

<sup>1</sup> Does age matter in trees' growth response to longer growing season?

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## <sup>4</sup> 1 Introduction

### <sup>5</sup> 1.1 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  
<sup>12</sup> affected 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> spring and autumn phenology—the timing of recurring life history events (Parmesan & Yohe, 2003; Cleland  
<sup>21</sup> *et al.*, 2007; Lieth *et al.*, 1974; Woolway *et al.*, 2021; Menzel *et al.*, 2006). Together, shifts in spring and au-  
<sup>22</sup> tumn phenology modify when the growing season starts and when it ends. Understanding the consequences  
<sup>23</sup> of changing growing season length on ecosystems requires understanding how much, and why it has changed  
<sup>24</sup> (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. These differences may be  
<sup>36</sup> caused in part by the lesser attention payed to autumn phenology (Piao *et al.*, 2019) and because the data  
<sup>37</sup> is often noisier (Wu *et al.*, 2024). However, some of these differences are likely due to different drivers of  
<sup>38</sup> autumn phenology, as these phenophases appear to be driven by shortening photoperiod and colder temper-  
<sup>39</sup> atures (Cooke *et al.*, 2012; Flynn & Wolkovich, 2018; Körner & Basler, 2010; Delpierre *et al.*, 2016). Given  
<sup>40</sup> that colder temperatures can accelerate senescence, warmer autumns may delay leaf senescence, possibly by  
<sup>41</sup> extending the activity of photosynthetic enzymes which causes decreases the degradation rate of chlorophyll  
<sup>42</sup> (Körner & Basler, 2010; Delpierre *et al.*, 2016).

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

49 **50 Uncertainty of how shifts in spring and autumn phenology affect trees and forests**

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

59 Understanding these findings requires answering why trees do not grow more despite longer growing seasons.  
60 While carbon allocation to above-ground biomass is one of the largest carbon sinks, how this carbon is  
61 allocated into wood is poorly understood. Indeed, the assumption of a linear relationship between wood  
62 growth and carbon assimilation is not well supported mechanistically and represents an important limitation  
63 of vegetation models (Cabon *et al.*, 2022). Net primary production represents the difference between  
64 photosynthesis and plant respiration, but this commonly used metric completely omits the representation  
65 of growth processes. This is perhaps because of a long-lasting paradigm of source-limited photosynthesis  
66 (Friend *et al.*, 2019; Parent *et al.*, 2010). Whether a tree's growth is source (photosynthetic activity de-  
67 termines sink activity) or sink (growth, respiration, and other metabolic processes determines the carbon  
68 source) controlled depends upon a closely coordinated sequence of dynamic responses and is still an active  
69 research question. However, Gessler & Zweifel (2024) recently suggested that neither source or sink control  
70 systematically dominate. This complex dynamic enforces the importance of understanding the temperature  
71 sensitivity relationship between growth activity and photosynthesis. Growing evidence suggests that cambial  
72 activity may be more sensitive than photosynthesis to a range of environmental conditions, such as water  
73 and nutrient availability, and temperature (Cabon *et al.*, 2022, 2020; Muller *et al.*, 2011; Peters *et al.*, 2021).  
74 Thus, this demonstrates that carbon projection models that solely rely on vegetation alone may mislead  
75 carbon sequestration dynamics of our forests.

76 **77 1.1.3. Growing season shifts and consequences on forest ecosystems and services**

78 Spring and fall phenological events are shifting with debatable consequences on tree growth. The sensitivity  
79 of cambial activity to water, temperature and nutrients has the potential to have far-reaching consequences  
80 given the hard-to-predict nature of future climate change, where any of these variables could vary from low  
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 **1.2 Experiments and observations to understand the future of growth and sea-  
86 son length relationship**

87 **1.2.1. 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  
90 to warming are very likely to be non-linear (Ettinger *et al.*, 2020; Fu *et al.*, 2013). Indeed, accurate pre-  
91 dictions require an in-depth, accurate mechanistic understanding of phenophases and their sensitivities to  
92 environmental drivers, especially to temperature and photoperiod (Fu *et al.*, 2013). Therefore, the very  
93 foundation of the assumption that longer seasons increase growth may shift with future climate change. The  
94 well-observed advance in spring phenology may decelerate, and delayed fall phenology may shift towards  
95 earlier leaf senescence (through summer drought-induced growth cessation).

