

1 Does age matter in trees' growth response to longer growing season?

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3 January 22, 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 (Ipcc), 2023; Laurance, 2007; Parmesan & Yohe, 2003). This can be through land use change and  
9 loss, 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  
12 affected Earth's climate and are projected to keep changing it for many centuries (Intergovernmental Panel  
13 On Climate Change (Ipcc), 2023). Yet, the extent of the consequences that a warming climate will have on  
14 biological processes is still debated (Huey *et al.*, 2012), in part because it requires accurate predictions of  
15 current and future trends in some of the most reported and direct biological impacts of climate change, as  
16 I review below. And also because it requires understanding the complex additional effects of these impacts,  
17 which I propose 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 spring and autumn phenology—the timing of recurring life history events (Parmesan & Yohe, 2003; Cleland  
21 *et al.*, 2007; Lieth *et al.*, 1974; Woolway *et al.*, 2021; Menzel *et al.*, 2006). Together, shifts in spring and au-  
22 tumn phenology modify when the growing season starts and when it ends. Understanding the consequences  
23 of changing growing season length on ecosystems requires understanding how much, and why it has changed  
24 (Duputié *et al.*, 2015).

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

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

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  
55 earlier growth onset, longer seasons did not increase the growth rate nor overall annual increment in trees.  
56 This could substantially affect forest carbon-cycle model projections on and thus feedbacks to future climate  
57 (Richardson *et al.*, 2013; Swidrak *et al.*, 2013). Starting to grow earlier and stopping later both have different  
58 effects on trees (Figure 1).

59

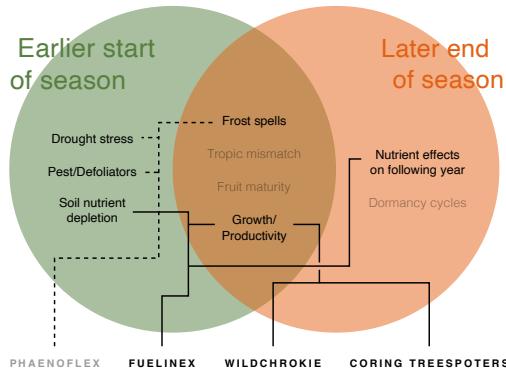


Figure 1: The effects that an earlier start and later end of season can have on trees. Solid lines connect effects studied over the course of this thesis. Phaeonflex (in grey) and its dashed lines represent other effects I investigated in a related experimental project that is not part of this thesis, 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  
62 allocated into wood is poorly understood. Indeed, the assumption of a linear relationship between wood  
63 growth and carbon assimilation is not well supported mechanistically and represents an important limita-  
64 tion of vegetation models (Cabon *et al.*, 2022). Net primary production represents the difference between  
65 photosynthesis and plant respiration, but this commonly used metric completely omits the representation  
66 of growth processes. This is perhaps because of a long-lasting paradigm of source-limited photosynthesis  
67 (Friend *et al.*, 2019; Parent *et al.*, 2010). Whether a tree's growth is source (photosynthetic activity de-  
68 termines sink activity) or sink (growth, respiration, and other metabolic processes determine the carbon  
69 source) controlled depends upon a closely coordinated sequence of dynamic responses and is still an active  
70 research question. However, Gessler & Zweifel (2024) recently suggested that neither source nor sink control  
71 systematically dominates. This complex dynamic enforces the importance of understanding the temperature  
72 sensitivity relationship between growth activity and photosynthesis. Growing evidence suggests that cambial  
73 activity may be more sensitive than photosynthesis to a range of environmental conditions, such as water  
74 and nutrient availability, and temperature (Cabon *et al.*, 2022, 2020; Muller *et al.*, 2011; Peters *et al.*, 2021).  
75 Thus, this demonstrates that carbon projection models that solely rely on vegetation alone may mislead  
76 carbon sequestration dynamics 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 overpassing important  
103 nuances 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). Different strategies can help understand how different species respond to warming and thus  
106 improve carbon sequestration projections.

