

¹ Does age matter in tree growth responses to longer growing season?

² Christophe Rouleau-Desrochers

³ January 28, 2026

⁴ Introduction

⁵ 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, 2023; Laurance, 2007; Parmesan & Yohe, 2003). This can be through land use change and loss,
⁹ pollution, invasive species, resource overexploitation and climate change (Driscoll *et al.*, 2018; Parmesan
¹⁰ *et al.*, 1999; Wu, 2013). Though some immediate actions can mitigate these impacts (e.g. Campbell *et al.*,
¹¹ 2014), reversing 150 years of human-induced greenhouse gas emissions is harder. These emissions have af-
¹² fected Earth's climate and are projected to keep changing it for many centuries (Intergovernmental Panel On
¹³ Climate Change, 2023). Yet, the extent of the consequences that a warming climate will have on biological
¹⁴ processes is still debated (Huey *et al.*, 2012), in part because it requires accurate predictions of current and
¹⁵ future trends in some of the most reported and direct biological impacts of climate change, as I review below.
¹⁶ And also because it requires understanding the complex additional effects of these impacts, which I propose
¹⁷ to study for my thesis.

¹⁸ Trends and drivers of spring and autumn phenological events

¹⁹ The most frequently observed biological impact of climate change over the past decades is major changes in
²⁰ phenology—the timing of recurring life history events (Parmesan & Yohe, 2003; Cleland *et al.*, 2007; Lieth
²¹ *et al.*, 1974; Woolway *et al.*, 2021; Menzel *et al.*, 2006). Shifts in spring and autumn phenology modify when
²² the growing season starts and when it ends. These shifts in growing season length could have impacts on
²³ ecosystems, but anticipating these consequences requires understanding how much, and why it has changed
²⁴ (Duputié *et al.*, 2015).

²⁵
²⁶ *Drivers of spring phenology:* Spring phenological events (e.g. budburst and leafout) have been advancing
²⁷ from 0.5 (Wolfe *et al.*, 2005) to 4.2 days/decade (Chmielewski & Rötzer, 2001; Fu *et al.*, 2014) and are
²⁸ mainly driven by temperature (Chuine, 2010; Cleland *et al.*, 2007; Peñuelas & Filella, 2001), especially for
²⁹ trees. In the winter, when trees are still in dormancy, they accumulate cold temperatures (chilling) for which
³⁰ a certain amount is required to be ready to accumulate heat (forcing) (Vitasse *et al.*, 2014). Then, in the
³¹ spring, a certain amount of forcing triggers budburst (Fu *et al.*, 2015). Heat requirements are met sooner
³² in warm springs, thus explaining the advancement of spring events and earlier onset of growing seasons over
³³ the last decades (Fu *et al.*, 2015, 2013; Laube *et al.*, 2014).

³⁴
³⁵
³⁶ *Drivers of autumn phenology:* In contrast, autumn phenology (e.g. budset and leaf senescence) has delayed
³⁷ with climate change—though shifts in the autumn have been much smaller than those in the spring (Gallinat
³⁸ *et al.*, 2015; Jeong & Medvigy, 2014)—and its drivers are also far less understood. Two realities could ex-
³⁹ plain these differences: lesser attention is paid to autumn phenology (Piao *et al.*, 2019) and the data is often
⁴⁰ noisier (Wu *et al.*, 2024). However, some of these disparities are likely due to different factors driving autumn
⁴¹ phenology, as these phenophases appear to be caused by shortening photoperiod and colder temperatures
⁴² (Cooke *et al.*, 2012; Flynn & Wolkovich, 2018; Körner & Basler, 2010; Delpierre *et al.*, 2016). Given that
⁴³ low temperatures can accelerate senescence, warmer autumns may delay autumn phenophases, possibly by
⁴⁴ extending the activity of photosynthetic enzymes, which decreases the degradation rate of chlorophyll (Yan

45 *et al.*, 2021). Additionally, summer droughts could pause the activity schedule of trees and delay senescence
46 to increase carbon assimilation (Dox *et al.*, 2022). Finally, there could be other factors affecting senescence
47 delays that we do not consider here, such an antagonistic effect of warming and atmospheric brightening
48 (Sanchez-Lorenzo *et al.*, 2015; Wu *et al.*, 2021).

49
50 **How shifts in spring and autumn phenology will affect trees and forests are not clear**
51 Shifts in spring and autumn phenology in trees support a long-lasting and intuitive assumption that earlier
52 spring and delayed autumn events extend seasons and thus increase growth (Keenan *et al.*, 2014; Stridbeck
53 *et al.*, 2022). However, research from recent years has cast doubt on this hypothesis (Dow *et al.*, 2022;
54 Green & Keenan, 2022; Silvestro *et al.*, 2023). For instance, Dow *et al.* (2022) showed that despite an earlier
55 growth onset, longer seasons did not increase the growth rate nor overall annual increment in trees. This could
56 substantially affect forest carbon-cycle model projections on and thus feedbacks to future climate (Richard-
57 son *et al.*, 2013; Swidrak *et al.*, 2013). These projections could be impacted by the different effects that an
58 earlier start and a later end of season have on trees, some of which I propose to study in my thesis (Figure 1).

59

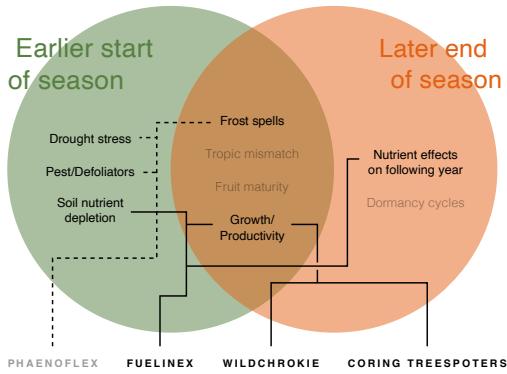


Figure 1: The effects that an earlier start and later end of season can have on trees. Solid lines connect effects studied over the course of this thesis. Phaenoflex (in grey) and its dashed lines represent other effects I investigated in a related experimental project that is not part of this thesis, but one I collaborated on in 2023 and 2024.

60 Understanding these findings requires answering why trees do not grow more despite longer growing seasons.
61 While carbon allocation to above-ground biomass is one of the largest carbon sinks, how this carbon is allo-
62 cated into wood is poorly understood. Indeed, the assumption of a linear relationship between wood growth
63 and carbon assimilation is not well supported mechanistically and represents an important limitation of
64 vegetation models (Cabon *et al.*, 2022). Net primary production represents the difference between photosyn-
65 thesis and plant respiration, but this commonly used metric omits the representation of growth processes.
66 This is perhaps because of a long-lasting paradigm of source-limited photosynthesis (Friend *et al.*, 2019;
67 Parent *et al.*, 2010). Whether a tree's growth is source (photosynthetic activity determines sink activity) or
68 sink (growth, respiration, and other metabolic processes determine the carbon source) controlled depends
69 upon a closely coordinated sequence of dynamic responses and is still an active research question. However,
70 Gessler & Zweifel (2024) recently suggested that neither source nor sink control systematically dominates.
71 This complex dynamic enforces the importance of understanding the temperature sensitivity relationship
72 between growth activity and photosynthesis. Growing evidence suggests that cambial activity may be more
73 sensitive than photosynthesis to a range of environmental conditions, such as water and nutrient availability,
74 and temperature (Cabon *et al.*, 2022, 2020; Muller *et al.*, 2011; Peters *et al.*, 2021). Thus, this demonstrates
75 that carbon projection models that solely rely on vegetation alone may mislead carbon sequestration dy-
76 namics of our forests.

77

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
81 to high amplitude (Almagro *et al.*, 2025; Cabon *et al.*, 2022). This expected asymmetry of future environ-
82 mental changes makes understanding the internal physiological constraints (via genetic and developmental
83 control), and external limits (via extreme temperatures or moisture deficit) to growth critical, which I aim
84 to investigate with experiments and observations.

85 Experiments and observations to anticipate the future of growth and season 86 length relationship

87 Past phenological trends can help (or not) predict future phenological changes

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

96 Growth drivers differences across species need to be considered

97 Recent work emphasizing the need to understand the drivers regulating growth across biomes highlights
98 strong species-level variation that may be critical to accurate projections. Phenology varies greatly across
99 species (e.g., closely related species tend to budburst at similar times under similar conditions Wolkovich
100 *et al.*, 2014), but so does the relationship between growth and season length, which may explain the wide
101 variation of this relationship within communities (Buckley & Kingsolver, 2012). This points out another
102 weakness of current carbon sequestration models that pool species together, likely missing important nu-
103 ancies in the growth responses plausibly explained by species differences. Excluding species differences in
104 models may mislead future carbon dynamic models (Green & Keenan, 2022; Cabon *et al.*, 2022; Wolkovich
105 *et al.*, 2025). We propose to address this issue by using experiments and ground-based observations to better
106 understand the responses of different species to warming. While both of these strategies have downsides,
107 they are likely to leverage valuable insights which are necessary to improve carbon sequestration projections
108 (Wolkovich *et al.*, 2025).

