses to Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, 43, 205–226.
- 281 Büntgen, U., Wacker, L., Galván, J.D., Arnold, S., Arseneault, D., Baillie, M., Beer, J., Bernabei, M.,
282 Bleicher, N., Boswijk, G., Bräuning, A., Carrer, M., Ljungqvist, F.C., Cherubini, P., Christl, M., Christie,
283 D.A., Clark, P.W., Cook, E.R., Esper, J., Fowler, A.M., Gennaretti, F., Grießinger, J., Grissino-Mayer,
284 H., Grudd, H., Gunnarson, B.E., Hantemirov, R., Herzig, F., Hessl, A., Heussner, K.U., Jull, A.J.T.,
285 Kukarskikh, V., Kirdyanov, A., Krusic, P.J., Kyncl, T., Lara, A., LeQuesne, C., Linderholm, H.W., Loader,
286 N.J., Luckman, B., Miyake, F., Myglan, V.S., Nicolussi, K., Oppenheimer, C., Palmer, J., Panyushkina, I.,
287 Pederson, N., Rybníček, M., Schweingruber, F.H., Seim, A., Sigl, M., Churakova, O., Speer, J.H., Synal,
288 H.A., Tegel, W., Treydte, K., Villalba, R., Wiles, G., Wilson, R., Winship, L.J., Wunder, J., Yang, B. &
289 Young, G.H.F. (2018). Tree rings reveal globally coherent signature of cosmogenic radiocarbon events in
290 774 and 993 CE. *Nature Communications*, 9, 3605.
- 291 Cabon, A., Fernández-de-Uña, L., Gea-Izquierdo, G., Meinzer, F.C., Woodruff, D.R., Martínez-Vilalta, J. &
292 De Cáceres, M. (2020). Water potential control of turgor-driven tracheid enlargement in Scots pine at its
293 xeric distribution edge. *New Phytologist*, 225, 209–221.
- 294 Cabon, A., Kannenberg, S.A., Arain, A., Babst, F., Baldocchi, D., Belmecheri, S., Delpierre, N., Guerrieri,
295 R., Maxwell, J.T., McKenzie, S., Meinzer, F.C., Moore, D.J.P., Pappas, C., Rocha, A.V., Szejner, P.,
296 Ueyama, M., Ulrich, D., Vincke, C., Voelker, S.L., Wei, J., Woodruff, D. & Anderegg, W.R.L. (2022).
297 Cross-biome synthesis of source versus sink limits to tree growth. *Science*, 376, 758–761.
- 298 Camarero, J.J., Olano, J.M. & Parras, A. (2010). Plastic bimodal xylogenesis in conifers from continental
299 Mediterranean climates. *New Phytologist*, 185, 471–480.
- 300 Campbell, L.M., Hagerman, S. & Gray, N.J. (2014). Producing Targets for Conservation: Science and Politics
301 at the Tenth Conference of the Parties to the Convention on Biological Diversity. *Global Environmental
302 Politics*, 14, 41–63.
- 303 Campbell, R., McCarroll, D., Loader, N.J., Grudd, H., Robertson, I. & Jalkanen, R. (2007). Blue intensity
304 in *Pinus sylvestris* tree-rings: developing a new palaeoclimate proxy. *The Holocene*, 17, 821–828.
- 305 Ceballos, G., Ehrlich, P.R. & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction
306 signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*,
307 114.
- 308 Change, I.P.O.C. (2014). Detection and Attribution of Climate Change: from Global to Regional. In:
309 *Climate Change 2013 – The Physical Science Basis*. Cambridge University Press, pp. 867–952. 1st edn.
- 310 Chiang, F., Mazdiyasni, O. & AghaKouchak, A. (2021). Evidence of anthropogenic impacts on global drought
311 frequency, duration, and intensity. *Nature Communications*, 12, 2754.
- 312 Chmielewski, F.M. & Rötzer, T. (2001). Response of tree phenology to climate change across Europe.
313 *Agricultural and Forest Meteorology*, 108, 101–112.
- 314 Choat, B., Brodribb, T.J., Brodersen, C.R., Duursma, R.A., López, R. & Medlyn, B.E. (2018). Triggers of
315 tree mortality under drought. *Nature*, 558, 531–539.