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

118 *Ground based observations:* Second, leaf phenology can provide valuable and accessible insights into the  
119 growth temporality of trees that are not suitable for experimental trials. Collecting cambial phenology  
120 data, which is a direct measure of wood growth, is time-consuming and expensive. In contrast, leaf phe-  
121 nology through ground-based observations are low-cost methods that provide direct evidence of changing  
122 phenophases (Piao *et al.*, 2019). Cambial and leaf phenology are often closely synchronized; therefore, the  
123 more accessible leaf phenology data can act as a reliable proxy for the onset and end of tree growth. In  
124 other words, knowing when leaves elongate and colour can guide as to when trees start and stop growing,  
125 which is a fundamental metric to determine the growing season length. Additionally, unlike other meth-  
126 ods, ground observations have the advantage of providing accurate measurements of phenological events

130 for specific sites and species. Recently, the widespread use of smartphones has considerably simplified the  
131 phenological monitoring by citizen scientists (Dickinson *et al.*, 2012; Hufkens *et al.*, 2019; Piao *et al.*, 2019).  
132 While there are drawbacks to observations by citizen science programs (e.g. non-standard protocols, highly  
133 uneven spatiotemporal distribution of these observations), they have the potential to vastly increase the  
134 range of studied species and areas.

135

### 136 **Goals of my thesis**

137 I aim to understand how different tree species, at different lifespan stages, vary in their growth responses  
138 to different season lengths. To achieve this, I worked across different methods (Figure 2). First, I deployed  
139 a large-scale experiment named Fuelinex during which I artificially controlled the growing season length for  
140 seven species of tree saplings (2-3 years old). During this experiment, I also tested nutrient effects later in  
141 the season. Under Wildchrokie, I leveraged vegetative phenology data from a common garden project of four  
142 species of juvenile trees (5-8 years old). Then, with coringTreespotters I used the phenology data collected  
143 by citizen scientists on eleven species of fully mature trees (>30 years old). Answering the growth patterns  
144 of the trees across these three projects requires defining growth and the growing season.

## 145 **Complexity of measuring growth and defining growing season length**

### 146 **What is a growing season?**

147 The definition of the growing season itself is not well-defined, and studies use an array of definitions. Recently,  
148 Körner *et al.* (2023) proposed four definitions addressing this issue: (1) true growing season, based on  
149 measurable growth; (2) phenological season, based on visible phenological markers; (3) the productive season,  
150 based on primary production and (4) meteorological season, based on environmental conditions.

151 Here, I will focus on how definition (2), incorporating (4), affects definition (1) as our data cannot address  
152 (3). I will use definition (2) to infer a "window of opportunity", to calculate growing degree days (GDD)—a  
153 measure of heat accumulation—using meteorological conditions. I am using the meteorological season within  
154 a constrained window, instead of simply using it irrespective of phenology because of the illusion that an  
155 absolute increase in GDD over the last decades—irrespective of the timing of phenophases—also increases  
156 growth. Springs are warmer, falls are also sometimes warmer, and summers are warmer, which together  
157 increase the number of GDD, which may appear to be a reliable proxy for better environmental conditions.  
158 However, models that accumulate GDD before and/or after trees grow could mislead about how this variable  
159 drives growth.

160

### 161 **What is growth?**

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

166

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

173

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

180

## 181 Objectives

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

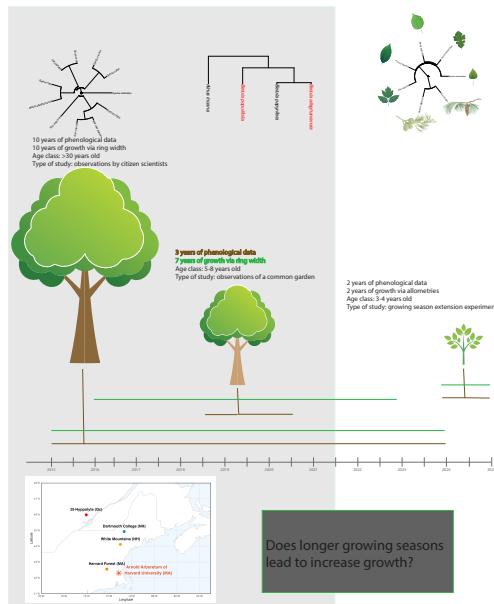


Figure 2: Overview of the age class, species, provenance of the trees used in each study along with the type of study each project consist of.