109
110 *Experiments:* First, experiments are extremely useful in teasing apart co-occurring realities in natural en-
111 vironments. For example, warm springs and severe droughts later in the summer often happen together
112 within a single year, making it difficult to tease these effects apart from observational data. Manipulative
113 experiments, in contrast, have the capacity to separate the relative effect of each phenomenon (Morin *et al.*,
114 2010; Primack *et al.*, 2015), but also have major limitations, especially when working on trees. Logistical
115 constraints of working with adult trees mean that experiments are most often performed on juvenile trees.
116 While saplings are critical for their role in forest regeneration projections, their responses often do not directly
117 translate to mature trees, which hold the overwhelming carbon biomass proportion of forests (Augspurger &
118 Bartlett, 2003; Silvestro *et al.*, 2023; Vitasse, 2013). However, even if young trees are often more plastic than
119 adult forms, their responses can still provide valuable insights into differences across species and populations
120 (Wolkovich *et al.*, 2025).

121
122 *Ground-based observations:* Second, leaf phenology can provide valuable and accessible insights into the
123 growth temporality of trees that are not suitable for experimental trials. Collecting cambial phenology
124 data, which is a direct measure of wood growth, is time-consuming and expensive. In contrast, leaf phe-
125 nology through ground-based observations are low-cost methods that provide direct evidence of changing
126 phenophases (Piao *et al.*, 2019). Cambial and leaf phenology are often closely synchronized (Stridbeck *et al.*,
127 2022); therefore, the more accessible leaf phenology data can act as a reliable proxy for the onset and end of
128 tree growth. In other words, knowing when leaves elongate and colour can guide us to when trees start and
129

130 stop growing, which is a fundamental metric to determine the growing season length. Additionally, unlike
131 other methods, ground observations have the advantage of providing accurate measurements of phenological
132 events for specific sites and species. Recently, the widespread use of smartphones has considerably simplified
133 the phenological monitoring by citizen scientists (Dickinson *et al.*, 2012; Hufkens *et al.*, 2019; Piao *et al.*,
134 2019). While there are drawbacks to observations by citizen science programs (e.g. non-standard protocols,
135 highly uneven spatiotemporal distribution of these observations), they have the potential to vastly increase
136 the range of studied species and areas (Chandler *et al.*, 2017; Feldman *et al.*, 2018).

137

138 **Goals of my thesis**

139 I aim to understand how different tree species, at different lifespan stages, vary in their growth responses to
140 different season lengths. To achieve this, I worked across different methods (Figure 2). First, I deployed a
141 large-scale experiment, named Fuelinex, during which I artificially controlled the growing season length for
142 seven species of tree saplings (2-3 years old). During this experiment, I also tested nutrient effects later in
143 the season. Second, I leveraged observational data from older trees across two projects. One of them, which
144 I named Wildchrokie, leverages vegetative phenology data from a common garden project of four species
145 of juvenile trees (5-8 years old). With the other observational project, named coringTreepotters, I used
146 phenology data collected by citizen scientists on eleven species of fully mature trees (>30 years old). With
147 these projects, I hope to explain the growth patterns of trees, but it requires defining growth and the growing
148 season.

149 **Complexity of measuring growth and defining growing season length**

150 **What is a growing season?**

151 The definition of the growing season itself is not well-defined, and studies use an array of definitions. Recently,
152 Körner *et al.* (2023) proposed four definitions addressing this issue: (1) true growing season, based on
153 measurable growth; (2) phenological season, based on visible phenological markers; (3) the productive season,
154 based on primary production and (4) meteorological season, based on environmental conditions.
155 Here, I will focus on how the phenological season (2), incorporating how the meteorological season (4) affects
156 the true growing season (1), as our data cannot address the productive season (3). I will use the phenological
157 season (2) to infer a “window of opportunity”, to calculate growing degree days (GDD)—a measure of heat
158 accumulation—using meteorological conditions.

159

160 **What is growth?**

161 Wood formation (xylogenesis) consists of allocating carbon for long-term storage in woody plants. Xylo-
162 genesis starts with cambial activation and cell production, which produces xylem and phloem cells (Etzold
163 *et al.*, 2022; Silvestro *et al.*, 2025). The rate and duration of these phases lead to irreversible radial growth
164 increments usually represented through tree rings (Plomion *et al.*, 2001; Rathgeber *et al.*, 2016).

165

166 Foresters have measured tree diameter and height for decades, but these measurements may not be suitable
167 for determining relationships between growth and environmental conditions. The widely used method in
168 forestry is to measure diameter at breast height at punctual time intervals. Combined with height, these
169 data help develop allometries foresters can use to estimate how much wood they can harvest in a forest (e.g.,
170 Meyer, 1940; Saunders & Wagner, 2008). These metrics work to determine wood in forests, but their coarse
171 temporal scale—measuring every 5 or more years—is likely to miss extreme events affecting growth.

172

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

179

180 **Objectives**

181 The objectives for my experiment (Fuelinex) are to assess tree species' potential to prolong or stretch their
182 activity schedule by artificially manipulating growing season length and analyze how this translates (or not)
183 into growth, during the current year (2024) and in the following year (2025). I will also conduct a secondary
184 experiment to examine whether trees can absorb nutrients late in the season and if that translates into growth
185 during the following season. For the observational data projects (Wildchrokie and coringTreespotters), I will
186 investigate how the timing of phenological events affects growth across years for juvenile and mature trees,
187 using observational phenology data and tree rings. The duration and type of study, the age classes and species
188 used in each project are presented in Figure 2). Together, my two chapters will allow me to investigate the
189 decoupling between growth increment in response to longer growing seasons.

190 **Research questions**

191 Fuelinex: How do extended growing seasons affect tree growth across different species, both immediately
192 (in the same year as the extended season) and in the subsequent year? Wildchrokie and coringTreespotters:
193 How does phenology regulate tree growth in urban ecosystems?

194

195 **Methodology**

196 **Chapter 1: Fuelinex**

197 **Species selection and growing conditions** We used seven species of tree saplings for our experiment
198 (Fuelinex). We purchased Paper birch (*Betula papyfera*), Choke Cherry (*Prunus virginiana*), Bur oak (*Quer-*
199 *cus macrocarpa*) from Peel's nursery in November 2023 and the trees arrived at Totem Field studios (49.26
200 °N, -123.25 °W), where the other four species were stored until the spring of 2023. Manitoba maple (*Acer*
201 *negundo*), Eastern white pine (*Pinus strobus*), Balsam poplar (*Populus balsamifera*) and Giant sequoia (*Se-*
202 *quoiaadendron giganteum*) were leftover trees that we purchased in 2022 for 2023 for a previous experiment.
203 We watered them weekly, and they remained at ambient conditions for the 2023 growing season. We ran-
204 domly selected 90 individuals of each species among them. We propagated *P. balsamifera* from 30 cm whips
205 while the trees were still dormant (Mc Carthy *et al.*, 2018). In May 2024, we repotted all the trees in
206 2-gallon plastic pots with a medium for perennials consisting of 50 % peat, 25% crushed pumice and 25%
207 crushed bark (purchased from www.westcreekfarm.com). In February 2025, we repotted the trees with the
208 same medium in 3-gallon pots. We arranged the trees in three blocks, each containing all 6 treatments and 7
209 species, with two of these blocks placed under an open-walled and well-ventilated polytunnel greenhouse. All
210 saplings were connected to a drip irrigation system (40 PVC frame from Netafilm 54 with a Toro controller)
211 to maintain constant irrigation across the season. Using fertilizer premix, we fertilized the trees twice during
212 the growing season of 2024 (except for the nutrient-boosted trees) and three times during 2025, just enough
213 to keep the trees alive (Table S4).

214

215 **Tree measurements and biomass:**

216 Using red paint, we marked the trees on their trunk at 3 cm from the soil in February 2024. Then we
217 measured the diameter at the top of that mark using a digital calliper (accuracy ± 0.01cm). From that
218 mark to the bottom of the highest apical bud, for angiosperms, and the top of the apical meristem for
219 gymnosperms, we measured height with a metal ruler (accuracy ± 0.1cm). We measured those two same
220 points in the winter (2024 growing season) and in the fall (2025 growing season) of 2025. For those two
221 subsequent measurements, if the measured shoot died (because of insects, accidentally snapped off, etc.), we
222 noted the previous measurement as invalid and measured the highest lateral shoot. In the fall of 2025, when
223 all the individuals from a species had lost all their leaves, we removed the trees from their pots and gently
224 washed the soil off the roots with a water hose. We dried the trees by placing them in drying ovens at 70°C
225 for 72 hours and weighed the roots and stem separately (accuracy ± 0.01 gram).

