

<sup>1</sup> Does age matter in tree growth responses to longer growing season?

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## <sup>4</sup> Introduction

### <sup>5</sup> Climate change impacts on tree phenology

<sup>6</sup> Research from the past decades has shown convincing evidence that human activity is increasingly affecting  
<sup>7</sup> many worldwide environmental processes (Ceballos *et al.*, 2017; Intergovernmental Panel On Climate  
<sup>8</sup> Change (Ipcc), 2023; Laurance, 2007; Parmesan & Yohe, 2003). This can be through land use change and  
<sup>9</sup> loss, pollution, invasive species, resource overexploitation and climate change (Driscoll *et al.*, 2018; Parmesan  
<sup>10</sup> *et al.*, 1999; Wu, 2013). Though some immediate actions can mitigate these impacts (e.g. Campbell *et al.*,  
<sup>11</sup> 2014), reversing 150 years of human-induced greenhouse gas emissions is harder. These emissions have af-  
<sup>12</sup> fected Earth's climate and are projected to keep changing it for many centuries (Intergovernmental Panel  
<sup>13</sup> On Climate Change (Ipcc), 2023). Yet, the extent of the consequences that a warming climate will have on  
<sup>14</sup> biological processes is still debated (Huey *et al.*, 2012), in part because it requires accurate predictions of  
<sup>15</sup> current and future trends in some of the most reported and direct biological impacts of climate change, as  
<sup>16</sup> I review below. And also because it requires understanding the complex additional effects of these impacts,  
<sup>17</sup> which I propose to study for my thesis.

### <sup>18</sup> Trends and drivers of spring and autumn phenological events

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

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

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

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; Green  
54 & Keenan, 2022; Silvestro *et al.*, 2023). For instance, Dow *et al.* (2022) showed that despite an earlier growth  
55 onset, longer seasons did not increase the growth rate nor overall annual increment in trees. This could sub-  
56 stantially affect forest carbon-cycle model projections on and thus feedbacks to future climate (Richardson  
57 *et al.*, 2013; Swidrak *et al.*, 2013). Starting to grow earlier and stopping later both have different effects on  
58 trees (Figure 1).

59

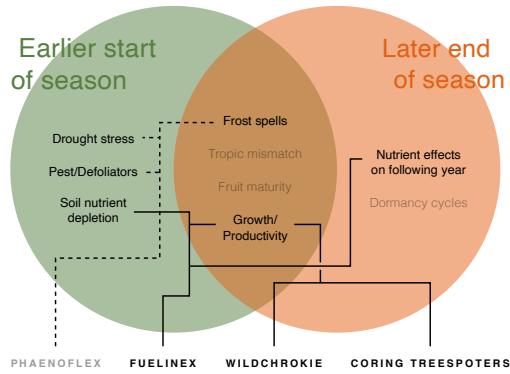


Figure 1: The effects that an earlier start and later end of season can have on trees. Solid lines connect effects studied over the course of this thesis. Phaeonflex (in grey) and its dashed lines represent other effects I investigated in a related experimental project that is not part of this thesis, 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 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 nuances  
103 in the growth responses plausibly explained by species differences. Excluding species differences in models  
104 may mislead future carbon dynamic models (Green & Keenan, 2022; Cabon *et al.*, 2022; Wolkovich *et al.*,  
105 2025). We propose to  
106 Strategies such as experiments and ground-based observations can help understand how different species  
107 respond to warming and thus improve carbon sequestration projections.

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

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

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

136

### 137 **Goals of my thesis**

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

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

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

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

158

### 159 **What is growth?**

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

164

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

171

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

178

## 179 Objectives

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

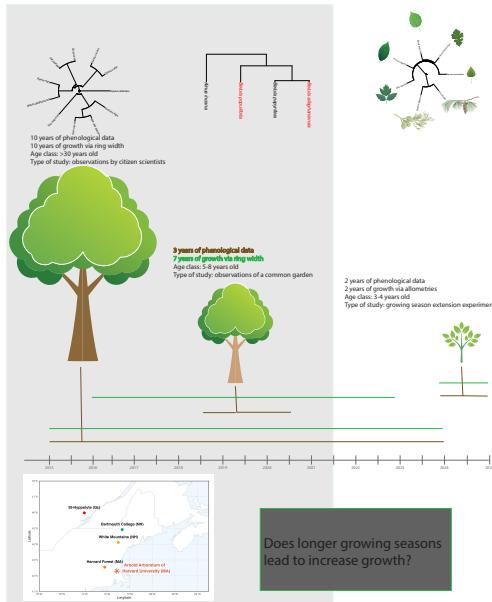


Figure 2: Overview of the age class, species, provenance of the trees used in each study along with the type of study each project consist of.