## 191 Research questions

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

195

## 196 Methodology

### 197 Chapter 1: Fuelinex

198 **Species selection and growing conditions** We used seven species of tree saplings for our experiment  
199 (Fuelinex). We purchased Paper birch (*Betula papyfera*), Choke Cherry (*Prunus virginiana*), Bur oak (*Quer-*  
200 *cus macrocarpa*) from Peel's nursery in November 2023 and the trees arrived at Totem Field studios 49.26  
201 °N, -123.25 °W, where the other four species were stored until the spring of 2023. Manitoba maple (*Acer*  
202 *negundo*), Eastern white pine (*Pinus strobus*), Balsam poplar (*Populus balsamifera*) and Giant sequoia (*Se-*  
203 *quoia巨树 giganteum*) are leftover trees that we purchased in 2022 for 2023 for a previous experiment. We  
204 watered them weekly, and they remained at ambient condition for the 2023 growing season. We randomly  
205 selected 90 individuals of each species among them. We propagated B. poplar from 30 cm whips while the

206 trees were still dormant Mc Carthy *et al.* (2018). In May 2024, we repotted all the trees in 2-gallon plastic  
207 pots with a medium for perennials consisting of 50 % peat, 25% crushed pumice and 25% crushed bark  
208 ([www.westcreekfarm.com](http://www.westcreekfarm.com)). In February 2025, we repotted the trees with the same medium in 3-gallon pots.  
209 We arranged the trees in three blocks, each containing all 6 treatments and 7 species, with two of these  
210 blocks placed under an open-walled and well-ventilated polytunnel greenhouse. All saplings were connected  
211 to a drip irrigation system (40 PVC frame from Netafilm 54 with a Toro controller) to maintain constant  
212 irrigation across the season. Using fertilizer premix, we fertilized the trees twice during the growing season  
213 of 2024 (except for the nutrient-boosted trees) and three times during 2025, just enough to keep the trees  
214 alive (Table S4).

215  
216 **Tree measurements and biomass** Using red paint, we marked the trees on their trunk at 3 cm from  
217 the soil in February 2024. Then we measured the diameter at the top of that mark using a digital calliper  
218 (accuracy  $\pm$  0.01cm). From that mark to the bottom of the highest apical bud, for angiosperms, and the top  
219 of the apical meristem for gymnosperms, we measured height with a metal ruler (accuracy  $\pm$  0.1cm). We  
220 measured those two same points in the winter (2024 growing season) and in the fall (2025 growing season) of  
221 2025. For those two subsequent measurements, if the measured shoot died (because of insects, accidentally  
222 snapped off, etc.), we noted the previous measurement as invalid and measured the highest lateral shoot.  
223 In the fall of 2025, when all the individuals from a species had lost all their leaves, we removed the trees  
224 from their pots and gently washed the soil off the roots with a water hose. We dried the trees by placing  
225 them in drying ovens at 70°C for 72 hours and weighed the roots and stem separately (accuracy  $\pm$  0.01 gram).

226  
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  
234 either the new-year apical or the highest lateral shoot. To facilitate and improve the quality of the shoot  
235 elongation measurements, we attached paper rulers (accuracy  $\pm$  0.1cm) on *A. negundo*, *B. papyfera*, *P.*  
236 *balsamifera* and *Q. macrocarpa*. For species not suitable for those paper rulers, we took those same mea-  
237 surements, but with a metal ruler (accuracy  $\pm$  0.1cm). We measured shoot elongation weekly from the red  
238 mark to the base of the bud for angiosperms, and at the top of the apical meristem for gymnosperms. For  
239 determinate growth species ((*A. negundo*, *P. virginiana* and *Q. macrocarpa*), when the trees did not elongate  
240 for two weeks, we 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 chloro-  
244 phyll content meter. We also recorded the date of loss of green leaf cover and leaf drop.