226

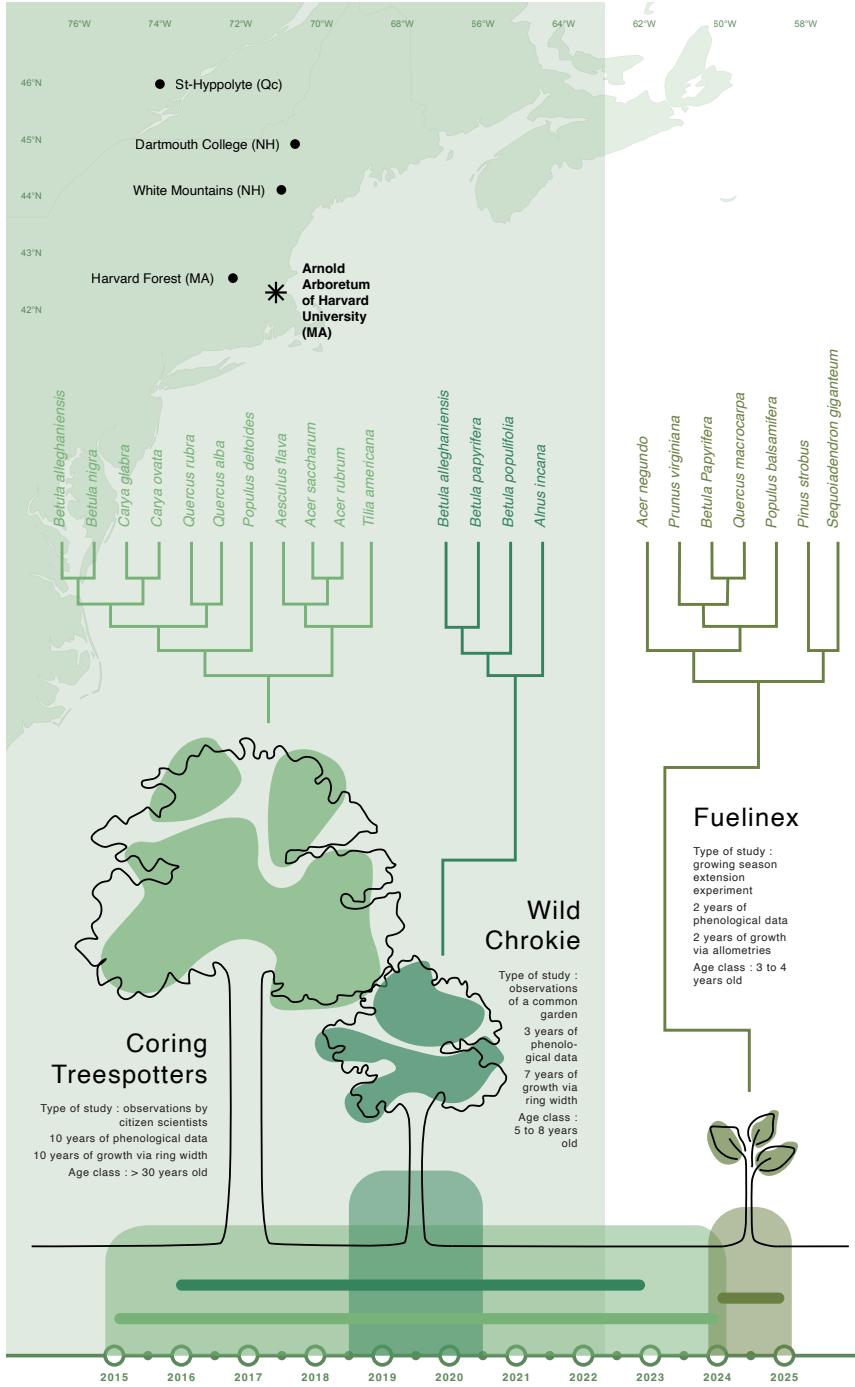


Figure 2: Overview of the age class, species, provenance of the trees used in each study along with the type of study each project consists of. The colored lines represent the period of the growth data and the shaded areas are the phenological data. Each phylogram illustrates the species used in each project. The map illustrates the four different provenances used in Wildchrokic and the start represents the location of Wildchrokic and coringTreespotters.

227 **Phenology and shoot elongation monitoring:**

228 *Leaf phenology:* We started monitoring phenology of all the trees on 11 April 2024, missing the initial leaf

229 phenology for most individuals, but we monitored subsequent phenophases twice a week until the leaves
230 had fully elongated. In the late summer and fall, we monitored budset every week until full bud dormancy.
231 Phenophases are described in Table 1. Phenophases of *S. giganteum* were not recorded.

232
233 *Shoot elongation:* Before shoot elongation onset, we marked a reference point with red paint at the base of ei-
234 ther the new-year apical or the highest lateral shoot. To facilitate and improve the quality of the shoot elonga-
235 tion measurements, we attached paper rulers (accuracy $\pm 0.1\text{cm}$) on *A. negundo*, *B. papyfera*, *P. balsamifera*
236 and *Q. macrocarpa*. For species not suitable for those paper rulers, we took those same measurements, but
237 with a metal ruler (accuracy $\pm 0.1\text{cm}$). We measured shoot elongation weekly from the red mark to the base
238 of the bud for angiosperms, and at the top of the apical meristem for gymnosperms. For determinate growth
239 species (*A. negundo*, *P. virginiana* and *Q. macrocarpa*), when the trees did not elongate for two weeks, we
240 started monitoring them every other week until September 1st for both growing seasons.

241
242 *Senescence:* Every week, starting on 4 September 2024, we monitored senescence by a visual assessment of
243 the remaining green leaf cover in percentage and by measuring the chlorophyll content meter with a SPAD-
244 502 chlorophyll meter (Minolta Camera Co. Japan). We also recorded the date of loss of green leaf cover
245 and leaf drop.

246

Table 1: Phenological stages and their descriptions for deciduous species and pine (From Baumgarten,
unpublished) and (Vitasse, 2013)

Group	Scale	Phenostage	Description
<i>Deciduous species</i>			
	0	dormant	no bud development visible
	1	bud swelling	swollen and/or elongating buds
	2	budburst	bud scales open and leaves partially visible
	3	leaf-out	leaves fully emerged from bud but still folded, crin- kled or pendant
	4	leaf unfolding	leaves fully unfolded
<i>Pine</i>			
	0	dormant	no signs of activity
	1	swelling	swelling or elongation of shoot visible
	2	budburst	green needle tips along the shoot visible
	3	leaf-out	scales open along the shoot and first needles become visible
	4	leaf-unfolding	green needles emerging away from the shoot

247 **Experimental design** Individuals from each species were randomly selected for a full factorial design of
248 Warm/Cool, Spring/Fall treatments (Figure S1) with two additional treatments to test nutrient effects in the
249 fall (Figure 3), for a total of 15 replicates/treatment/species. On 6 March 2024, we placed the Cool Spring
250 individuals in climate chambers to delay the start of their growing season, while the Warm Spring replicates
251 remained at ambient conditions. Once all Warm Spring individuals had fully leafed out, we removed the
252 Cool Spring replicates from the chambers and placed them back at ambient conditions for the whole sum-
253 mer. On 4 September 2024, we placed the trees for the Warm Fall treatments in the climate chambers. The
254 temperature was set to fit the mean 30-year weekly maximum temperature of the previous month (e.g. 1st
255 week of September set to the average of the 1st week of August). The Cool Fall treatment trees remained
256 at ambient conditions. For both climate chamber treatments, we rotated and watered the trees weekly to
257 minimize the climate chamber's effect. We also set the photoperiod regime to the corresponding sunrise and
258 sunset of the ongoing week and ramped it until it reached full light. To test for nutrient limitation at the
259 end of the season, we added a supplemental dose of nutrients (Table S4) to two treatments (Figure 3). In
260 2025, all the trees were kept at ambient conditions together at Totem field during which we recorded the

²⁶¹ same phenophases.

²⁶²

²⁶³ **Leaf count** To determine if nutrient addition treatments in the fall affected leaf primordia formation, we
²⁶⁴ counted the apical meristem leaves on 27 May 2025 for the determinate growth species only (*A. negundo*,
²⁶⁵ *P. virginiana* and *Q. macrocarpa*).

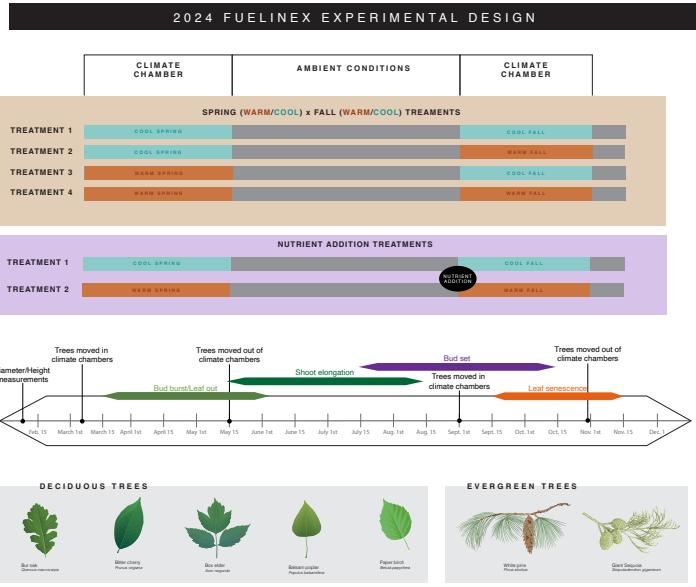


Figure 3: Experimental design during the 2024 growing season. Cooling treatments are represented in blue, and warming treatments are in orange. The grey zone in the middle represents an approximate period during the growing season where all treatments were together at ambient conditions. The colored arrows represent the approximated periods during which we recorded the phenostages.

266 Chapter 2: Wildchrokie and coringTreespotters

267 Wildchrokie

268 *Common garden setup (direct quote from Buonaiuto, in review)*

269 “In 2014-2015, we collected seeds from four field sites in northeastern North America spanning approximately
270 a 3.5° latitudinal gradient. The four field sites included Harvard Forest (42.55 °N, 72.20°W), the White
271 Mountains (44.11 °N, 71.40 °W), Second College Grant, (44.79 °N, 71.15 °W), and St. Hippolyte, QC, CAN
272 (45.98 °N, 74.01 °W) (Figure 4). We transported all seeds back to the Weld Hill Research Building at the
273 Arnold Arboretum in Boston Massachusetts (42.30 °N, 71.13 °W) where we germinated seeds following stan-
274 dard germination protocols, and grew them to seedling stages in the research greenhouse. In the spring of
275 2017, we out-planted seedlings to establish the garden. Plots were regularly weeded and watered throughout
276 the duration of the study and were pruned in the fall of 2020.”