97 **1.2.2. The assumption that longer seasons lead to increased growth is called into question**  
98 Recent work emphasizing the need to understand the drivers regulating growth across biomes highlights  
99 strong species-level variation that may be critical to accurate projections. Phenology varies greatly across  
100 species (e.g. closely related species tend to budburst at similar times under similar conditions) (Wolkovich  
101 *et al.*, 2014), but so does the relationship between growth and season length, which may explain the wide  
102 variation of this relationship within communities (Buckley & Kingsolver, 2012). This points out another  
103 weakness of current carbon sequestration models that pool species together, likely overpassing important  
104 nuances in the growth responses that could be explained by species differences. Excluding species differences  
105 in models may mislead future carbon dynamic models (Green & Keenan, 2022; Cabon *et al.*, 2022; Wolkovich  
106 *et al.*, 2025). Different strategies can help understanding how different species respond to warming and thus  
107 improve carbon sequestration projections.

108  
109 **1.2.2.1. Experiments:** First, experiments are extremely useful in teasing apart co-occurring realities in  
110 natural environments. For example, warm springs, and severe droughts later in the summer often happen  
111 together within a single year making it difficult to tease these effects apart from observational data. Manipu-  
112 lative experiments, in contrast, have the capacity to separate the relative effect of each phenomenon (Morin  
113 *et al.*, 2010; Primack *et al.*, 2015), but also have major limitations, especially when working on trees. Logis-  
114 tical constraints of working with adult trees, mean that experiments are most often performed on juvenile  
115 trees. While saplings are critical for their role in forest regeneration projections, their responses often do  
116 not directly translate to mature trees, which hold the overwhelming carbon biomass proportion of forests  
117 (Augspurger & Bartlett, 2003; Silvestro *et al.*, 2023; Vitasse, 2013). However, even if young trees are often  
118 more plastic than adult forms, their responses can still provide valuable insights in differences across species  
119 and populations (Wolkovich *et al.*, 2025).

120  
121 **1.2.2.2. Ground based observations:** Second, leaf phenology can provide valuable and accessible insights into  
122 the 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, therefore, the  
126 more accessible leaf phenology data can act as a reliable proxy for the onset and end of tree growth. In other  
127 words, knowing when leaves elongate and colour can guide as to when trees start and stop growing, which is  
128 a fundamental metric to determine the growing season length. Additionally, unlike other methods, ground  
129 observations have the advantage of providing accurate measurements of phenological events for specific sites  
130 and species. Recently, the widespread use of smartphones has considerably simplified the phenological moni-  
131 toring by citizen scientists which has the potential to vastly increase the range of studied species and areas.  
132 (Dickinson *et al.*, 2012; Hufkens *et al.*, 2019; Piao *et al.*, 2019). While there are drawbacks to observations  
133 by citizen science programs (e.g. non-standard protocols, highly uneven spatiotemporal distribution of these  
134 observations), they have a great potential to diversify the phenology data.

135  
136 **1.2.3. 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 length. To achieve this, I worked across different methods. First, for my large-scale  
139 experiment named Fuelinex, I artificially controlled the growing season length for seven species of tree  
140 saplings (2-3 years old). During this experiment, I also tested nutrient effects late in the season. Under  
141 Wildchrokie, I leveraged vegetative phenology data from a common garden project of four species of juvenile  
142 trees (5-8 years old). Then, with coringTreespotters I used the phenology data collected by citizen scientists  
143 on eleven species of fully mature trees (>30 years old). Answering the growth patterns of the trees across  
144 these three projects requires specifying the definitions of growth and the growing season.