245  
246 **Experimental design** Individuals from each species were randomly selected for a full factorial design of  
247 Warm/Cool, Spring/Fall treatments (Figure S1) with two additional treatments to test nutrient effects in the  
248 fall (Figure 3), for a total of 15 replicates/treatment/species. On 6 March 2024, we placed the Cool Spring  
249 individuals in climate chambers to delay the start of their growing season, while the Warm Spring replicates  
250 remained at ambient conditions. Once all Warm Spring individuals have fully leafed out, we removed the  
251 Cool Spring replicates from the chambers and placed them back at ambient conditions for the whole sum-  
252 mer. On 4 September 2024, we placed the trees for the Warm Fall treatments in the climate chambers. The  
253 temperature was set to fit the mean 30-year weekly maximum temperature of the previous month (e.g. 1st  
254 week of September set to the average of the 1st week of August). The Cool Fall treatment trees remained  
255 at ambient conditions. For both climate chamber treatments, we rotated and watered the trees weekly to  
256 minimize the climate chamber's effect. We also set the photoperiod regime to the corresponding sunrise and  
257 sunset of the ongoing week and ramped it until it reached full light. To test for nutrient limitation at the  
258 end of the season, we added a supplemental dose of nutrients (Table S4) to two treatments (Figure 3). In  
259 2025, all the trees were kept at ambient conditions together at Totem field during which we recorder the

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

<b>Group</b>	<b>Scale</b>	<b>Phenostage</b>	<b>Description</b>
<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, crinkled 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

<sup>260</sup> same phenophases.

<sup>261</sup>

<sup>262</sup> **Leaf count** To determine if nutrient addition treatments in the fall affected leaf primordia formation, we  
<sup>263</sup> counted the apical meristem leaves on 27 May 2025 for the determinate growth species only (*A. negundo*, *P.*  
<sup>264</sup> *virginiana* and *Q. macrocarpa*).

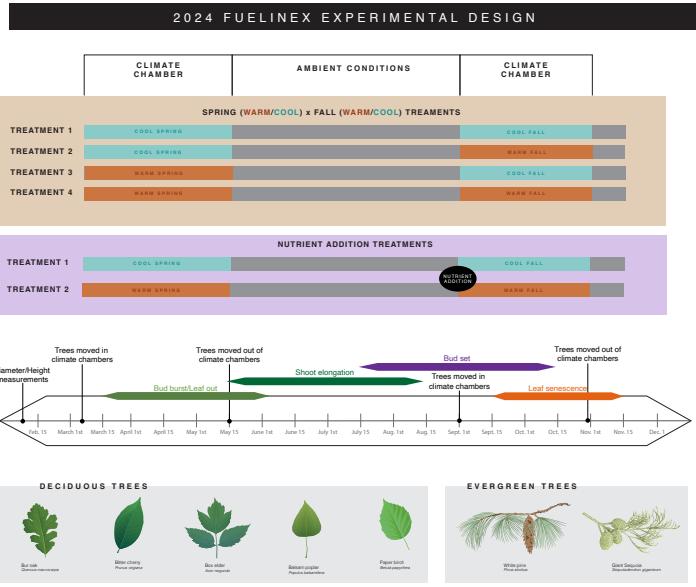


Figure 3: Experimental design during the 2024 growing season. Cooling treatments are represented in blue, and warming treatments are in orange. The grey zone in the middle represents an approximate period during the growing season where all treatments were together at ambient conditions.

## 265 Chapter 2: Wildchrokie and coringTreespotters

### 266 Wildchrokie

#### 267 Common garden setup (*Buonaiuto, in review*)

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

276

#### 277 Phenological monitoring and sample collection (*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.

287

### 288 Coringtreespotters

#### 289 Citizen science program

290 The Treespotters was a citizen science program that started in 2015 and aimed to train citizen scientists for  
 291 accurate and rigorous phenological monitoring. From 2015 to 2024, hundreds of citizen scientists monitored