- 316 Chuine, I. (2010). Why does phenology drive species distribution? *Philosophical Transactions of the Royal
317 Society B: Biological Sciences*, 365, 3149–3160.
- 318 Chuine, I. & Régnière, J. (2017). Process-Based Models of Phenology for Plants and Animals. *Annual
319 Review of Ecology, Evolution, and Systematics*, 48, 159–182.

- 320 Cleland, E., Chuine, I., Menzel, A., Mooney, H. & Schwartz, M. (2007). Shifting plant phenology in response
321 to global change. *Trends in Ecology & Evolution*, 22, 357–365.
- 322 Cooke, J.E.K., Eriksson, M.E. & Junntila, O. (2012). The dynamic nature of bud dormancy in trees:
323 environmental control and molecular mechanisms. *Plant, Cell & Environment*, 35, 1707–1728.
- 324 Delpierre, N., Vitasse, Y., Chuine, I., Guillemot, J., Bazot, S., Rutishauser, T. & Rathgeber, C.B.K. (2016).
325 Temperate and boreal forest tree phenology: from organ-scale processes to terrestrial ecosystem models.
326 *Annals of Forest Science*, 73, 5–25.
- 327 Dickinson, J.L., Shirk, J., Bonter, D., Bonney, R., Crain, R.L., Martin, J., Phillips, T. & Purcell, K. (2012).
328 The current state of citizen science as a tool for ecological research and public engagement. *Frontiers in
329 Ecology and the Environment*, 10, 291–297.
- 330 Dosio, A., Mentaschi, L., Fischer, E.M. & Wyser, K. (2018). Extreme heat waves under 1.5 °C and 2 °C
331 global warming. *Environmental Research Letters*, 13, 054006.
- 332 Douglass, A. (1928). Climate and trees. *Nature Magazine*, 12, 51–53.
- 333 Dow, C., Kim, A.Y., D'Orangeville, L., Gonzalez-Akre, E.B., Helcoski, R., Herrmann, V., Harley, G.L.,
334 Maxwell, J.T., McGregor, I.R., McShea, W.J., McMahon, S.M., Pederson, N., Tepley, A.J. & Anderson-
335 Teixeira, K.J. (2022). Warm springs alter timing but not total growth of temperate deciduous trees.
336 *Nature*, 608, 552–557.
- 337 Dox, I., Skrøppa, T., Decoster, M., Prislan, P., Gascó, A., Gričar, J., Lange, H. & Campioli, M. (2022).
338 Severe drought can delay autumn senescence of silver birch in the current year but advance it in the next
339 year. *Agricultural and Forest Meteorology*, 316, 108879.
- 340 Driscoll, D.A., Bland, L.M., Bryan, B.A., Newsome, T.M., Nicholson, E., Ritchie, E.G. & Doherty, T.S.
341 (2018). A biodiversity-crisis hierarchy to evaluate and refine conservation indicators. *Nature Ecology &
342 Evolution*, 2, 775–781.
- 343 Duputié, A., Rutschmann, A., Ronce, O. & Chuine, I. (2015). Phenological plasticity will not help all species
344 adapt to climate change. *Global Change Biology*, 21, 3062–3073.
- 345 Ettinger, A.K., Chamberlain, C.J., Morales-Castilla, I., Buonaiuto, D.M., Flynn, D.F.B., Savas, T., Samaha,
346 J.A. & Wolkovich, E.M. (2020). Winter temperatures predominate in spring phenological responses to
347 warming. *Nature Climate Change*, 10, 1137–1142.
- 348 Etzold, S., Sterck, F., Bose, A.K., Braun, S., Buchmann, N., Eugster, W., Gessler, A., Kahmen, A., Peters,
349 R.L., Vitasse, Y., Walthert, L., Ziemińska, K. & Zweifel, R. (2022). Number of growth days and not length
350 of the growth period determines radial stem growth of temperate trees. *Ecology Letters*, 25, 427–439.
- 351 Flynn, D.F.B. & Wolkovich, E.M. (2018). Temperature and photoperiod drive spring phenology across all
352 species in a temperate forest community. *New Phytologist*, 219, 1353–1362.