277 *Phenological monitoring and sample collection (direct quote from Buonaiuto, in review)*
278 “For the years 2018-2019, we made phenological observations of all individuals in the common garden twice
279 per week from February to December. In 2020 due to the COVID 19 pandemic, we monitored them once per
280 week from March to November. We describe phenological stages using a modified BBCH scale, a common
281 metric for quantifying woody plant phenological progression (Finn *et al.*, 2007). We observed all major veg-
282 etative stages (budburst BBCH 07, leafout BBCH 15, end of leaf expansion BBCH 19, leaf coloration/drop
283 BBCH 97, reproductive phases flowering BBCH 60-65, fruiting BBCH 72-79 and fruit/cones fully ripe BBCH
284 89). We added additional phases for budset and labelled the full budset as BBCH 102.” In the spring of
285 2023, we collected cross-sections for most trees and 1 tree core on a few individuals. Both the cores and
286 cross-sections were left to dry at ambient temperature for three months.”

288 **289 Coringtreespotters**
290 *Citizen science program*
291 The Treespotters was a citizen science program that started in 2015 and aimed to train citizen scientists for

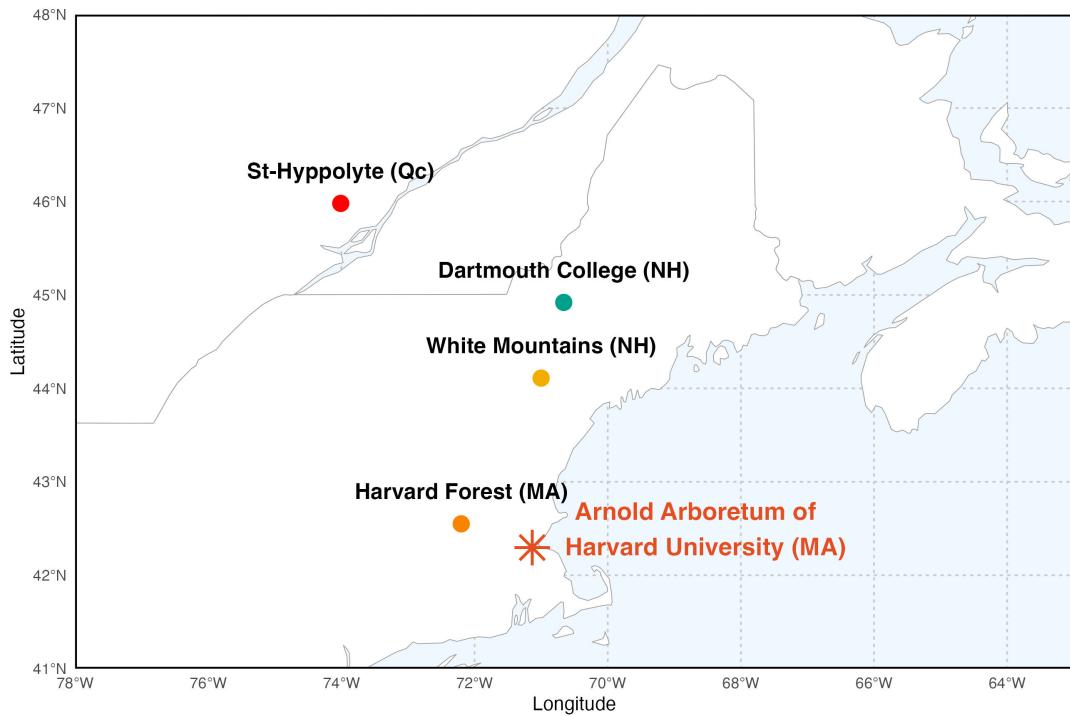


Figure 4: Locations of the provenance study for the common garden study (Wildchrokie). The common garden and the citizen science project (coringTreespotters) took place at the Arnold Arboretum of Harvard University, represented by the orange star.

292 accurate and rigorous phenological monitoring at the Arnold Arboretum of Harvard University (42.30°N ,
 293 -71.12°W) (Figure 4). From 2015 to 2024, hundreds of citizen scientists monitored 50 trees of 11 species.
 294 They regularly followed those individuals from budburst in the spring to leaf colouring in the fall using the
 295 National Phenology Network (NPN) phenophases (Denny *et al.*, 2014): Leaves (483), Colored leaves (498),
 296 Fruits (516), Ripe Fruits (390), Falling leaves(471), Recent fruit or seed drop (504), Increasing leaf size (467),
 297 Breaking leaf buds (371), Flowers or flower buds (500), Open flowers (501), Pollen release (502). Not all
 298 phenophases were recorded for every tree, for every year, and some trees miss several years of data.

299 *Phenological monitoring and sample collection*

300 From 20 to 22 April 2025, we collected two 5-mm diameter cores, 15-cm length at 1.3 meters above ground
 301 from 50 trees of the 11 species (Table S3) that were previously monitored for phenology, using an increment
 302 borer (Mora Borer, Haglöfs Sweden, Bromma, Stockholm, Sweden). We collected the cores perpendicular to
 303 the slope and at 180 degrees from each other, cleaning the increment borer with alcohol (70% ethanol) and
 304 the inside with a brush before collecting each core. We stored the cores at ambient temperature for three
 305 months in paper straws that were previously labelled and punched to help with drying.

306 **Sample processing, imaging and measuring**

307 We mounted the cores on wooden mounts, and sanded the cores and cross-sections using progressively finer
 308 sandpaper grits: 150, 300, 400, 600, 800, 1000. We scanned the cores and cross-sections at a resolution
 309 of 6250 dpi, with a high-resolution treering scanner (Fong, unpublished). We used the digitized images to
 310 measure the tree ring widths with ImageJ (Schneider *et al.*, 2012). Then, we performed visual crossdating
 311 using DplR (Bunn, 2010), we did not perform statistical crossdating because of the short chronologies that
 312 limit the capacity of these analyses (Raden *et al.*, 2020).

313 **Statistical analyses**

317 For both projects, we used Bayesian hierarchical models coded in Stan with the rstan package version 2.32.7
 318 (Carpenter *et al.*, 2017) to run the Stan code in R. With these models, we estimated ringwidth as a function
 319 of growing degree days, accumulated from the leafout date to the budset date. We had three grouping
 320 factors for Wildchrokie (species, site and treeid) and two for coringTreespotters (species and treeid). We
 321 ran four chains with each 2000 warmup, which we discarded, and 2000 sampling iterations, which we kept
 322 for posterior distribution estimates. The models did not have any divergent transitions and \hat{R} was below 1.01.
 323

324 *Wildchrokie model structure*

$$\begin{aligned} \text{ringwidth}_i &\sim \text{Normal}(\mu, \sigma_y) \\ \mu &= \alpha + \alpha_{\text{species}} + \alpha_{\text{site}} + \alpha_{\text{treeid}} + \beta_{\text{species}} * \text{gdd} \\ \alpha_{\text{species}} &\sim \text{Normal}(0, 0.5) \\ \alpha_{\text{site}} &\sim \text{Normal}(0, 0.5) \\ \alpha_{\text{treeid}} &\sim \text{Normal}(0, \sigma_{\alpha \text{ treeid}}) \\ \sigma_{\alpha \text{ treeid}} &\sim \text{Normal}(0, 0.2) \end{aligned}$$

325 *coringTreespotters model structure*

$$\begin{aligned} \text{ringwidth}_i &\sim \text{Normal}(\mu, \sigma_y) \\ \mu &= \alpha + \alpha_{\text{species}} + \alpha_{\text{site}} + \alpha_{\text{treeid}} + \beta_{\text{species}} * \text{gdd} \\ \alpha_{\text{species}} &\sim \text{Normal}(0, 0.5) \\ \alpha_{\text{treeid}} &\sim \text{Normal}(0, \sigma_{\alpha \text{ treeid}}) \\ \sigma_{\alpha \text{ treeid}} &\sim \text{Normal}(0, 0.2) \end{aligned}$$

