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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). The
38 drivers regulating autumn phenology are far less understood than those of spring because it has attracted
39 much less attention compared to spring (Piao *et al.*, 2019) and because the data is often noisier (Wu *et al.*,
40 2024). However, there is a general belief that autumn phenophases are driven by shortening photoperiod and
41 colder temperatures (Cooke *et al.*, 2012; Flynn & Wolkovich, 2018; Körner & Basler, 2010; Delpierre *et al.*,
42 2016). Different hypotheses are proposed to explain delayed autumn phenophases. First, warmer autumn
43 temperatures may extend the activity of photosynthetic enzymes which causes decreases the degradation
44 rate of chlorophyll, thus delaying the timing of leaf senescence (Yan *et al.*, 2021). Second, summer droughts

45 could pause the activity schedule of trees and delay senescence to increase carbon assimilation (Dox *et al.*,
46 2022). Third, there could be an antagonistic effect of warming and brightening—caused by reductions in
47 atmospheric pollution and cloud cover (Sanchez-Lorenzo *et al.*, 2015)—on leaf senescence (Wu *et al.*, 2021).
48 Brightening accelerates the leaf senescence processes and reduces the temperature sensitivity during that
49 period, counteracting the 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, neither growth rate nor overall annual increment was increased by longer seasons. This
58 could substantially affect carbon-cycle model projections and thus feedbacks to future climate (Richardson
59 *et al.*, 2013; Swidrak *et al.*, 2013). Starting to grow earlier and stopping later both have pros and cons
60 (Figure 1).

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

76 **1.1.3. Growing season shifts and consequences on forest ecosystems and services**

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

85 **1.2 Nature of the problem, and how to address it**

86 **1.2.1. Past phenological trends can help (or not) predict future phenological changes**

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

95

96 **1.2.2. The assumption that longer seasons lead to increased growth is called into question**

97 1.2.2.1. *Absence of growth despite better conditions and strategies that can be used* Recent work shows
98 an absence of increased growth despite apparent better environmental conditions, thus casting doubt on a
99 simple and intuitive positive relationship between growing season length and growth. This paradox further
100 emphasizes the need to better understand the drivers regulating growth across biomes, but also how these
101 drivers vary across the species within these biomes. Phenology varies greatly across species (e.g. closely
102 related species tend to budburst at similar times under similar conditions) (Wolkovich *et al.*, 2014), but
103 so does the relationship between growth and season length, which may explain the wide variation of this
104 relationship within communities (Buckley & Kingsolver, 2012). This highlights another weakness of current
105 carbon sequestration models that pool species together, which likely overpasses important nuances in the
106 growth responses that could be explained by species differences. This may mislead the future of forest carbon
107 source-sink ratios (Green & Keenan, 2022; Cabon *et al.*, 2022). To better understand how different species
108 respond to warming, different strategies can be used.

109
110 1.2.2.2. *Experiments:* First, experiments are paramount to robustly tease apart the external vs internal
111 drivers (e.g. warmer springs from severe drought later in the season—a common co-occurring reality in natu-
112 ral environments) (Morin *et al.*, 2010; Primack *et al.*, 2015). However, experiments are most often performed
113 on juvenile trees, which are critical for their role in forest regeneration projections, but their responses can
114 hardly be translated to mature trees, which hold the overwhelming carbon biomass proportion of forests
115 (Augspurger & Bartlett, 2003; Silvestro *et al.*, 2023b; Vitasse, 2013).

116
117 1.2.2.3. *Ground based observations:* Second, leaf phenology through ground-based observations can pro-
118 vide valuable insights into the growth temporality trees that are not suitable for experimental trials. Since
119 cambial and leaf phenology are closely linked to the other, having the more accessible leaf phenology data
120 can act as a reliable proxy for the onset and end of tree growth. It is to say that knowing when leaves
121 elongate and colour can guide when trees start and stop growing—fundamental metrics to determine the
122 growing season length. Ground observations have the advantage of providing accurate data on phenological
123 events for specific sites and species. Recently, the widespread use of smartphones has opened a whole new
124 world of possible phenological monitoring through citizen scientists' records of data over much larger areas
125 and for a wider range of species (Dickinson *et al.*, 2012; Hufkens *et al.*, 2019; Piao *et al.*, 2019). While there
126 are drawbacks to these observations (e.g. non-standard protocols, highly uneven spatiotemporal distribution
127 of these observations), these methods have a huge potential to diversify the phenology data.