- 353 Friend, A.D., Eckes-Shephard, A.H., Fonti, P., Rademacher, T.T., Rathgeber, C.B.K., Richardson, A.D. &
354 Turton, R.H. (2019). On the need to consider wood formation processes in global vegetation models and
355 a suggested approach. *Annals of Forest Science*, 76, 49.
- 356 Fritts, H. & Swetnam, T. (1989). Dendroecology: A Tool for Evaluating Variations in Past and Present
357 Forest Environments. In: *Advances in Ecological Research*. Elsevier, vol. 19, pp. 111–188.
- 358 Fu, Y.H., Campioli, M., Deckmyn, G. & Janssens, I.A. (2013). Sensitivity of leaf unfolding to experimental
359 warming in three temperate tree species. *Agricultural and Forest Meteorology*, 181, 125–132.
- 360 Fu, Y.H., Piao, S., Op De Beeck, M., Cong, N., Zhao, H., Zhang, Y., Menzel, A. & Janssens, I.A. (2014).
361 Recent spring phenology shifts in western Central Europe based on multiscale observations. *Global Ecology
362 and Biogeography*, 23, 1255–1263.

- 363 Fu, Y.H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., Ciais, P., Huang, M., Menzel, A., Peñuelas,
364 J., Song, Y., Vitassee, Y., Zeng, Z. & Janssens, I.A. (2015). Declining global warming effects on the
365 phenology of spring leaf unfolding. *Nature*, 526, 104–107. Publisher: Nature Publishing Group.
- 366 Gagne, M.A., Smith, D.D. & McCulloh, K.A. (2020). Limited physiological acclimation to recurrent heat-
367 waves in two boreal tree species. *Tree Physiology*, 40, 1680–1696.
- 368 Gallinat, A.S., Primack, R.B. & Wagner, D.L. (2015). Autumn, the neglected season in climate change
369 research. *Trends in Ecology & Evolution*, 30, 169–176.
- 370 Gazol, A., Camarero, J.J., Vicente-Serrano, S.M., Sánchez-Salguero, R., Gutiérrez, E., De Luis, M.,
371 Sangüesa-Barreda, G., Novak, K., Rozas, V., Tíscar, P.A., Linares, J.C., Martín-Hernández, N., Martínez
372 Del Castillo, E., Ribas, M., García-González, I., Silla, F., Camisón, A., Génova, M., Olano, J.M., Longares,
373 L.A., Hevia, A., Tomás-Burguera, M. & Galván, J.D. (2018). Forest resilience to drought varies across
374 biomes. *Global Change Biology*, 24, 2143–2158.
- 375 Gilmore, E.C. & Rogers, J.S. (1958). Heat Units as a Method of Measuring Maturity in Corn. *Agronomy
376 Journal*, 50, 611–615.
- 377 Green, J.K. & Keenan, T.F. (2022). The limits of forest carbon sequestration. *Science*, 376, 692–693.
- 378 Griffin, D., Porter, S.T., Trumper, M.L., Carlson, K.E., Crawford, D.J., Schwalen, D. & McFadden, C.H.
379 (2021). Gigapixel Macro Photography of Tree Rings. *Tree-Ring Research*, 77.
- 380 Hauck, M., Schneider, T., Bahlinger, S., Fischbach, J., Oswald, G., Csapek, G. & Dulamsuren, C. (2025).
381 Heat tolerance of temperate tree species from Central Europe. *Forest Ecology and Management*, 580,
382 122541.
- 383 Helama, S. (2023). Distinguishing Type I and II errors in statistical tree-ring dating. *Quaternary Geochronol-
384 ogy*, 78, 101470.
- 385 Hidalgo, H.G., Das, T., Dettinger, M.D., Cayan, D.R., Pierce, D.W., Barnett, T.P., Bala, G., Mirin, A.,
386 Wood, A.W., Bonfils, C., Santer, B.D. & Nozawa, T. (2009). Detection and Attribution of Streamflow
387 Timing Changes to Climate Change in the Western United States. *Journal of Climate*, 22, 3838–3855.
- 388 Huey, R.B., Kearney, M.R., Krockenberger, A., Holtum, J.A.M., Jess, M. & Williams, S.E. (2012). Predicting
389 organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philosophical
390 Transactions of the Royal Society B: Biological Sciences*, 367, 1665–1679.
- 391 Hufkens, K., Melaas, E.K., Mann, M.L., Foster, T., Ceballos, F., Robles, M. & Kramer, B. (2019). Monitoring
392 crop phenology using a smartphone based near-surface remote sensing approach. *Agricultural and Forest
393 Meteorology*, 265, 327–337.
- 394 Intergovernmental panel on climate change (ed.) (2007). *Climate change 2007: the physical science basis*.