## 189 Research questions

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

193

## 194 Methodology

### 195 Chapter 1: Fuelinex

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

204 while the trees were still dormant (McCarthy *et al.*, 2018). In May 2024, we repotted all the trees in  
205 2-gallon plastic pots with a medium for perennials consisting of 50 % peat, 25% crushed pumice and 25%  
206 crushed bark (purchased from [www.westcreekfarm.com](http://www.westcreekfarm.com)). In February 2025, we repotted the trees with the  
207 same medium in 3-gallon pots. We arranged the trees in three blocks, each containing all 6 treatments and 7  
208 species, with two of these blocks placed under an open-walled and well-ventilated polytunnel greenhouse. All  
209 saplings were connected to a drip irrigation system (40 PVC frame from Netafilm 54 with a Toro controller)  
210 to maintain constant irrigation across the season. Using fertilizer premix, we fertilized the trees twice during  
211 the growing season of 2024 (except for the nutrient-boosted trees) and three times during 2025, just enough  
212 to keep the trees alive (Table S4).

213

#### 214 **Tree measurements and biomass:**

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

225

#### 226 **Phenology and shoot elongation monitoring:**

227 *Leaf phenology:* We started monitoring phenology of all the trees on 11 April 2024, missing the initial leaf  
228 phenology for most individuals, but we monitored subsequent phenophases twice a week until the leaves  
229 had fully elongated. In the late summer and fall, we monitored budset every week until full bud dormancy.  
230 Phenophases are described in Table 1. Phenophases of *S. giganteum* were not recorded.

231

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

240

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

244

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

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

258 2025, all the trees were kept at ambient conditions together at Totem field during which we recorded the  
 259 same phenophases.

260  
 261 **Leaf count** To determine if nutrient addition treatments in the fall affected leaf primordia formation, we  
 262 counted the apical meristem leaves on 27 May 2025 for the determinate growth species only (*A. negundo*,  
 263 *P. virginiana* and *Q. macrocarpa*).

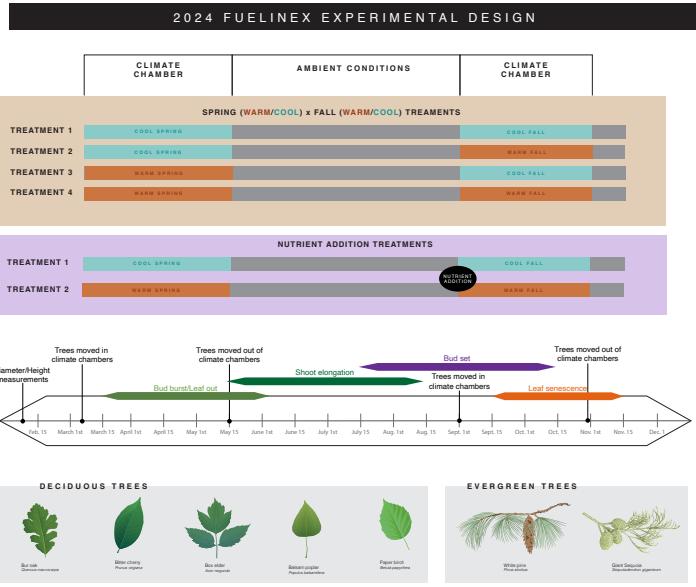


Figure 3: Experimental design during the 2024 growing season. Cooling treatments are represented in blue, and warming treatments are in orange. The grey zone in the middle represents an approximate period during the growing season where all treatments were together at ambient conditions.

## 264 Chapter 2: Wildchrokie and coringTreespotters

### 265 Wildchrokie

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

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

275

276 *Phenological monitoring and sample collection (direct quote from Buonaiuto, in review)*

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

286

### 287 Coringtreespotters

288 *Citizen science program*

289 The Treespotters was a citizen science program that started in 2015 and aimed to train citizen scientists for  
290 accurate and rigorous phenological monitoring at the Arnold Arboretum of Harvard University (42.30 °N,