128
129 1.2.3. **Goals of my thesis**
130 Using citizen science data, a common garden study and a large-scale experiment, I aim to better understand
131 how different tree species, at different lifespan stages, vary in their growth responses to different season
132 length. Answering these patterns requires defining growth and the growing season.

133 1.3 Complexity of measuring growth and defining growing season length

134 1.3.1.1. *What is a growing season?*

135 To understand how trees respond to growing season conditions, it is important to clarify what a growing
136 season and growth are.
137 First, a problem that arises when one tries to quantify how shifting growing seasons affect growth comes from
138 the definition of the growing season itself. Recently, Körner *et al.* (2023) proposed four definitions addressing
139 this issue: (1) true growing season, based on measurable growth; (2) phenological season, based on visible
140 phenological markers; (3) the productive season, based on primary production and (4) meteorological season,
141 based on environmental conditions.

142 Here, I will focus on how definition (2), incorporating (4) affects definition (1) as the data collected
143 for this thesis can't address (3). I will use definition (2) to infer a "window of opportunity" during which
144 meteorological conditions will be used to calculate growing degree days (GDD). I am using the meteorological
145 season within a constrained window, instead of simply using it irrespective of phenology because of the illusion
146 that an absolute increase in GDD over the last decades—is irrespective of the timing of phenophases—also
147 increases growth. Springs are warmer, falls are also sometimes warmer, and summers are warmer, which
148 together increase the number of GDD, which may appear to be a reliable proxy for better environmental

149 conditions. However, models that accumulate GDD before and/or after trees grow could mislead about how
150 this variable drives growth.

151 *1.3.1.2. What is growth?*

152 Wood formation (xylogenesis) is the major biological process by which carbon is allocated and long-term
153 stored in woody plants. Radial growth is determined by the production of xylem and phloem cells that
154 begins with cambial activation and cell production (Etzold *et al.*, 2022; Silvestro *et al.*, 2025). The rate and
155 duration of these phases lead to irreversible radial growth increments usually represented through tree rings.
156 In these, secondary xylem cells account disproportionately to the number of cells produced because they
157 divide more than phloem cells (Plomion *et al.*, 2001; Rathgeber *et al.*, 2016).

158

159 **1.3.2. Traditional diameter measurements miss the resolution of annual growth increment**

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

169

170 Alongside the diameter-height allometric relationship, dendroecology—applications of dendrochronological
171 techniques to problems in ecology (Fritts & Swetnam, 1989)—emerged to answer ecological problems as
172 well as to hindcast (e.g. (Bergeron *et al.*, 2004)) and forecast ecological processes both at the regional (Gazol
173 *et al.*, 2018) and global scale (Manzanedo & Pederson, 2019; Büntgen *et al.*, 2018). Now, these methods
174 can be used to understand more precise growth patterns and their relationship with different environmental
175 factors.

176

177 **1.3.3. 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 mentioned:
192 determinate and indeterminate growth, though it appears that species exist along a gradient of these (Baum-
193 garten *et al.*, 2025). Indeterminate growth is usually associated with short-lived and fast growth species,
194 where these life-history strategies may give them a competing advantage as tissue growth can be produced
195 quickly in response to changing environmental conditions, but this comes with a higher risk of late spring
196 and early fall frost as well as late droughts (Baumgarten *et al.*, 2025; Brienen *et al.*, 2020). At the opposite
197 side of the spectrum, determinate species are usually long-lived and slow-growing and are mainly constrained
198 by conditions during bud formation; this may increase bud survival at the detriment of opportunistic growth
199 in face of better-than-expected conditions (Baumgarten *et al.*, 2025).