326

References

- 327 Almagro, D., Martin-Benito, D., Rossi, S., Conde, M., Fernández-de-Uña, L. & Gea-Izquierdo, G. (2025).
 328 Long-Term Cambial Phenology Reveals Diverging Growth Responses of Two Tree Species in a Mixed
 329 Forest Under Climate Change. *Global Change Biology*, 31, e70503.
- 330 Augspurger, C.K. & Bartlett, E.A. (2003). Differences in leaf phenology between juvenile and adult trees in
 331 a temperate deciduous forest. *Tree Physiology*, 23, 517–525.
- 332 Bergeron, Y., Gauthier, S., Flannigan, M. & Kafka, V. (2004). Fire regimes at the transition between
 333 mixedwood and coniferous boreal forest in northwestern Quebec. *Ecology*, 85, 1916–1932.
- 334 Buckley, L.B. & Kingsolver, J.G. (2012). Functional and Phylogenetic Approaches to Forecasting Species'
 335 Responses to Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, 43, 205–226.
- 336 Bunn, A.G. (2010). Statistical and visual crossdating in R using the dplR library. *Dendrochronologia*, 28,
 337 251–258.
- 338 Büntgen, U., Wacker, L., Galván, J.D., Arnold, S., Arseneault, D., Baillie, M., Beer, J., Bernabei, M.,
 339 Bleicher, N., Boswijk, G., Bräuning, A., Carrer, M., Ljungqvist, F.C., Cherubini, P., Christl, M., Christie,
 340 D.A., Clark, P.W., Cook, E.R., Esper, J., Fowler, A.M., Gennaretti, F., Grießinger, J., Grissino-Mayer,
 341 H., Grudd, H., Gunnarson, B.E., Hantemirov, R., Herzog, F., Hessl, A., Heussner, K.U., Jull, A.J.T.,
 342 Kukarskikh, V., Kirdyanov, A., Krusic, P.J., Kyncl, T., Lara, A., LeQuesne, C., Linderholm, H.W., Loader,
 343 N.J., Luckman, B., Miyake, F., Myglan, V.S., Nicolussi, K., Oppenheimer, C., Palmer, J., Panyushkina, I.,
 344 Pederson, N., Rybníček, M., Schweingruber, F.H., Seim, A., Sigl, M., Churakova, O., Speer, J.H., Synal,
 345 H.A., Tegel, W., Treydte, K., Villalba, R., Wiles, G., Wilson, R., Winship, L.J., Wunder, J., Yang, B. &
 346 Young, G.H.F. (2018). Tree rings reveal globally coherent signature of cosmogenic radiocarbon events in
 347 774 and 993 CE. *Nature Communications*, 9, 3605.
- 348 Cabon, A., Fernández-de-Uña, L., Gea-Izquierdo, G., Meinzer, F.C., Woodruff, D.R., Martínez-Vilalta, J. &
 349 De Cáceres, M. (2020). Water potential control of turgor-driven tracheid enlargement in Scots pine at its
 350 xeric distribution edge. *New Phytologist*, 225, 209–221.

- 351 Cabon, A., Kannenberg, S.A., Arain, A., Babst, F., Baldocchi, D., Belmecheri, S., Delpierre, N., Guerrieri,
 352 R., Maxwell, J.T., McKenzie, S., Meinzer, F.C., Moore, D.J.P., Pappas, C., Rocha, A.V., Szejner, P.,
 353 Ueyama, M., Ulrich, D., Vincke, C., Voelker, S.L., Wei, J., Woodruff, D. & Anderegg, W.R.L. (2022).
 354 Cross-biome synthesis of source versus sink limits to tree growth. *Science*, 376, 758–761.
- 355 Campbell, L.M., Hagerman, S. & Gray, N.J. (2014). Producing Targets for Conservation: Science and Politics
 356 at the Tenth Conference of the Parties to the Convention on Biological Diversity. *Global Environmental
 357 Politics*, 14, 41–63.
- 358 Carpenter, B., Gelman, A., Hoffman, M.D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo,
 359 J., Li, P. & Riddell, A. (2017). Stan : A Probabilistic Programming Language. *Journal of Statistical
 360 Software*, 76.
- 361 Ceballos, G., Ehrlich, P.R. & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction
 362 signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*,
 363 114.
- 364 Chandler, M., See, L., Copas, K., Bonde, A.M., López, B.C., Danielsen, F., Legind, J.K., Masinde, S.,
 365 Miller-Rushing, A.J., Newman, G., Rosemartin, A. & Turak, E. (2017). Contribution of citizen science
 366 towards international biodiversity monitoring. *Biological Conservation*, 213, 280–294.
- 367 Change, I.P.O.C. (2014). Detection and Attribution of Climate Change: from Global to Regional. In:
 368 *Climate Change 2013 – The Physical Science Basis*. Cambridge University Press, pp. 867–952. 1st edn.
- 369 Chiang, F., Mazdiyasni, O. & AghaKouchak, A. (2021). Evidence of anthropogenic impacts on global drought
 370 frequency, duration, and intensity. *Nature Communications*, 12, 2754.
- 371 Chmielewski, F.M. & Rötzer, T. (2001). Response of tree phenology to climate change across Europe.
 372 *Agricultural and Forest Meteorology*, 108, 101–112.
- 373 Choat, B., Brodribb, T.J., Brodersen, C.R., Duursma, R.A., López, R. & Medlyn, B.E. (2018). Triggers of
 374 tree mortality under drought. *Nature*, 558, 531–539.
- 375 Chuine, I. (2010). Why does phenology drive species distribution? *Philosophical Transactions of the Royal
 376 Society B: Biological Sciences*, 365, 3149–3160.
- 377 Cleland, E., Chuine, I., Menzel, A., Mooney, H. & Schwartz, M. (2007). Shifting plant phenology in response
 378 to global change. *Trends in Ecology & Evolution*, 22, 357–365.
- 379 Cooke, J.E.K., Eriksson, M.E. & Junntila, O. (2012). The dynamic nature of bud dormancy in trees:
 380 environmental control and molecular mechanisms. *Plant, Cell & Environment*, 35, 1707–1728.
- 381 Delpierre, N., Vitasse, Y., Chuine, I., Guillemot, J., Bazot, S., Rutishauser, T. & Rathgeber, C.B.K. (2016).
 382 Temperate and boreal forest tree phenology: from organ-scale processes to terrestrial ecosystem models.
 383 *Annals of Forest Science*, 73, 5–25.
- 384 Denny, E.G., Gerst, K.L., Miller-Rushing, A.J., Tierney, G.L., Crimmins, T.M., Enquist, C.A.F., Guertin,
 385 P., Rosemartin, A.H., Schwartz, M.D., Thomas, K.A. & Weltzin, J.F. (2014). Standardized phenology
 386 monitoring methods to track plant and animal activity for science and resource management applications.
 387 *International Journal of Biometeorology*, 58, 591–601.
- 388 Dickinson, J.L., Shirk, J., Bonter, D., Bonney, R., Crain, R.L., Martin, J., Phillips, T. & Purcell, K. (2012).
 389 The current state of citizen science as a tool for ecological research and public engagement. *Frontiers in
 390 Ecology and the Environment*, 10, 291–297.
- 391 Dosio, A., Mentaschi, L., Fischer, E.M. & Wyser, K. (2018). Extreme heat waves under 1.5 °C and 2 °C
 392 global warming. *Environmental Research Letters*, 13, 054006.

- 393 Dow, C., Kim, A.Y., D'Orangeville, L., Gonzalez-Akre, E.B., Helcoski, R., Herrmann, V., Harley, G.L.,
394 Maxwell, J.T., McGregor, I.R., McShea, W.J., McMahon, S.M., Pederson, N., Tepley, A.J. & Anderson-
395 Teixeira, K.J. (2022). Warm springs alter timing but not total growth of temperate deciduous trees.
396 *Nature*, 608, 552–557.
- 397 Dox, I., Skrøppa, T., Decoster, M., Prislan, P., Gascó, A., Gričar, J., Lange, H. & Campioli, M. (2022).
398 Severe drought can delay autumn senescence of silver birch in the current year but advance it in the next
399 year. *Agricultural and Forest Meteorology*, 316, 108879.
- 400 Driscoll, D.A., Bland, L.M., Bryan, B.A., Newsome, T.M., Nicholson, E., Ritchie, E.G. & Doherty, T.S.
401 (2018). A biodiversity-crisis hierarchy to evaluate and refine conservation indicators. *Nature Ecology &*
402 *Evolution*, 2, 775–781.
- 403 Duputié, A., Rutschmann, A., Ronce, O. & Chuine, I. (2015). Phenological plasticity will not help all species
404 adapt to climate change. *Global Change Biology*, 21, 3062–3073.
- 405 Ettinger, A.K., Chamberlain, C.J., Morales-Castilla, I., Buonaiuto, D.M., Flynn, D.F.B., Savas, T., Samaha,
406 J.A. & Wolkovich, E.M. (2020). Winter temperatures predominate in spring phenological responses to
407 warming. *Nature Climate Change*, 10, 1137–1142.
- 408 Etzold, S., Sterck, F., Bose, A.K., Braun, S., Buchmann, N., Eugster, W., Gessler, A., Kahmen, A., Peters,
409 R.L., Vitasse, Y., Walthert, L., Ziemińska, K. & Zweifel, R. (2022). Number of growth days and not length
410 of the growth period determines radial stem growth of temperate trees. *Ecology Letters*, 25, 427–439.
- 411 Feldman, R.E., Žemaitė, I. & Miller-Rushing, A.J. (2018). How training citizen scientists affects the accuracy
412 and precision of phenological data. *International Journal of Biometeorology*, 62, 1421–1435.
- 413 Finn, G., Straszewski, A. & Peterson, V. (2007). A general growth stage key for describing trees and woody
414 plants. *Annals of Applied Biology*, 151, 127–131.
- 415 Flynn, D.F.B. & Wolkovich, E.M. (2018). Temperature and photoperiod drive spring phenology across all
416 species in a temperate forest community. *New Phytologist*, 219, 1353–1362.
- 417 Friend, A.D., Eckes-Shephard, A.H., Fonti, P., Rademacher, T.T., Rathgeber, C.B.K., Richardson, A.D. &
418 Turton, R.H. (2019). On the need to consider wood formation processes in global vegetation models and
419 a suggested approach. *Annals of Forest Science*, 76, 49.
- 420 Fritts, H. & Swetnam, T. (1989). Dendroecology: A Tool for Evaluating Variations in Past and Present
421 Forest Environments. In: *Advances in Ecological Research*. Elsevier, vol. 19, pp. 111–188.
- 422 Fu, Y.H., Campioli, M., Deckmyn, G. & Janssens, I.A. (2013). Sensitivity of leaf unfolding to experimental
423 warming in three temperate tree species. *Agricultural and Forest Meteorology*, 181, 125–132.
- 424 Fu, Y.H., Piao, S., Op De Beeck, M., Cong, N., Zhao, H., Zhang, Y., Menzel, A. & Janssens, I.A. (2014).
425 Recent spring phenology shifts in western Central Europe based on multiscale observations. *Global Ecology
426 and Biogeography*, 23, 1255–1263.
- 427 Fu, Y.H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., Ciais, P., Huang, M., Menzel, A., Peñuelas,
428 J., Song, Y., Vitasse, Y., Zeng, Z. & Janssens, I.A. (2015). Declining global warming effects on the
429 phenology of spring leaf unfolding. *Nature*, 526, 104–107.
- 430 Gagne, M.A., Smith, D.D. & McCulloh, K.A. (2020). Limited physiological acclimation to recurrent heat-
431 waves in two boreal tree species. *Tree Physiology*, 40, 1680–1696.
- 432 Gallatin, A.S., Primack, R.B. & Wagner, D.L. (2015). Autumn, the neglected season in climate change
433 research. *Trends in Ecology & Evolution*, 30, 169–176.