### 145 **1.3 Complexity of measuring growth and defining growing season length**

146 **1.3.1.1. What is a growing season?**

147  
148 The definition of the growing season itself is not well-defined and an array of definitions are used differently

149 accross studies. Recently, Körner *et al.* (2023) proposed four definitions addressing this issue: (1) true growing  
150 season, based on measurable growth; (2) phenological season, based on visible phenological markers; (3)  
151 the productive season, based on primary production and (4) meteorological season, based on environmental  
152 conditions.

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

#### 162 *1.3.1.2. What is growth?*

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

167 **1.3.2. Traditional diameter measurements miss the resolution of annual growth increment**  
168 Foresters have measured tree diameter and height for decades, but these measurements may not be suitable  
169 for determining relationships between growth and environmental conditions. The widely used method in  
170 forestry is to measure diameter at breast height at punctual time intervals. Combined with height, these  
171 data help develop allometries foresters can use to estimate how much wood they can harvest in a forest  
172 (e.g. (Meyer, 1940; Saunders & Wagner, 2008)). These metrics work to determine wood in forests, but their  
173 coarse temporal scale—measuring every 5 or more years—are likely to miss extreme events affecting growth.  
174 **1.3.3. Dendroecology to analyses growth responses to changing growing season length** Alongside  
175 the diameter-height allometric relationship, dendroecology—applications of dendrochronological techniques  
176 to problems in ecology (Fritts & Swetnam, 1989)—emerged to answer ecological problems as well as to hind-  
177 cast (e.g. (Bergeron *et al.*, 2004)) and forecast ecological processes both at the regional (Gazol *et al.*, 2018)  
178 and global scale (Manzanedo & Pederson, 2019; Büntgen *et al.*, 2018). Now, these methods are used to  
179 understand more precise growth patterns and their relationship with different environmental factors. This  
180 is why I will use tree rings as a proxy for how much trees grew in any given year.  
181