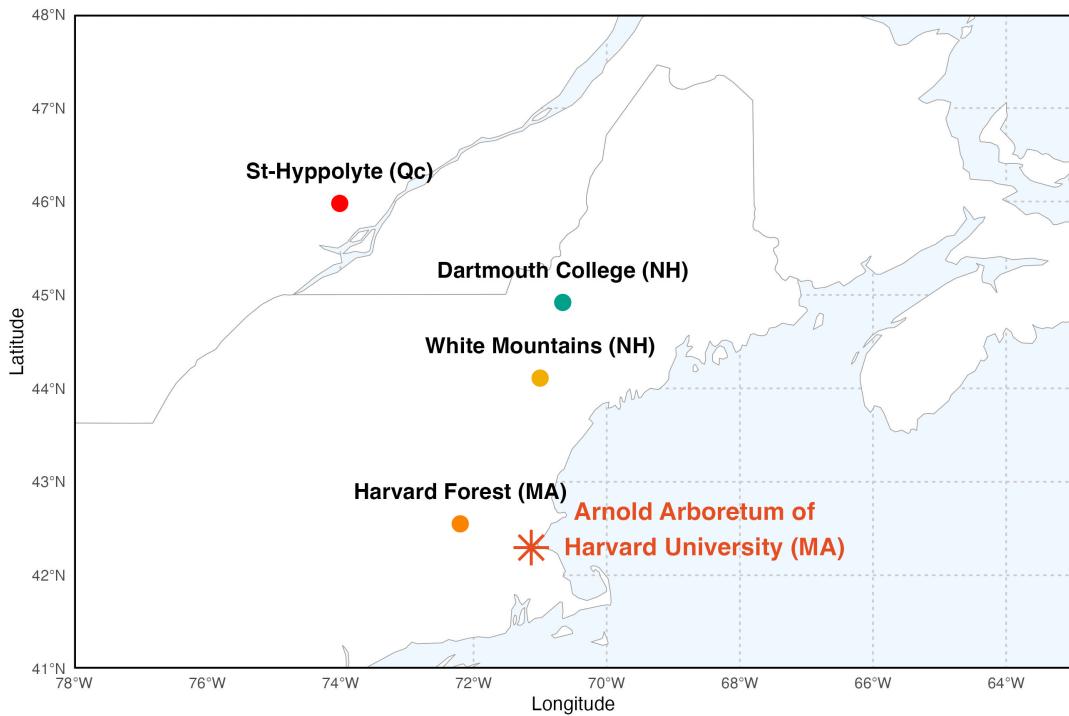


Figure 4: Locations of the provenance study for the common garden study (Wildchrokie). The common garden and the citizen science project (coringTreespotters) took place at the Arnold Arboretum of Harvard University, represented by the orange star.

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

#### 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). The cores were collected perpendicular  
 303 to the slope and at 180 degrees from each other. We cleaned the increment borer with alcohol (70% ethanol)  
 304 and the inside with a brush before collecting each core. We stored the cores in paper straws that were pre-  
 305 viously labelled and punched to help with drying. They were stored at ambient temperature for three months.  
 306

#### 307 **Sample processing, imaging and measuring**

308 We mounted the cores on wooden mounts, and sanded the cores and cross-sections using progressively fine  
 309 grit (150, 300, 400, 600, 800, 1000). We scanned the cores and cross-sections at a resolution of 6250 dpi,  
 310 with a high resolution treering scanner (Fong, unpublished). We used the digitized images to measure the  
 311 tree ring widths with Fiji ImageJ. Then, we performed visual crossdating using DplR (Bunn, 2010), we did  
 312 not perform statistical crossdating because of the short chronologies that limit the capacity of these analyses.  
 313

#### 314 **Statistical analyses**

315 For both projects, we used Bayesian hierarchical models coded in Stan with the rstan package version 2.32.7  
 316 (Carpenter *et al.*, 2017) to run the Stan code in R. With these models, we estimated ringwidth as a function

317 of growing degree days, accumulated from the leafout date to the budset date. We had three grouping  
 318 factors for Wildchrokie (species, site and treeid) and two for coringTreespotters (species and treeid). We ran  
 319 four chains with each 2000 warmup, which we discarded and 2000 sampling iterations, which we kept for  
 320 posterior distribution estimates. The models did not have any divergent transitions and Rhat was below 1.01.