- 434 Gazol, A., Camarero, J.J., Vicente-Serrano, S.M., Sánchez-Salguero, R., Gutiérrez, E., De Luis, M.,
435 Sangüesa-Barreda, G., Novak, K., Rozas, V., Tíscar, P.A., Linares, J.C., Martín-Hernández, N., Martínez
436 Del Castillo, E., Ribas, M., García-González, I., Silla, F., Camisón, A., Génova, M., Olano, J.M., Longares,
437 L.A., Hevia, A., Tomás-Burguera, M. & Galván, J.D. (2018). Forest resilience to drought varies across
438 biomes. *Global Change Biology*, 24, 2143–2158.
- 439 Gessler, A. & Zweifel, R. (2024). Beyond source and sink control – toward an integrated approach to
440 understand the carbon balance in plants. *New Phytologist*, 242, 858–869.
- 441 Green, J.K. & Keenan, T.F. (2022). The limits of forest carbon sequestration. *Science*, 376, 692–693.
- 442 Hauck, M., Schneider, T., Bahlinger, S., Fischbach, J., Oswald, G., Csapek, G. & Dulamsuren, C. (2025).
443 Heat tolerance of temperate tree species from Central Europe. *Forest Ecology and Management*, 580,
444 122541.
- 445 Hidalgo, H.G., Das, T., Dettinger, M.D., Cayan, D.R., Pierce, D.W., Barnett, T.P., Bala, G., Mirin, A.,
446 Wood, A.W., Bonfils, C., Santer, B.D. & Nozawa, T. (2009). Detection and Attribution of Streamflow
447 Timing Changes to Climate Change in the Western United States. *Journal of Climate*, 22, 3838–3855.
- 448 Huey, R.B., Kearney, M.R., Krockenberger, A., Holtum, J.A.M., Jess, M. & Williams, S.E. (2012). Predicting
449 organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philosophical
450 Transactions of the Royal Society B: Biological Sciences*, 367, 1665–1679.
- 451 Hufkens, K., Melaas, E.K., Mann, M.L., Foster, T., Ceballos, F., Robles, M. & Kramer, B. (2019). Monitoring
452 crop phenology using a smartphone based near-surface remote sensing approach. *Agricultural and Forest
453 Meteorology*, 265, 327–337.
- 454 Intergovernmental panel on climate change (ed.) (2007). *Climate change 2007: the physical science basis*.
455 Cambridge university press, Cambridge.
- 456 Intergovernmental Panel On Climate Change (2023). *Climate Change 2021 – The Physical Science Basis:
457 Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate
458 Change*. 1st edn. Cambridge University Press.
- 459 Jeong, S. & Medvigy, D. (2014). Macroscale prediction of autumn leaf coloration throughout the continental
460 United States. *Global Ecology and Biogeography*, 23, 1245–1254.
- 461 Keenan, T.F., Gray, J., Friedl, M.A., Toomey, M., Bohrer, G., Hollinger, D.Y., Munger, J.W., O'Keefe, J.,
462 Schmid, H.P., Wing, I.S., Yang, B. & Richardson, A.D. (2014). Net carbon uptake has increased through
463 warming-induced changes in temperate forest phenology. *Nature Climate Change*, 4, 598–604.
- 464 Kurnik, B., Barbosa, P. & Vogt, J. (2011). Testing two different precipitation datasets to compute the
465 standardized precipitation index over the Horn of Africa. *International Journal of Remote Sensing*, 32,
466 5947–5964.
- 467 Körner, C. & Basler, D. (2010). Phenology Under Global Warming. *Science*, 327, 1461–1462.
- 468 Körner, C., Möhl, P. & Hiltbrunner, E. (2023). Four ways to define the growing season. *Ecology Letters*, 26,
469 1277–1292.
- 470 Laube, J., Sparks, T.H., Estrella, N., Höfler, J., Ankerst, D.P. & Menzel, A. (2014). Chilling outweighs
471 photoperiod in preventing precocious spring development. *Global Change Biology*, 20, 170–182.
- 472 Laurance, W.F. (2007). Have we overstated the tropical biodiversity crisis? *Trends in Ecology & Evolution*,
473 22, 65–70.
- 474 Li, Y., Zhang, W., Schwalm, C.R., Gentine, P., Smith, W.K., Ciais, P., Kimball, J.S., Gazol, A., Kannenberg,
475 S.A., Chen, A., Piao, S., Liu, H., Chen, D. & Wu, X. (2023). Widespread spring phenology effects on
476 drought recovery of Northern Hemisphere ecosystems. *Nature Climate Change*, 13, 182–188.

- 477 Lieth, H., Jacobs, J., Lange, O.L., Olson, J.S. & Wieser, W. (eds.) (1974). *Phenology and Seasonality*
478 *Modeling*. vol. 8 of *Ecological Studies*. Springer Berlin Heidelberg, Berlin, Heidelberg.
- 479 Manzanedo, R.D. & Pederson, N. (2019). Towards a More Ecological Dendroecology. *Tree-Ring Research*,
480 75, 152.
- 481 Marvel, K., Cook, B.I., Bonfils, C.J.W., Durack, P.J., Smerdon, J.E. & Williams, A.P. (2019). Twentieth-
482 century hydroclimate changes consistent with human influence. *Nature*, 569, 59–65.
- 483 Marx, W., Haunschild, R. & Bornmann, L. (2021). Heat waves: a hot topic in climate change research.
484 *Theoretical and Applied Climatology*, 146, 781–800.
- 485 Mc Carthy, R., Löf, M. & Gardiner, E.S. (2018). Early root development of poplars (*Populus* spp.) in
486 relation to moist and saturated soil conditions. *Scandinavian Journal of Forest Research*, 33, 125–132.
- 487 Meehl, G.A. & Tebaldi, C. (2004). More Intense, More Frequent, and Longer Lasting Heat Waves in the
488 21st Century. *Science*, 305, 994–997.
- 489 Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská,
490 O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Defila, C., Donnelly, A., Filella, Y., Jatczak,
491 K., Mestre, A., Peñuelas, J., Pirinen, P., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wiel-
492 golaski, F., Zach, S. & Zust, A. (2006). European phenological response to climate change matches the
493 warming pattern. *Global Change Biology*, 12, 1969–1976.
- 494 Meyer, B.F., Buras, A., Gregor, K., Layritz, L.S., Principe, A., Kreyling, J., Rammig, A. & Zang, C.S.
495 (2024). Frost matters: incorporating late-spring frost into a dynamic vegetation model regulates regional
496 productivity dynamics in European beech forests. *Biogeosciences*, 21, 1355–1370.
- 497 Meyer, H.A. (1940). A Mathematical Expression for Height Curves. *Journal of Forestry*, 38, 415–420.
- 498 Morin, X., Roy, J., Sonié, L. & Chuine, I. (2010). Changes in leaf phenology of three European oak species
499 in response to experimental climate change. *New Phytologist*, 186, 900–910.
- 500 Muller, B., Pantin, F., Génard, M., Turc, O., Freixes, S., Piques, M. & Gibon, Y. (2011). Water deficits
501 uncouple growth from photosynthesis, increase C content, and modify the relationships between C and
502 growth in sink organs. *Journal of Experimental Botany*, 62, 1715–1729.
- 503 Parent, B., Turc, O., Gibon, Y., Stitt, M. & Tardieu, F. (2010). Modelling temperature-compensated
504 physiological rates, based on the co-ordination of responses to temperature of developmental processes.
505 *Journal of Experimental Botany*, 61, 2057–2069.
- 506 Parmesan, C., Ryhrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila,
507 L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A. & Warren, M. (1999). Poleward shifts in
508 geographical ranges of butterfly species associated with regional warming. *Nature*, 399, 579–583.
- 509 Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural
510 systems. *Nature*, 421, 37–42.
- 511 Peters, R.L., Steppe, K., Cuny, H.E., De Pauw, D.J., Frank, D.C., Schaub, M., Rathgeber, C.B., Cabon, A.
512 & Fonti, P. (2021). Turgor – a limiting factor for radial growth in mature conifers along an elevational
513 gradient. *New Phytologist*, 229, 213–229.
- 514 Peñuelas, J. & Filella, I. (2001). Responses to a Warming World. *Science*, 294, 793–795.
- 515 Piao, S., Liu, Q., Chen, A., Janssens, I.A., Fu, Y., Dai, J., Liu, L., Lian, X., Shen, M. & Zhu, X. (2019).
516 Plant phenology and global climate change: Current progresses and challenges. *Global Change Biology*,
517 25, 1922–1940.
- 518 Plomion, C., Leprovost, G. & Stokes, A. (2001). Wood Formation in Trees. *Plant Physiology*, 127, 1513–1523.