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

204 1.4 Objectives

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

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

213 1.5 Research questions

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

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

219 2 Methodology

220 2.1 Coringtreespotters

221 2.1. Studies locations **Common garden** In 2014-2015, we collected seeds from four field sites in northeastern
 222 North America spanning approximately a 3.5° latitudinal gradient. The four field sites included Harvard
 223 Forest (42.55°N, 72.20°W), the White Mountains (44.11°N, 71.40°W), Second College Grant, (44.79°N,
 224 71.15°W), and St. Hippolyte, QC, CAN (45.98°N, 74.01°W). We transported all seeds back to the Weld
 225 Hill Research Building at the Arnold Arboretum in Boston Massachusetts (42.30°N, 71.13°W) where we
 226 germinated seeds following standard germination protocols, and grew them to seedling stages in the research
 227 greenhouse. In the spring of 2017 we out-planted seedlings to establish the garden. Plots were regularly
 228 weeded and watered throughout the duration of the study and were pruned in the fall of 2020.

229 **2.1. Coringtreespotters** The citizen science programs, the Treespotters was started in 2015 and aimed
 230 to train citizen scientist for accurate and rigorous phenological monitoring. From 2015 to 2024, hundreds of
 231 citizen scientists monitored * trees of * species regularly from the early phenostage in the spring until leaf
 232 colouring in the fall. The BBC scale was used (check if that's true).

233 In 2018, with Lizzie's move to UBC, the Tree Spotters became an official program of the Arnold Arbore-
 234 tum of Harvard University. From 2015-2020, the Tree Spotters program trained hundreds of citizen scientists
 235 to observe 75 trees and shrubs representing 15 native species. During that time, volunteers submitted over
 236 330,000 phenological observations to the National Phenology's Database.

²³⁷ **3 Supplemental material**

²³⁸ **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	

240

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)
241	<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))
242	<p>Differences across species/provenance</p>

243

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>
244 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)

245 References

- 246 Aitken, S.N. & Bemmels, J.B. (2016). Time to get moving: assisted gene flow of forest trees. *Evolutionary Applications*, 9, 271–290.
- 247
- 248 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.
- 249
- 250
- 251 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.
- 252
- 253 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.
- 254
- 255
- 256 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*.
- 257
- 258 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.
- 259
- 260 Bonhomme, R. (2000). Bases and limits to using ‘degree.day’ units. *European Journal of Agronomy*, 13, 1–10.
- 261