## 183 **1.4 Objectives**

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

## 193 **1.5 Research questions**

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

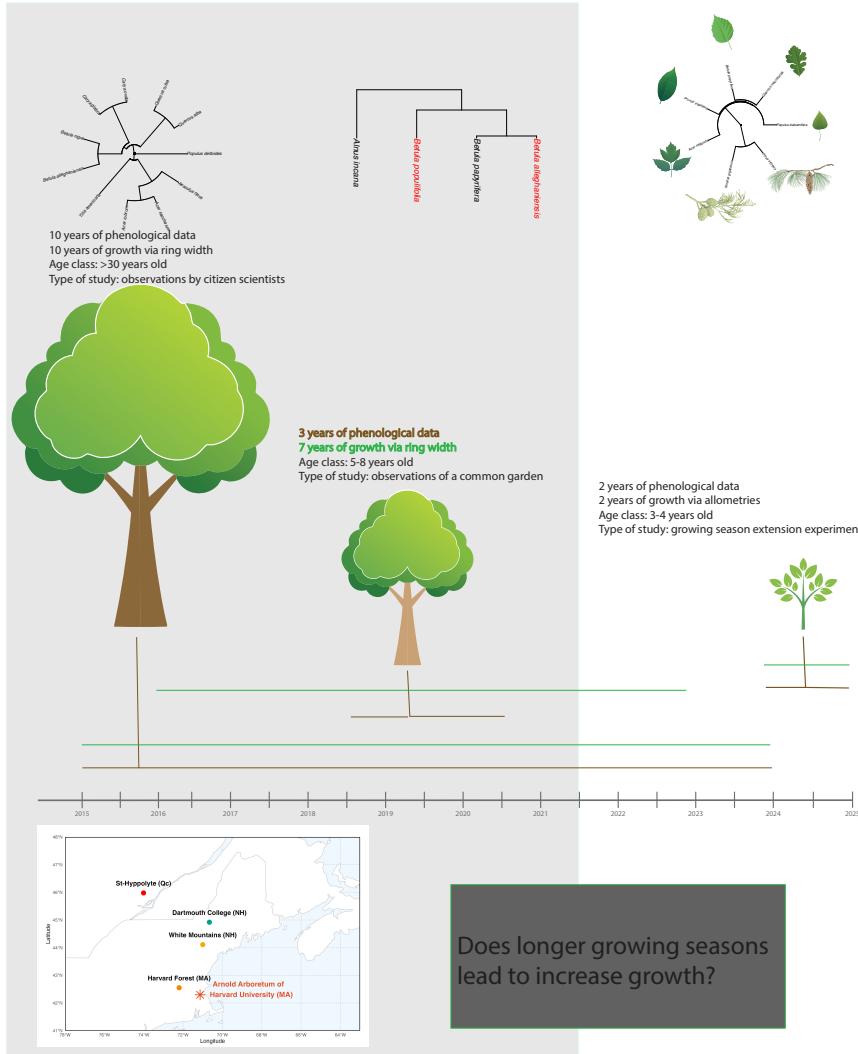


Figure 1: The effects that an earlier start and later end of season can have on trees. In bold are the effects that were studied over the course of this thesis. Phaenoflex (in grey) is a related experimental project, that is not part of this thesis, but one I collaborated on in 2023 and 2024.

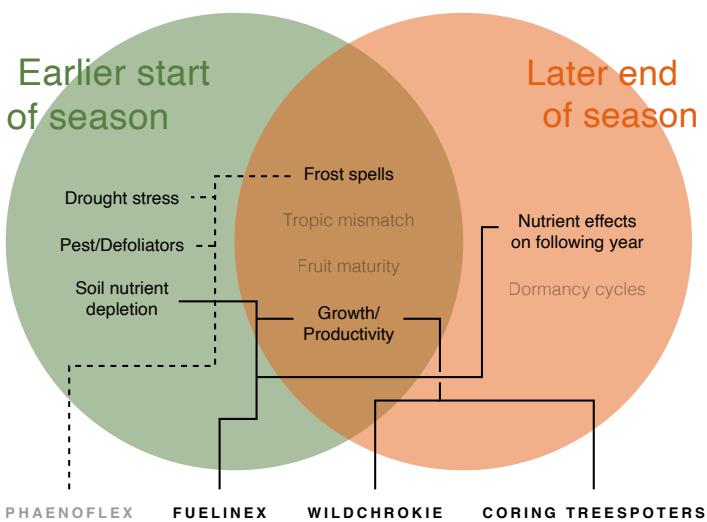


Figure 2: The effects that an earlier start and later end of season can have on trees. In bold are the effects that were studied over the course of this thesis. Phaenoflex (in grey) is a related experimental project, that is not part of this thesis, but one I collaborated on in 2023 and 2024.

198 **Methodology**

199 **Wildchrokic**

200 *Common garden setup (Buonaiuto (in review))*

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

209 *Phenological monitoring*

210 For the years of 2018-2019, we made phenological observations of all individuals in the common garden  
211 twice per week from February to December. In 2020 due to the COVID 19 pandemic, we monitored once  
212 per week from March to November. We describe phenological stages using a modified BBCH scale (?) a  
213 common metrics for quantify woody plant phenological progression. We observed all major vegetative stages  
214 (budburst BBCH 07, leafout BBCH 15, end of leaf expansion BBCH 19, leaf coloration/drop BBCH 97,  
215 reproductive phases flowering BBCH 60-65, fruiting BBCH 72-79 and fruit/cones fully ripe BBCH 89). We  
216 added additional phases for budset and labelled full budset as BBCH 102. In the spring of 2023, we collected  
217 cross-sections for most trees and 1 tree core on a few individuals. Both the cores and cross-sections were left  
218 to dry at ambient temperature for three months.