- 519 Polgar, C.A. & Primack, R.B. (2011). Leaf-out phenology of temperate woody plants: from trees to ecosys-
520 tems. *New Phytologist*, 191, 926–941.
- 521 Primack, R.B., Laube, J., Gallinat, A.S. & Menzel, A. (2015). From observations to experiments in phenology
522 research: investigating climate change impacts on trees and shrubs using dormant twigs. *Annals of Botany*,
523 116, 889–897.
- 524 Raden, M., Mattheis, A., Spiecker, H., Backofen, R. & Kahle, H.P. (2020). The potential of intra-annual
525 density information for crossdating of short tree-ring series. *Dendrochronologia*, 60, 125679.
- 526 Rathgeber, C.B.K., Cuny, H.E. & Fonti, P. (2016). Biological Basis of Tree-Ring Formation: A Crash Course.
527 *Frontiers in Plant Science*, 7.
- 528 Reinmann, A.B., Bowers, J.T., Kaur, P. & Kohler, C. (2023). Compensatory responses of leaf physiology
529 reduce effects of spring frost defoliation on temperate forest tree carbon uptake. *Frontiers in Forests and*
530 *Global Change*, 6, 988233.
- 531 Richardson, A.D., Keenan, T.F., Migliavacca, M., Ryu, Y., Sonnentag, O. & Toomey, M. (2013). Climate
532 change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural*
533 *and Forest Meteorology*, 169, 156–173.
- 534 Sanchez-Lorenzo, A., Wild, M., Brunetti, M., Guijarro, J.A., Hakuba, M.Z., Calbó, J., Mystakidis, S. &
535 Bartok, B. (2015). Reassessment and update of long-term trends in downward surface shortwave radiation
536 over Europe (1939–2012). *Journal of Geophysical Research: Atmospheres*, 120, 9555–9569.
- 537 Saunders, M.R. & Wagner, R.G. (2008). Height-diameter models with random coefficients and site variables
538 for tree species of Central Maine. *Annals of Forest Science*, 65, 203–203.
- 539 Schneider, C.A., Rasband, W.S. & Eliceiri, K.W. (2012). NIH Image to ImageJ: 25 years of image analysis.
540 *Nature Methods*, 9, 671–675.
- 541 Sgubin, G., Swingedouw, D., Dayon, G., García De Cortázar-Atauri, I., Ollat, N., Pagé, C. & Van Leeuwen,
542 C. (2018). The risk of tardive frost damage in French vineyards in a changing climate. *Agricultural and*
543 *Forest Meteorology*, 250–251, 226–242.
- 544 Silvestro, R., Deslauriers, A., Prislan, P., Rademacher, T., Rezaie, N., Richardson, A.D., Vitasse, Y. &
545 Rossi, S. (2025). From Roots to Leaves: Tree Growth Phenology in Forest Ecosystems. *Current Forestry*
546 *Reports*, 11, 12.
- 547 Silvestro, R., Zeng, Q., Buttò, V., Sylvain, J.D., Drolet, G., Mencuccini, M., Thiffault, N., Yuan, S. & Rossi,
548 S. (2023). A longer wood growing season does not lead to higher carbon sequestration. *Scientific Reports*,
549 13, 4059.
- 550 Spinoni, J., Naumann, G., Carrao, H., Barbosa, P. & Vogt, J. (2014). World drought frequency, duration,
551 and severity for 1951–2010. *International Journal of Climatology*, 34, 2792–2804.
- 552 Spinoni, J., Vogt, J.V., Naumann, G., Barbosa, P. & Dosio, A. (2018). Will drought events become more
553 frequent and severe in Europe? *International Journal of Climatology*, 38, 1718–1736.
- 554 Stridbeck, P., Björklund, J., Fuentes, M., Gunnarson, B.E., Jönsson, A.M., Linderholm, H.W., Ljungqvist,
555 F.C., Olsson, C., Rayner, D., Rocha, E., Zhang, P. & Seftigen, K. (2022). Partly decoupled tree-ring
556 width and leaf phenology response to 20th century temperature change in Sweden. *Dendrochronologia*,
557 75, 125993.
- 558 Swidrak, I., Schuster, R. & Oberhuber, W. (2013). Comparing growth phenology of co-occurring deciduous
559 and evergreen conifers exposed to drought. *Flora: Morphology, Distribution, Functional Ecology of Plants*,
560 208, 609–617.
- 561 Teskey, R., Werten, T., Bauweraerts, I., Ameye, M., McGuire, M.A. & Steppe, K. (2015). Responses of tree
562 species to heat waves and extreme heat events. *Plant, Cell & Environment*, 38, 1699–1712.

- 563 Trenberth, K.E., Dai, A., Van Der Schrier, G., Jones, P.D., Barichivich, J., Briffa, K.R. & Sheffield, J.
564 (2014). Global warming and changes in drought. *Nature Climate Change*, 4, 17–22.
- 565 Tyree, M.T. & Zimmermann, M.H. (2002). *Xylem Structure and the Ascent of Sap*. Springer Series in Wood
566 Science. Springer Berlin Heidelberg, Berlin, Heidelberg.
- 567 Vitasse, Y. (2013). Ontogenetic changes rather than difference in temperature cause understory trees to leaf
568 out earlier. *New Phytologist*, 198, 149–155.
- 569 Vitasse, Y., eLenz, A. & eKoerner, C. (2014). The interaction between freezing tolerance and phenology in
570 temperate deciduous trees. *Frontiers in Plant Science*, 5.
- 571 Wolfe, D.W., Schwartz, M.D., Lakso, A.N., Otsuki, Y., Pool, R.M. & Shaulis, N.J. (2005). Climate change
572 and shifts in spring phenology of three horticultural woody perennials in northeastern USA. *International
573 Journal of Biometeorology*, 49, 303–309.
- 574 Wolkovich, E.M., Cook, B.I. & Davies, T.J. (2014). Progress towards an interdisciplinary science of plant
575 phenology: building predictions across space, time and species diversity. *New Phytologist*, 201, 1156–1162.
576 _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/nph.12599>.
- 577 Wolkovich, E.M., Ettinger, A.K., Chin, A.R., Chamberlain, C.J., Baumgarten, F., Pradhan, K., Manzanedo,
578 R.D. & Hille Ris Lambers, J. (2025). Why longer seasons with climate change may not increase tree growth.
579 *Nature Climate Change*, 15, 1283–1292.
- 580 Woolway, R.I., Sharma, S., Weyhenmeyer, G.A., Debolskiy, A., Golub, M., Mercado-Bettín, D., Perroud,
581 Stepanenko, V., Tan, Z., Grant, L., Ladwig, R., Mesman, J., Moore, T.N., Shatwell, T., Vanderkelen,
582 I., Austin, J.A., DeGasperi, C.L., Dokulil, M., La Fuente, S., Mackay, E.B., Schladow, S.G., Watanabe,
583 S., Marcé, R., Pierson, D.C., Thiery, W. & Jennings, E. (2021). Phenological shifts in lake stratification
584 under climate change. *Nature Communications*, 12, 2318.
- 585 Wu, J. (2013). Key concepts and research topics in landscape ecology revisited: 30 years after the Allerton
586 Park workshop. *Landscape Ecology*, 28, 1–11.
- 587 Wu, X., Niu, C., Liu, X., Hu, T., Feng, Y., Zhao, Y., Liu, S., Liu, Z., Dai, G., Zhang, Y., Van Meerbeek, K.,
588 Wu, J., Liu, L., Guo, Q. & Su, Y. (2024). Canopy structure regulates autumn phenology by mediating
589 the microclimate in temperate forests. *Nature Climate Change*, 14, 1299–1305.
- 590 Wu, Z., Chen, S., De Boeck, H.J., Stenseth, N.C., Tang, J., Vitasse, Y., Wang, S., Zohner, C. & Fu, Y.H.
591 (2021). Atmospheric brightening counteracts warming-induced delays in autumn phenology of temperate
592 trees in Europe. *Global Ecology and Biogeography*, 30, 2477–2487.
- 593 Yan, T., Fu, Y.H., Campioli, M., Peñuelas, J. & Wang, X. (2021). Divergent responses of phenology and
594 growth to summer and autumnal warming. *Global Change Biology*, 27, null.
- 595 Zohner, C.M., Mo, L., Renner, S.S., Svenning, J.C., Vitasse, Y., Benito, B.M., Ordonez, A., Baumgarten,
596 F., Bastin, J.F., Sebald, V., Reich, P.B., Liang, J., Nabuurs, G.J., de Miguel, S., Alberti, G., Antón-
597 Fernández, C., Balazy, R., Brändli, U.B., Chen, H.Y.H., Chisholm, C., Cienciala, E., Dayanandan, S.,
598 Fayle, T.M., Frizzera, L., Gianelle, D., Jagodzinski, A.M., Jaroszewicz, B., Jucker, T., Kepfer-Rojas, S.,
599 Khan, M.L., Kim, H.S., Korjus, H., Johannsen, V.K., Laarmann, D., Lang, M., Zawila-Niedzwiecki, T.,
600 Niklaus, P.A., Paquette, A., Pretzsch, H., Saikia, P., Schall, P., Šeben, V., Svoboda, M., Tikhonova, E.,
601 Viana, H., Zhang, C., Zhao, X. & Crowther, T.W. (2020). Late-spring frost risk between 1959 and 2017
602 decreased in North America but increased in Europe and Asia. *Proceedings of the National Academy of
603 Sciences*, 117, 12192–12200.