395 Cambridge university press, Cambridge.
- 396 Intergovernmental Panel On Climate Change (Ipcc) (2023). *Climate Change 2022 – Impacts, Adaptation and
397 Vulnerability: Working Group II Contribution to the Sixth Assessment Report of the Intergovernmental
398 Panel on Climate Change*. 1st edn. Cambridge University Press.
- 399 Jeong, S. & Medvigy, D. (2014). Macroscale prediction of autumn leaf coloration throughout the continental
400 United States. *Global Ecology and Biogeography*, 23, 1245–1254.
- 401 Keenan, T.F., Gray, J., Friedl, M.A., Toomey, M., Bohrer, G., Hollinger, D.Y., Munger, J.W., O'Keefe, J.,
402 Schmid, H.P., Wing, I.S., Yang, B. & Richardson, A.D. (2014). Net carbon uptake has increased through
403 warming-induced changes in temperate forest phenology. *Nature Climate Change*, 4, 598–604.
- 404 Kolář, T., Giagli, K., Trnka, M., Bednářová, E., Vavrčík, H. & Rybníček, M. (2016). Response of the leaf
405 phenology and tree-ring width of European beech to climate variability. *Silva Fennica*, 50.

- 406 Kurnik, B., Barbosa, P. & Vogt, J. (2011). Testing two different precipitation datasets to compute the
 407 standardized precipitation index over the Horn of Africa. *International Journal of Remote Sensing*, 32,
 408 5947–5964.
- 409 Körner, C. & Basler, D. (2010). Phenology Under Global Warming. *Science*, 327, 1461–1462. Publisher:
 410 American Association for the Advancement of Science.
- 411 Körner, C., Möhl, P. & Hiltbrunner, E. (2023). Four ways to define the growing season. *Ecology Letters*, 26,
 412 1277–1292.
- 413 Laube, J., Sparks, T.H., Estrella, N., Höfler, J., Ankerst, D.P. & Menzel, A. (2014). Chilling outweighs
 414 photoperiod in preventing precocious spring development. *Global Change Biology*, 20, 170–182.
- 415 Laurance, W.F. (2007). Have we overstated the tropical biodiversity crisis? *Trends in Ecology & Evolution*,
 416 22, 65–70.
- 417 Levanič, T. (2007). Atrics – A New System for Image Acquisition in Dendrochronology. *Tree-Ring Research*,
 418 63, 117–122.
- 419 Li, Y., Zhang, W., Schwalm, C.R., Gentine, P., Smith, W.K., Ciais, P., Kimball, J.S., Gazol, A., Kannenberg,
 420 S.A., Chen, A., Piao, S., Liu, H., Chen, D. & Wu, X. (2023). Widespread spring phenology effects on
 421 drought recovery of Northern Hemisphere ecosystems. *Nature Climate Change*, 13, 182–188.
- 422 Lieth, H., Jacobs, J., Lange, O.L., Olson, J.S. & Wieser, W. (eds.) (1974). *Phenology and Seasonality
 423 Modeling*. vol. 8 of *Ecological Studies*. Springer Berlin Heidelberg, Berlin, Heidelberg.
- 424 Lynas, M., Houlton, B.Z. & Perry, S. (2021). Greater than 99% consensus on human caused climate change
 425 in the peer-reviewed scientific literature. *Environmental Research Letters*, 16, 114005.
- 426 Manzanedo, R.D. & Pederson, N. (2019). Towards a More Ecological Dendroecology. *Tree-Ring Research*,
 427 75, 152.
- 428 Marvel, K., Cook, B.I., Bonfils, C.J.W., Durack, P.J., Smerdon, J.E. & Williams, A.P. (2019). Twentieth-
 429 century hydroclimate changes consistent with human influence. *Nature*, 569, 59–65.