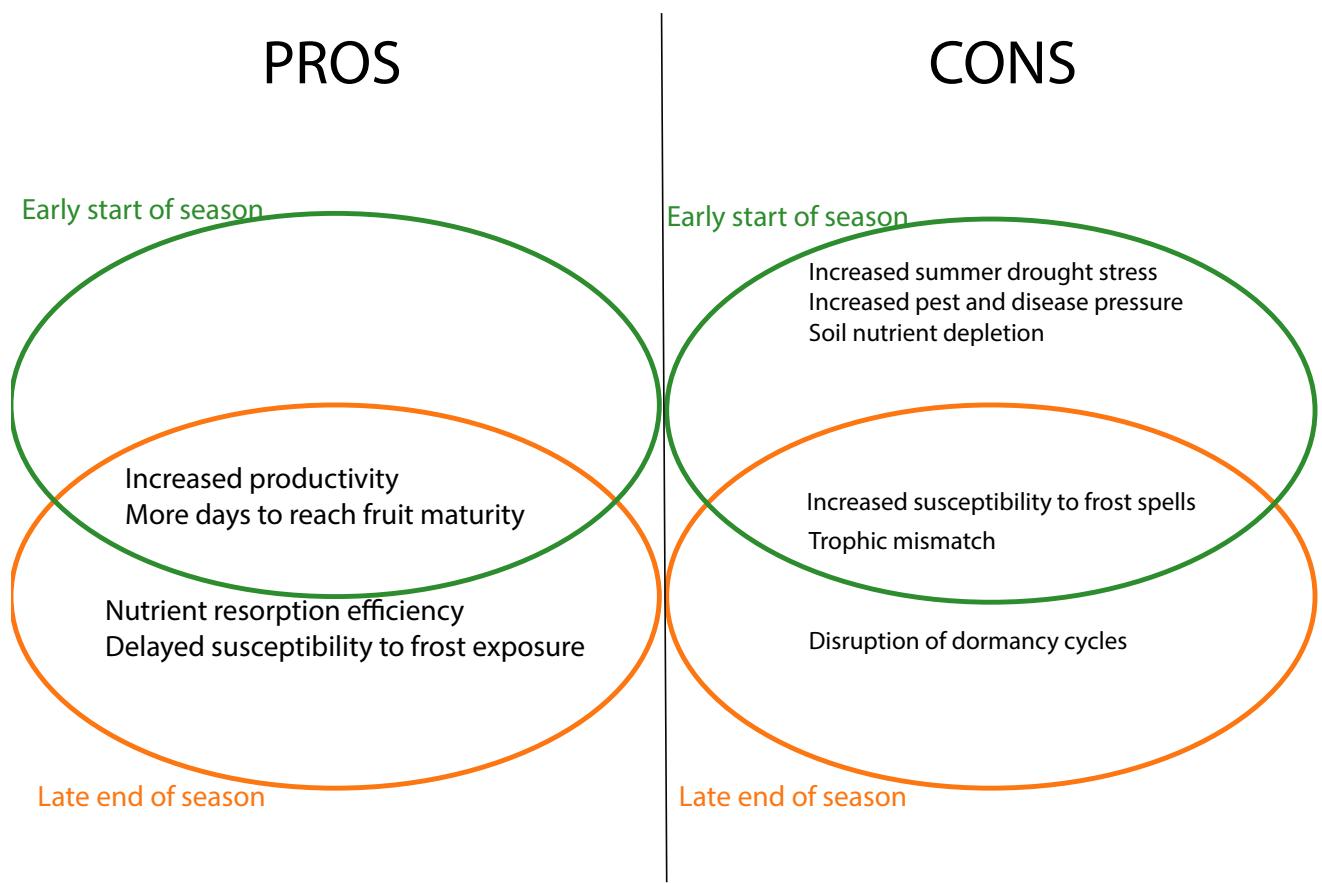


Figure 1: Pros and cons of early start and late end of growing season.