219 **Coringtreespotters**

220 The Treespotters was a citizen science program that started in 2015 and aimed to train citizen scientist for  
221 accurate and rigorous phenological monitoring. From 2015 to 2024, hundreds of citizen scientists monitored  
222 50 trees of 11 species regularly from budburst in the spring to leaf colouring in the fall using NPN phenophases  
223 (DENNY2014): Leaves (483), Colored leaves (498), Fruits (516), Ripe Fruits (390), Falling leaves(471),  
224 Recent fruit or seed drop (504), Increasing leaf size (467), Breaking leaf buds (371), Flowers or flower buds  
225 (500), Open flowers (501), Pollen release (502). Not all phenophases were recorded for every tree, for every  
226 year, and some trees miss several several years of data.

227 From 20 to 22 April 2025, we collected two 5-mm diameter core, 15-cm length at 1.3 meter above ground  
228 from 50 trees of the 11 species (Table XX) that were previously monitored for phenology, using an increment  
229 borer (Mora Borer, Haglöfs Sweden, Bromma, Stockholm, Sweden). The cores were collected perpendicularly  
230 to the slope and at 180 degrees from each other. We cleaned the increment borer with alcohol (70%  
231 ethanol?) and the inside with a brush before collecting each core. We stored the cores in paper straws that  
232 were previously labelled and punched to help drying. They were stored at ambient temperature for three  
233 months.

234 **Sample processing, imaging and measuring for Wildchrokic and coringTreespotters** We mounted  
235 the cores on wooden mounts, and sanded the cores and cross-sections using progressively fine grit (150, 300,  
236 400, 600, 800, 1000). We scanned the cores and cross-sections at a resolution of \*\*\*dpi using a homemade  
237 great scanner (Tina2026?) We used the digitalized images to measure the tree ring widths with Fiji ImageJ.  
238 Then, we performed visual crossdating using Dpl, we did not performed statistical crossdating because of  
239 the short chronologies that limit the capacity of these analyses.

240 **Statistical analyses**

241

246 **1.6 Fuelinex**

247 **1.7 Species selection and growing conditions**

248 We used seven species of tree sapling for our experiment (Fuelinex). We purchased Paper birch (*Betula*  
249 *papyfera*), Choke Cherry (*Prunus virginiana*), Bur oak (*Quercus macrocarpa*) from Peel's nursery in November  
250 2023 and the trees arrived at Totem Field studios 49.26 °N, -123.25 °W where the other four species were  
251 stored until the spring of 2023. Manitoba maple (*Acer negundo*), Eastern white pine (*Pinus strobus*),  
252 Balsam poplar (*Populus balsamifera*) and Giant sequoia (*Sequoiaadendron giganteum*) are leftover trees that  
253 we purchased in 2022 for 2023 for a previous experiment. We watered them weekly and they remained at  
254 ambient condition for the 2023 growing season. We randomly selected 90 individuals of each species among  
255 them. We propagated B. poplar from 30 cm whips while the trees were still dormant (McCartyEARLY2017).  
256 In May 2024, we repotted all the trees in 2-gallon plastic pots with a medium for perennials consisting of 50 %  
257 peat, 25% crushed pumice and 25% crushed bark ([www.westcreekfarm.com](http://www.westcreekfarm.com)). In February 2025, we repotted  
258 the trees with the same medium in 3-gallon pots. We arranged the trees in three blocs, each containing all 6  
259 treatments and 7 species, with two of these blocs placed under an open-walled and well ventilled polytunnel  
260 greenhouse. All saplings were connected to a drip irrigation system (40 PVC frame from Netafilm 54 with  
261 a Toro controler) to maintain constant irrigation across the season. Using fertilizer premix from XXX, we  
262 fertilized the trees twice during the growing season of 2024 (except for the nutrient boosted trees) and three  
263 times during 2025, just enough to keep the trees alive (Table XXX).