- 430 Marx, W., Haunschild, R. & Bornmann, L. (2021). Heat waves: a hot topic in climate change research.
 431 *Theoretical and Applied Climatology*, 146, 781–800.
- 432 McMaster, G. (1997). Growing degree-days: one equation, two interpretations. *Agricultural and Forest
 433 Meteorology*, 87, 291–300.
- 434 Meehl, G.A. & Tebaldi, C. (2004). More Intense, More Frequent, and Longer Lasting Heat Waves in the
 435 21st Century. *Science*, 305, 994–997.
- 436 Meng, L., Mao, J., Zhou, Y., Richardson, A.D., Lee, X., Thornton, P.E., Ricciuto, D.M., Li, X., Dai, Y., Shi,
 437 X. & Jia, G. (2020). Urban warming advances spring phenology but reduces the response of phenology
 438 to temperature in the conterminous United States. *Proceedings of the National Academy of Sciences*, 117,
 439 4228–4233.
- 440 Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská,
 441 O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Defila, C., Donnelly, A., Filella, Y., Jatczak,
 442 K., Mestre, A., Peñuelas, J., Pirinen, P., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wiel-
 443 golaski, F., Zach, S. & Zust, A. (2006). European phenological response to climate change matches the
 444 warming pattern. *Global Change Biology*, 12, 1969–1976.
- 445 Meyer, B.F., Buras, A., Gregor, K., Layritz, L.S., Principe, A., Kreyling, J., Rammig, A. & Zang, C.S.
 446 (2024). Frost matters: incorporating late-spring frost into a dynamic vegetation model regulates regional
 447 productivity dynamics in European beech forests. *Biogeosciences*, 21, 1355–1370.
- 448 Meyer, H.A. (1940). A Mathematical Expression for Height Curves. *Journal of Forestry*, 38, 415–420.

- 449 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.
- 450
- 451 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.
- 452
- 453 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.
- 454
- 455
- 456 Oreskes, N. (2004). The Scientific Consensus on Climate Change. *Science*, 306, 1686–1686.
- 457 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.
- 458
- 459
- 460 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.
- 461
- 462
- 463 Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42.
- 464
- 465 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.
- 466
- 467 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.
- 468
- 469
- 470 Peñuelas, J. & Filella, I. (2001). Responses to a Warming World. *Science*, 294, 793–795. Publisher: American Association for the Advancement of Science.
- 471
- 472 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.
- 473
- 474
- 475 Plomion, C., Leprovost, G. & Stokes, A. (2001). Wood Formation in Trees. *Plant Physiology*, 127, 1513–1523.
- 476
- 477 Polgar, C.A. & Primack, R.B. (2011). Leaf-out phenology of temperate woody plants: from trees to ecosystems. *New Phytologist*, 191, 926–941.
- 478
- 479 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.
- 480
- 481 Rathgeber, C.B.K., Cuny, H.E. & Fonti, P. (2016). Biological Basis of Tree-Ring Formation: A Crash Course. *Frontiers in Plant Science*, 7.
- 482
- 483 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.
- 484
- 485
- 486
- 487
- 488
- 489
- 490 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.
- 491
- 492

- 493 Richardson, A.D., Keenan, T.F., Migliavacca, M., Ryu, Y., Sonnentag, O. & Toomey, M. (2013). Climate
 494 change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural*
 495 and *Forest Meteorology*, 169, 156–173.
- 496 Rossi, S., Anfodillo, T. & Menardi, R. (2006). Trephor: A New Tool for Sampling Microcores from tree
 497 stems. *IAWA Journal*, 27, 89–97.
- 498 Sanchez-Lorenzo, A., Wild, M., Brunetti, M., Guijarro, J.A., Hakuba, M.Z., Calbó, J., Mystakidis, S. &
 499 Bartok, B. (2015). Reassessment and update of long-term trends in downward surface shortwave radiation
 500 over Europe (1939–2012). *Journal of Geophysical Research: Atmospheres*, 120, 9555–9569.
- 501 Saunders, M.R. & Wagner, R.G. (2008). Height-diameter models with random coefficients and site variables
 502 for tree species of Central Maine. *Annals of Forest Science*, 65, 203–203.