- 262 Brienen, R.J.W., Caldwell, L., Duchesne, L., Voelker, S., Barichivich, J., Baliva, M., Ceccantini, G., Di Fil-
263 ippo, A., Helama, S., Locosselli, G.M., Lopez, L., Piovesan, G., Schöngart, J., Villalba, R. & Gloor, E.
264 (2020). Forest carbon sink neutralized by pervasive growth-lifespan trade-offs. *Nature Communications*,
265 11, 4241.
- 266 Buckley, L.B. & Kingsolver, J.G. (2012). Functional and Phylogenetic Approaches to Forecasting Species'
267 Responses to Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, 43, 205–226.
- 268 Büntgen, U., Wacker, L., Galván, J.D., Arnold, S., Arseneault, D., Baillie, M., Beer, J., Bernabei, M.,
269 Bleicher, N., Boswijk, G., Bräuning, A., Carrer, M., Ljungqvist, F.C., Cherubini, P., Christl, M., Christie,
270 D.A., Clark, P.W., Cook, E.R., Esper, J., Fowler, A.M., Gennaretti, F., Grießinger, J., Grissino-Mayer,
271 H., Grudd, H., Gunnarson, B.E., Hantemirov, R., Herzig, F., Hessl, A., Heussner, K.U., Jull, A.J.T.,
272 Kukarskikh, V., Kirdyanov, A., Krusic, P.J., Kyncl, T., Lara, A., LeQuesne, C., Linderholm, H.W., Loader,
273 N.J., Luckman, B., Miyake, F., Myglan, V.S., Nicolussi, K., Oppenheimer, C., Palmer, J., Panyushkina, I.,
274 Pederson, N., Rybníček, M., Schweingruber, F.H., Seim, A., Sigl, M., Churakova, O., Speer, J.H., Synal,
275 H.A., Tegel, W., Treydte, K., Villalba, R., Wiles, G., Wilson, R., Winship, L.J., Wunder, J., Yang, B. &
276 Young, G.H.F. (2018). Tree rings reveal globally coherent signature of cosmogenic radiocarbon events in
277 774 and 993 CE. *Nature Communications*, 9, 3605.
- 278 Cabon, A., Fernández-de-Uña, L., Gea-Izquierdo, G., Meinzer, F.C., Woodruff, D.R., Martínez-Vilalta, J. &
279 De Cáceres, M. (2020). Water potential control of turgor-driven tracheid enlargement in Scots pine at its
280 xeric distribution edge. *New Phytologist*, 225, 209–221.
- 281 Cabon, A., Kannenberg, S.A., Arain, A., Babst, F., Baldocchi, D., Belmecheri, S., Delpierre, N., Guerrieri,
282 R., Maxwell, J.T., McKenzie, S., Meinzer, F.C., Moore, D.J.P., Pappas, C., Rocha, A.V., Szejner, P.,
283 Ueyama, M., Ulrich, D., Vincke, C., Voelker, S.L., Wei, J., Woodruff, D. & Anderegg, W.R.L. (2022).
284 Cross-biome synthesis of source versus sink limits to tree growth. *Science*, 376, 758–761.
- 285 Camarero, J.J., Olano, J.M. & Parras, A. (2010). Plastic bimodal xylogenesis in conifers from continental
286 Mediterranean climates. *New Phytologist*, 185, 471–480.
- 287 Campbell, L.M., Hagerman, S. & Gray, N.J. (2014). Producing Targets for Conservation: Science and Politics
288 at the Tenth Conference of the Parties to the Convention on Biological Diversity. *Global Environmental
289 Politics*, 14, 41–63.
- 290 Campbell, R., McCarroll, D., Loader, N.J., Grudd, H., Robertson, I. & Jalkanen, R. (2007). Blue intensity
291 in *Pinus sylvestris* tree-rings: developing a new palaeoclimate proxy. *The Holocene*, 17, 821–828.
- 292 Ceballos, G., Ehrlich, P.R. & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction
293 signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*,
294 114.
- 295 Change, I.P.O.C. (2014). Detection and Attribution of Climate Change: from Global to Regional. In:
296 *Climate Change 2013 – The Physical Science Basis*. Cambridge University Press, pp. 867–952. 1st edn.
- 297 Chiang, F., Mazdiyasni, O. & AghaKouchak, A. (2021). Evidence of anthropogenic impacts on global drought
298 frequency, duration, and intensity. *Nature Communications*, 12, 2754.
- 299 Chmielewski, F.M. & Rötzer, T. (2001). Response of tree phenology to climate change across Europe.
300 *Agricultural and Forest Meteorology*, 108, 101–112.
- 301 Choat, B., Brodribb, T.J., Brodersen, C.R., Duursma, R.A., López, R. & Medlyn, B.E. (2018). Triggers of
302 tree mortality under drought. *Nature*, 558, 531–539.
- 303 Chuine, I. (2010). Why does phenology drive species distribution? *Philosophical Transactions of the Royal
304 Society B: Biological Sciences*, 365, 3149–3160.
- 305 Chuine, I. & Régnière, J. (2017). Process-Based Models of Phenology for Plants and Animals. *Annual
306 Review of Ecology, Evolution, and Systematics*, 48, 159–182.