321

322 *Wildchrokie model structure*

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

323 *coringTreespotters model structure*

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

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595 **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>Sequoiadendron giganteum</i> )	Slow-growth, long life	Non-porous	54

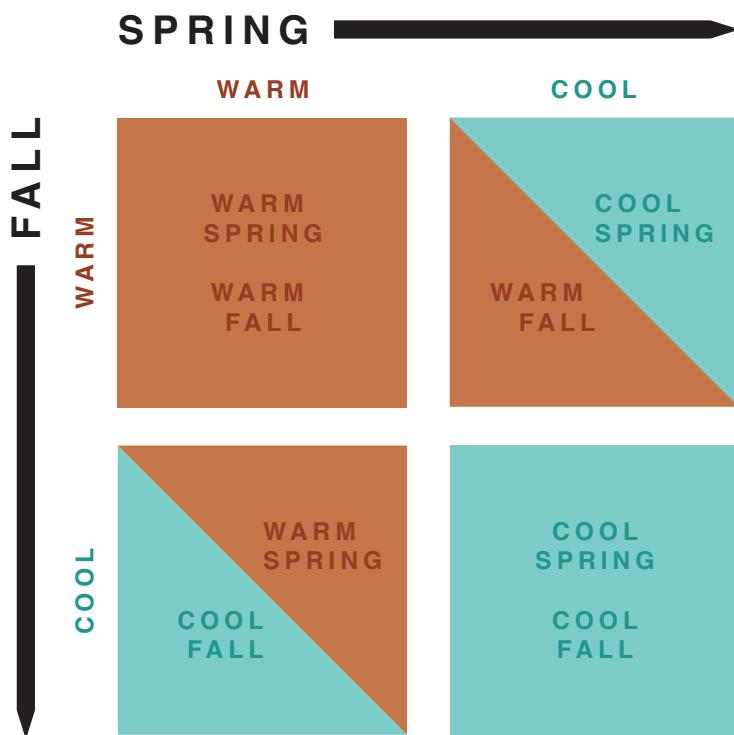


Figure S1: Arrangement of the Fuelinex four main treatments in a full factorial design

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
<b>Subtotal (2024)</b>	<b>375</b>	<b>125</b>
10 April 2025	0	125
9 May 2025	0	125
June 2025	62.5	62.5
July 2025	62.5	62.5
<b>Subtotal (2025)</b>	<b>125</b>	<b>375</b>
<b>2-year total</b>	<b>500</b>	<b>500</b>

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

<b>Definition:</b>	Late spring frosts are below-freezing temperatures in late spring (Zohner <i>et al.</i> , 2020)
<b>Mechanisms</b>	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)
<b>Global trend of occurrence</b>	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)
<b>Consequences (Individual and ecosystem level)</b>	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

<b>Definition:</b>	“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).
<b>Mechanisms</b>	<ul style="list-style-type: none"> <li>— Hot temperature + low precipitation (global-change-type drought (Tyree &amp; Zimmermann, 2002)) = ↑ evapotranspiration → less water in soil → cavitation → embolism → hydraulic failure (Tyree &amp; Zimmermann, 2002) = tissue death (Choat <i>et al.</i>, 2018);</li> <li>— Earlier spring phenology = longer GS → increased vegetative growth → increased evapotranspiration → increased drawdown of soil moisture = progressive water stress (Li <i>et al.</i>, 2023);</li> <li>— Long-term vs short-term stomatal responses and consequences on tissue death (Choat <i>et al.</i>, 2018);</li> <li>— Recovery and its determinants (Choat <i>et al.</i>, 2018; Li <i>et al.</i>, 2023).</li> </ul>
<b>Global trend of occurrence</b>	<ul style="list-style-type: none"> <li>— ↑ precipitation anomalies since 1990 (Trenberth <i>et al.</i>, 2014);</li> <li>— Climate models often exclude PDO/ENSO, limiting the attribution of increasing droughts to climate change (Trenberth <i>et al.</i>, 2014);</li> <li>— Weak evidence for detection and attribution of changes in meteorological drought since the mid-20th century (Change, 2014);</li> <li>— 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).</li> </ul>
<b>Consequences (Individual and ecosystem level)</b>	<ul style="list-style-type: none"> <li>— Recurring droughts may limit trees’ ability to recover from other types of stress;</li> <li>— 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)).</li> </ul>

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

<b>Definition:</b>	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).
<b>Mechanisms</b>	↑ atmospheric CO <sub>2</sub> → ↑ 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).
<b>Global trend of occurrence</b>	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).
<b>Consequences (Individual and ecosystem level)</b>	— Reduced photosynthesis; — Increased mortality; — Loss of photosynthetic tissue (Gagne <i>et al.</i> , 2020).