- 503 Sgubin, G., Swingedouw, D., Dayon, G., García De Cortázar-Atauri, I., Ollat, N., Pagé, C. & Van Leeuwen,
 504 C. (2018). The risk of tardive frost damage in French vineyards in a changing climate. *Agricultural and*
 505 *Forest Meteorology*, 250–251, 226–242.
- 506 Silvestro, R., Deslauriers, A., Prislan, P., Rademacher, T., Rezaie, N., Richardson, A.D., Vitassee, Y. &
 507 Rossi, S. (2025). From Roots to Leaves: Tree Growth Phenology in Forest Ecosystems. *Current Forestry*
 508 *Reports*, 11, 12.
- 509 Silvestro, R., Mura, C., Alano Bonacini, D., De Lafontaine, G., Faubert, P., Mencuccini, M. & Rossi, S.
 510 (2023a). Local adaptation shapes functional traits and resource allocation in black spruce. *Scientific*
 511 *Reports*, 13, 21257.
- 512 Silvestro, R., Zeng, Q., Buttò, V., Sylvain, J.D., Drolet, G., Mencuccini, M., Thiffault, N., Yuan, S. & Rossi,
 513 S. (2023b). A longer wood growing season does not lead to higher carbon sequestration. *Scientific Reports*,
 514 13, 4059.
- 515 Soolanayakanahally, R.Y., Guy, R.D., Silim, S.N. & Song, M. (2013). Timing of photoperiodic competency
 516 causes phenological mismatch in balsam poplar (*Populus balsamifera* L.). *Plant, Cell & Environment*, 36,
 517 116–127.
- 518 Spinoni, J., Naumann, G., Carrao, H., Barbosa, P. & Vogt, J. (2014). World drought frequency, duration,
 519 and severity for 1951–2010. *International Journal of Climatology*, 34, 2792–2804.
- 520 Spinoni, J., Vogt, J.V., Naumann, G., Barbosa, P. & Dosio, A. (2018). Will drought events become more
 521 frequent and severe in Europe? *International Journal of Climatology*, 38, 1718–1736.
- 522 Stridbeck, P., Björklund, J., Fuentes, M., Gunnarson, B.E., Jönsson, A.M., Linderholm, H.W., Ljungqvist,
 523 F.C., Olsson, C., Rayner, D., Rocha, E., Zhang, P. & Seftigen, K. (2022). Partly decoupled tree-ring
 524 width and leaf phenology response to 20th century temperature change in Sweden. *Dendrochronologia*,
 525 75, 125993.
- 526 Swidrak, I., Schuster, R. & Oberhuber, W. (2013). Comparing growth phenology of co-occurring deciduous
 527 and evergreen conifers exposed to drought. *Flora: Morphology, Distribution, Functional Ecology of Plants*,
 528 208, 609–617.
- 529 Teskey, R., Werten, T., Bauweraerts, I., Ameye, M., McGuire, M.A. & Steppe, K. (2015). Responses of tree
 530 species to heat waves and extreme heat events. *Plant, Cell & Environment*, 38, 1699–1712.
- 531 Trenberth, K.E., Dai, A., Van Der Schrier, G., Jones, P.D., Barichivich, J., Briffa, K.R. & Sheffield, J.
 532 (2014). Global warming and changes in drought. *Nature Climate Change*, 4, 17–22.
- 533 Tyree, M.T. & Zimmermann, M.H. (2002). *Xylem Structure and the Ascent of Sap*. Springer Series in Wood
 534 Science. Springer Berlin Heidelberg, Berlin, Heidelberg.
- 535 Vitasse, Y. (2013). Ontogenetic changes rather than difference in temperature cause understory trees to leaf
 536 out earlier. *New Phytologist*, 198, 149–155.

- 537 Vitasse, Y., eLenz, A. & eKoerner, C. (2014). The interaction between freezing tolerance and phenology in
538 temperate deciduous trees. *Frontiers in Plant Science*, 5. Publisher: Frontiers Media S.A.
- 539 Von Arx, G. & Carrer, M. (2014). ROXAS – A new tool to build centuries-long tracheid-lumen chronologies
540 in conifers. *Dendrochronologia*, 32, 290–293.