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

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

- 393 Kurnik, B., Barbosa, P. & Vogt, J. (2011). Testing two different precipitation datasets to compute the
 394 standardized precipitation index over the Horn of Africa. *International Journal of Remote Sensing*, 32,
 395 5947–5964.
- 396 Körner, C. & Basler, D. (2010). Phenology Under Global Warming. *Science*, 327, 1461–1462. Publisher:
 397 American Association for the Advancement of Science.
- 398 Körner, C., Möhl, P. & Hiltbrunner, E. (2023). Four ways to define the growing season. *Ecology Letters*, 26,
 399 1277–1292.
- 400 Laube, J., Sparks, T.H., Estrella, N., Höfler, J., Ankerst, D.P. & Menzel, A. (2014). Chilling outweighs
 401 photoperiod in preventing precocious spring development. *Global Change Biology*, 20, 170–182.
- 402 Laurance, W.F. (2007). Have we overstated the tropical biodiversity crisis? *Trends in Ecology & Evolution*,
 403 22, 65–70.
- 404 Levanič, T. (2007). Atrics – A New System for Image Acquisition in Dendrochronology. *Tree-Ring Research*,
 405 63, 117–122.
- 406 Li, Y., Zhang, W., Schwalm, C.R., Gentine, P., Smith, W.K., Ciais, P., Kimball, J.S., Gazol, A., Kannenberg,
 407 S.A., Chen, A., Piao, S., Liu, H., Chen, D. & Wu, X. (2023). Widespread spring phenology effects on
 408 drought recovery of Northern Hemisphere ecosystems. *Nature Climate Change*, 13, 182–188.
- 409 Lieth, H., Jacobs, J., Lange, O.L., Olson, J.S. & Wieser, W. (eds.) (1974). *Phenology and Seasonality
 410 Modeling*. vol. 8 of *Ecological Studies*. Springer Berlin Heidelberg, Berlin, Heidelberg.
- 411 Lynas, M., Houlton, B.Z. & Perry, S. (2021). Greater than 99% consensus on human caused climate change
 412 in the peer-reviewed scientific literature. *Environmental Research Letters*, 16, 114005.
- 413 Manzanedo, R.D. & Pederson, N. (2019). Towards a More Ecological Dendroecology. *Tree-Ring Research*,
 414 75, 152.
- 415 Marvel, K., Cook, B.I., Bonfils, C.J.W., Durack, P.J., Smerdon, J.E. & Williams, A.P. (2019). Twentieth-
 416 century hydroclimate changes consistent with human influence. *Nature*, 569, 59–65.
- 417 Marx, W., Haunschild, R. & Bornmann, L. (2021). Heat waves: a hot topic in climate change research.
 418 *Theoretical and Applied Climatology*, 146, 781–800.
- 419 McMaster, G. (1997). Growing degree-days: one equation, two interpretations. *Agricultural and Forest
 420 Meteorology*, 87, 291–300.
- 421 Meehl, G.A. & Tebaldi, C. (2004). More Intense, More Frequent, and Longer Lasting Heat Waves in the
 422 21st Century. *Science*, 305, 994–997.
- 423 Meng, L., Mao, J., Zhou, Y., Richardson, A.D., Lee, X., Thornton, P.E., Ricciuto, D.M., Li, X., Dai, Y., Shi,
 424 X. & Jia, G. (2020). Urban warming advances spring phenology but reduces the response of phenology
 425 to temperature in the conterminous United States. *Proceedings of the National Academy of Sciences*, 117,
 426 4228–4233.
- 427 Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská,
 428 O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Defila, C., Donnelly, A., Filella, Y., Jatczak,
 429 K., Mestre, A., Peñuelas, J., Pirinen, P., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wiel-
 430 golaski, F., Zach, S. & Zust, A. (2006). European phenological response to climate change matches the
 431 warming pattern. *Global Change Biology*, 12, 1969–1976.
- 432 Meyer, B.F., Buras, A., Gregor, K., Layritz, L.S., Principe, A., Kreyling, J., Rammig, A. & Zang, C.S.
 433 (2024). Frost matters: incorporating late-spring frost into a dynamic vegetation model regulates regional
 434 productivity dynamics in European beech forests. *Biogeosciences*, 21, 1355–1370.
- 435 Meyer, H.A. (1940). A Mathematical Expression for Height Curves. *Journal of Forestry*, 38, 415–420.

- 436 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.
- 437
- 438 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.
- 439
- 440 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.
- 441
- 442
- 443 Oreskes, N. (2004). The Scientific Consensus on Climate Change. *Science*, 306, 1686–1686.
- 444 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.
- 445
- 446
- 447 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.
- 448
- 449
- 450 Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42.
- 451
- 452 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.
- 453
- 454 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.
- 455
- 456
- 457 Peñuelas, J. & Filella, I. (2001). Responses to a Warming World. *Science*, 294, 793–795. Publisher: American Association for the Advancement of Science.
- 458
- 459 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.
- 460
- 461
- 462 Plomion, C., Leprovost, G. & Stokes, A. (2001). Wood Formation in Trees. *Plant Physiology*, 127, 1513–1523.
- 463 Polgar, C.A. & Primack, R.B. (2011). Leaf-out phenology of temperate woody plants: from trees to ecosystems. *New Phytologist*, 191, 926–941.
- 464
- 465 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.
- 466
- 467
- 468 Rathgeber, C.B.K., Cuny, H.E. & Fonti, P. (2016). Biological Basis of Tree-Ring Formation: A Crash Course. *Frontiers in Plant Science*, 7.
- 469
- 470 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., Capone, 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.
- 471
- 472
- 473
- 474
- 475
- 476
- 477 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.
- 478
- 479

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

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

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