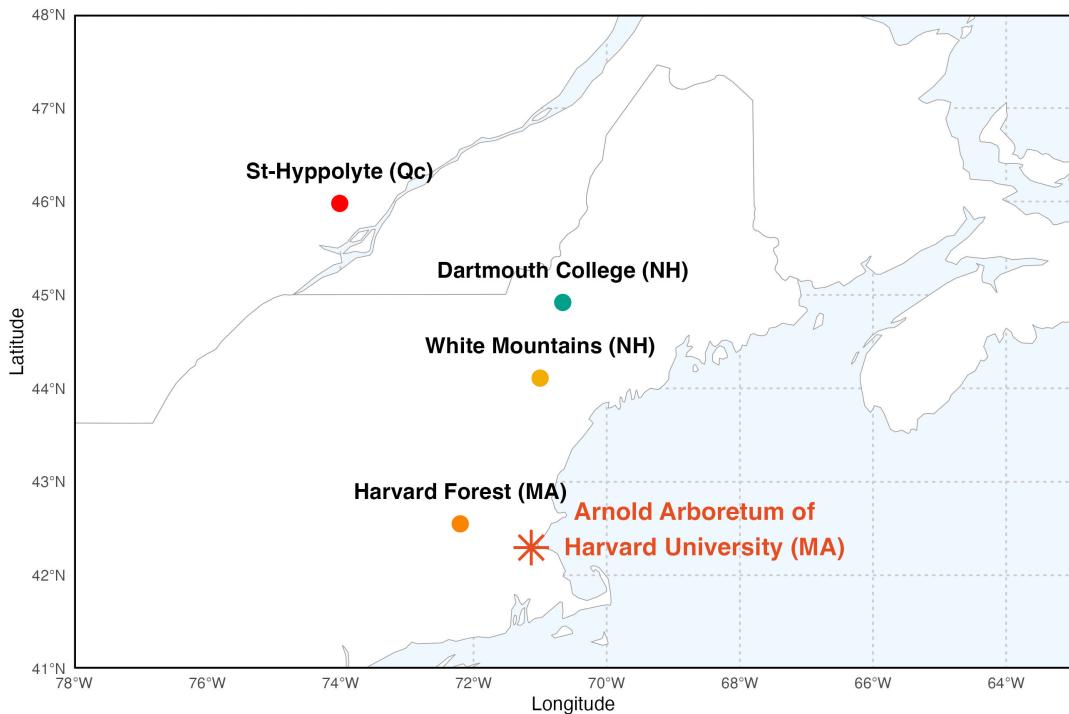


Figure 4: Locations of the provenance study for the common garden study (Wildchrokie). The common garden and the citizen science project (coringTreespotters) took place at the Arnold Arboretum of Harvard University, represented by the orange star.

291 -71.12 °W) (Figure 4). From 2015 to 2024, hundreds of citizen scientists monitored 50 trees of 11 species.  
 292 They regularly followed those individuals from budburst in the spring to leaf colouring in the fall using the  
 293 National Phenology Network (NPN) phenophases (Denny *et al.*, 2014): Leaves (483), Colored leaves (498),  
 294 Fruits (516), Ripe Fruits (390), Falling leaves(471), Recent fruit or seed drop (504), Increasing leaf size (467),  
 295 Breaking leaf buds (371), Flowers or flower buds (500), Open flowers (501), Pollen release (502). Not all  
 296 phenophases were recorded for every tree, for every year, and some trees miss several years of data.

#### 297 *Phenological monitoring and sample collection*

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

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

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

#### 311 **Statistical analyses**

312 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  
 319 ran four chains with each 2000 warmup, which we discarded, and 2000 sampling iterations, which we kept  
 320 for posterior distribution estimates. The models did not have any divergent transitions and  $\hat{R}$  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>Sequoiaadendron giganteum</i> )	Slow-growth, long life	Non-porous	54

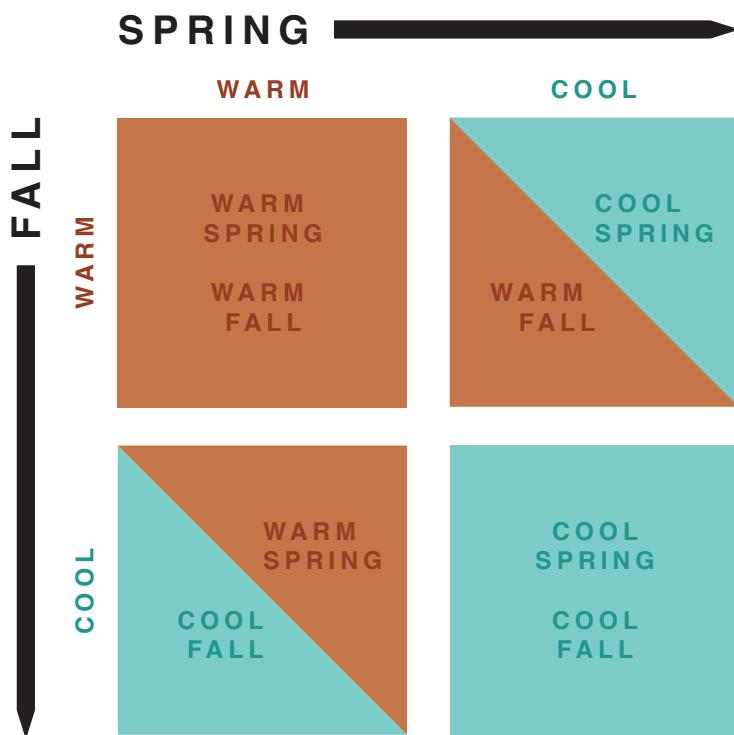


Figure S1: Arrangement of the Fuelinex four main treatments in a full factorial design

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
<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).