- 541 Way, D.A. & Montgomery, R.A. (2015). Photoperiod constraints on tree phenology, performance
542 and migration in a warming world. *Plant, Cell & Environment*, 38, 1725–1736. _eprint:
543 <https://onlinelibrary.wiley.com/doi/pdf/10.1111/pce.12431>.
- 544 Wolfe, D.W., Schwartz, M.D., Lakso, A.N., Otsuki, Y., Pool, R.M. & Shaulis, N.J. (2005). Climate change
545 and shifts in spring phenology of three horticultural woody perennials in northeastern USA. *International
546 Journal of Biometeorology*, 49, 303–309.
- 547 Wolkovich, E.M., Auerbach, J., Chamberlain, C.J., Buonaiuto, D.M., Ettinger, A.K., Morales-Castilla, I.
548 & Gelman, A. (2021). A simple explanation for declining temperature sensitivity with warming. *Global
549 Change Biology*, 27, 4947–4949.
- 550 Wolkovich, E.M., Cook, B.I. & Davies, T.J. (2014). Progress towards an interdisciplinary science of plant
551 phenology: building predictions across space, time and species diversity. *New Phytologist*, 201, 1156–1162.
552 _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/nph.12599>.
- 553 Wolkovich, E.M., Ettinger, A.K., Chin, A., Chamberlain, C.J., Baumgarten, F., Pradhan, K., Manzanedo,
554 R.D. & Lambers, J.H.R. (2025). Why longer seasons with climate change may not increase tree growth.
555 *In review*.
- 556 Woolway, R.I., Sharma, S., Weyhenmeyer, G.A., Debolskiy, A., Golub, M., Mercado-Bettín, D., Perroud,
557 M., Stepanenko, V., Tan, Z., Grant, L., Ladwig, R., Mesman, J., Moore, T.N., Shatwell, T., Vanderkelen,
558 I., Austin, J.A., DeGasperi, C.L., Dokulil, M., La Fuente, S., Mackay, E.B., Schladow, S.G., Watanabe,
559 S., Marcé, R., Pierson, D.C., Thiery, W. & Jennings, E. (2021). Phenological shifts in lake stratification
560 under climate change. *Nature Communications*, 12, 2318.
- 561 Wu, J. (2013). Key concepts and research topics in landscape ecology revisited: 30 years after the Allerton
562 Park workshop. *Landscape Ecology*, 28, 1–11.
- 563 Wu, X., Niu, C., Liu, X., Hu, T., Feng, Y., Zhao, Y., Liu, S., Liu, Z., Dai, G., Zhang, Y., Van Meerbeek, K.,
564 Wu, J., Liu, L., Guo, Q. & Su, Y. (2024). Canopy structure regulates autumn phenology by mediating
565 the microclimate in temperate forests. *Nature Climate Change*, 14, 1299–1305.
- 566 Wu, Z., Chen, S., De Boeck, H.J., Stenseth, N.C., Tang, J., Vitasse, Y., Wang, S., Zohner, C. & Fu, Y.H.
567 (2021). Atmospheric brightening counteracts warming-induced delays in autumn phenology of temperate
568 trees in Europe. *Global Ecology and Biogeography*, 30, 2477–2487.
- 569 Yan, T., Fu, Y.H., Campioli, M., Peñuelas, J. & Wang, X. (2021). Divergent responses of phenology and
570 growth to summer and autumnal warming. *Global Change Biology*, 27, null.
- 571 Yuancai, L. & Parresol, B.R. (2001). Remarks on Height-Diameter Modeling. Tech. Rep. SRS-RN-10, U.S.
572 Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.
- 573 Zani, D., Crowther, T.W., Mo, L., Renner, S.S. & Zohner, C.M. (2020). Increased growing-season productiv-
574 ity drives earlier autumn leaf senescence in temperate trees. *Science*, 370, 1066–1071. Publisher: American
575 Association for the Advancement of Science.
- 576 Zohner, C.M., Mirzagholi, L., Renner, S.S., Mo, L., Rebindaine, D., Bucher, R., Palouš, D., Vitasse, Y., Fu,
577 Y.H., Stocker, B.D. & Crowther, T.W. (2023). Effect of climate warming on the timing of autumn leaf
578 senescence reverses after the summer solstice. *Science*, 381.

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