604 **Supplemental material**

Table S1: Fuelinex species grouped by tree type, life history, and wood anatomy.

Deciduous Trees			
Common Name (Latin)	Life History Strategy	Wood Anatomy	n (ap- prox)
Bur oak (<i>Quercus macrocarpa</i>)	Slow-growth, long life	Ring-porous	87
Bitter cherry (<i>Prunus virginiana</i>)	Fast-growth, short life	Diffuse-porous	78
Box elder (<i>Acer negundo</i>)	Fast-growth, short life	Diffuse-porous	90
Balsam poplar (<i>Populus balsamifera</i>)	Fast-growth, short life	Diffuse-porous	84
Paper birch (<i>Betula papyrifera</i>)	Fast-growth, short life	Diffuse-porous	90
Evergreen Trees			
White pine (<i>Pinus strobus</i>)	Slow-growth, long life	Non-porous	89
Giant Sequoia (<i>Sequoiaadendron giganteum</i>)	Slow-growth, long life	Non-porous	54

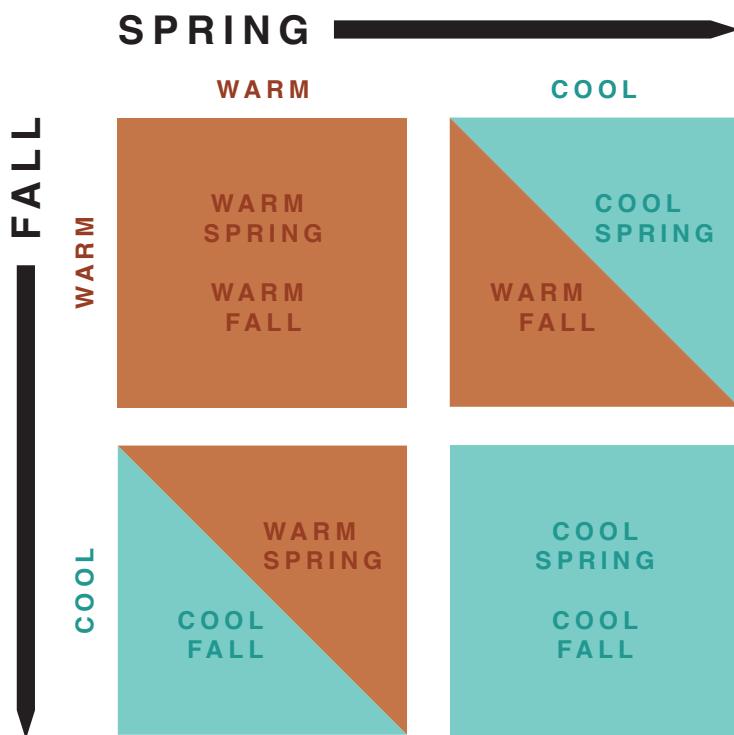


Figure S1: Arrangement of the Fuelinex four main treatments in a full factorial design

Table S2: Wilchrokic species grouped by tree type, life history, and wood anatomy.

Deciduous Trees			
Common Name (Latin)	Life History Strategy	Wood Anatomy	n
Paper birch (<i>Betula papyrifera</i>)	Fast-growth, short life	Diffuse-porous	8
Yellow birch (<i>Betula alleghaniensis</i>)	Moderate-growth, moderate life	Diffuse-porous	21
Grey birch (<i>Betula populifolia</i>)	Fast-growth, short life	Diffuse-porous	29
Grey alder (<i>Alnus incana</i>)	Fast-growth, short life	Diffuse-porous	31

Table S3: Treespotters species grouped by tree type, life history, and wood anatomy.

Deciduous Trees			
Common Name (Latin)	Life History Strategy	Wood Anatomy	n
American basswood (<i>Tilia americana</i>)	Fast-growth, moderate life	Diffuse-porous	5
Eastern cottonwood (<i>Populus deltoides</i>)	Fast-growth, short life	Diffuse-porous	4
Northern red oak (<i>Quercus rubra</i>)	Moderate-growth, long life	Ring-porous	4
White oak (<i>Quercus alba</i>)	Slow-growth, long life	Ring-porous	5
Pignut hickory (<i>Carya glabra</i>)	Slow-growth, long life	Ring-porous	4
Shagbark hickory (<i>Carya ovata</i>)	Slow-growth, long life	Ring-porous	4
River birch (<i>Betula nigra</i>)	Fast-growth, short life	Diffuse-porous	5
Yellow birch (<i>Betula alleghaniensis</i>)	Moderate-growth, moderate life	Diffuse-porous	4
Sugar maple (<i>Acer saccharum</i>)	Slow-growth, long life	Diffuse-porous	5
Red maple (<i>Acer rubrum</i>)	Slow-growth, long life	Diffuse-porous	4
Yellow buckeye (<i>Aesculus flava</i>)	Moderate-growth, moderate life	Diffuse-porous	5

Table S4: Nutrient addition over the two growing seasons for the nutrient addition treatment and the other treatments. The fertilizer is from Evergro (Delta, BC V4G 1B6), ID: Pepper Feed Main.

Date	Nutrient addition treatments	Regular treatments
7 June 2024	62.5	62.5
6 July 2024	62.5	62.5
1 Sept 2024	250	0
Subtotal (2024)	375	125
10 April 2025	0	125
9 May 2025	0	125
June 2025	62.5	62.5
July 2025	62.5	62.5
Subtotal (2025)	125	375
2-year total	500	500

Table S5: Summary of late spring frosts: definition, mechanisms, trends, and consequences

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 (<-2 °C) → 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 ↓ in North America; global trend is controversial (Reinmann <i>et al.</i> , 2023)
Consequences (Individual and ecosystem level)	Loss of vegetative tissue = ↓ photosynthesis = ↓ NSC and remobilization 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); Economic costs for orchards (Reinmann <i>et al.</i> , 2023)

Table S6: Summary of drought: definition, mechanisms, global trends, and consequences

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 (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 → increased vegetative growth → increased evapotranspiration → increased 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); — Climate models often exclude PDO/ENSO, limiting the attribution of increasing droughts to climate change (Trenberth <i>et al.</i>, 2014); — Weak evidence for detection and attribution of changes in meteorological drought since the mid-20th century (Change, 2014); — From a spatial, model-based perspective, anthropogenic forcing increased the frequency, duration, and intensity of SPI-based droughts in 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 East Asia (Chiang <i>et al.</i>, 2021; Marvel <i>et al.</i>, 2019; Spinoni <i>et al.</i>, 2014).
Consequences (Individual and ecosystem level)	<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, respectively (Li <i>et al.</i>, 2023)).

Table S7: Summary of heat waves: definition, mechanisms, global trends, and consequences

Definition:	A heat wave is a period of excessively hot weather (five or more consecutive days during which the daily maximum temperature exceeds the long-term average maximum temperature by 5 °C), which may be accompanied by high humidity (Marx <i>et al.</i> , 2021).
Mechanisms	↑ atmospheric CO ₂ → ↑ temperature → ↑ frequency and intensity of heat waves. More specifically, one proposed mechanism for the increased occurrence of heat waves is a weakening of the polar jet stream (a key weather driver in mid-latitude regions of North America, Europe, and Asia) caused by global warming, which increases the persistence of stationary weather patterns, resulting in prolonged heat waves or heavy rainfall events (Marx <i>et al.</i> , 2021). Extreme heat affects growth either (1) directly via disruption of cellular processes or (2) indirectly via increased leaf-to-air vapor pressure deficit (VPD) (Gagne <i>et al.</i> , 2020). Increased temperature leads to reduced photosynthesis, which can be attributed to: 1. Damage to photosynthetic machinery; 2. Inactivation of Rubisco; 3. Reduced RuBP regeneration; 4. Loss of membrane stability; 5. Increased mitochondrial respiration and photorespiration (Hauck <i>et al.</i> , 2025).
Global trend of occurrence	Heat waves have increased in frequency and intensity (Gagne <i>et al.</i> , 2020; Meehl & Tebaldi, 2004; Teskey <i>et al.</i> , 2015) and are expected to increase further 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 several weeks now impact approximately 10% of global land surfaces, compared to only 1% in the 1960s (Teskey <i>et al.</i> , 2015). These trends cannot be explained solely by natural climate variability and require anthropogenic climate change (Marx <i>et al.</i> , 2021).
Consequences (Individual and ecosystem level)	— Reduced photosynthesis; — Increased mortality; — Loss of photosynthetic tissue (Gagne <i>et al.</i> , 2020).