264 **1.8 Tree measurements and biomass**

265 Using red paint, we marked the trees on their trunk at 3 cm from the soil in February 2024. Then we  
266 measured the diameter at the top of that mark using a digital caliper (accuracy  $\pm$  0.01cm), and from that  
267 point to the bottom of the highest apical we measured height with a metal ruler (accuracy  $\pm$  0.1cm). We  
268 measured those two same points in the winter (2024 growing season) and in the fall (2025 growing season)  
269 of 2025. For those two subsequent measurements, if the measured shoot died (because of insects, accidentally  
270 broken it, etc.), we noted the previous measurement as invalid and measured the highest lateral shoot. In  
271 the fall of 2025, when all the individuals from a species have lost all their leaves, we removed the trees from  
272 their pots and gently washed the soil off the roots with a water hose. We dried the trees by placing them in  
273 drying ovens at 70°C for 72 hours and weighted the roots and stem separately (accuracy  $\pm$  0.01 gram).

274 **1.9 Phenology and shoot elongation monitoring**

275 : We started monitoring phenology of all the trees on 11 April 2024, missing the initial leaf phenology  
276 for most individuals, but we monitored subsequent phenophases twice a week until the leaves have fully  
277 elongated. In the late summer and fall, we monitored budset until full bud dormancy. Phenophases are  
278 described in Table 1.

279 Before shoot elongation onset, we marked a reference point with red pain at the base of either the new-year  
280 apical or highest lateral shoot. To facilitate and improve the quality of the shoot elongation measurements,  
281 we attached paper rulers (accuracy  $\pm$  0.1cm) on A. negundo, B. papyfera, P. balsamifera and Q. macrocarpa.  
282 For species not suitable for those paper rulers, we took those same measurements, but with a metal ruler  
283 (accuracy  $\pm$  0.1cm). We measured shoot elongation weekly from the red mark to the base of the bud (for  
284 deciduous species) and at the top of the apical meristem for conifers. For determinate growth species (Table  
285 XXX), after two weeks of little or no change in elongation, we started monitoring them every other week  
286 until September 1st for both growing seasons.

287 Every week, starting on 4 September 2024, we monitored senescence by a visual assessment of the remaining  
288 green leaf cover in percentage and by measuring the chlorophyll content meter with a chlorophyll content  
289 meter. We also recorded the date of loss of green leaf cover and leaf drop.

290 **1.10 Experimental design**

291 Individuals from each species were randomly selected for a full factorial design of Warm/Cool, Spring/Fall  
292 treatments (Suppl Figure XXX) with two addditional treatments to test nutrient effects in the fall (Figure

293 XXX exp design). On 6 March 2024, we placed the Cool Spring individuals in climate chambers to delay  
 294 the start of their growing season, while the Warm Spring replicates remained at ambient conditions. Once  
 295 all Warm Spring individuals have fully leaf out, we removed the Cool Spring replicates from the chambers  
 296 and placed them back at ambient conditions for the whole summer. On 4 September 2024, we placed the  
 297 trees for the Warm Fall treatments in the climate chambers. The temperature was set to fit the mean 30-  
 298 year weekly maximum temperature of the previous month (e.g. 1st week of September set to averaged 1st  
 299 week of August). The Cool Fall treatment trees remained at ambient conditions. For both climate chamber  
 300 treatment, we rotated and watered the trees weekly to minimize the climate chambers effect. We also set  
 301 the photoperiod regime to the corresponding sunrise and sunset of the ongoing week and was ramped until  
 302 it reached full light. To test for nutrient limitation at the end of the season, we added a supplemental dose  
 303 of nutrient (Supple Table XXX) to two treatments (Figure XXX).

### 304 1.11 Leaf count

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

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

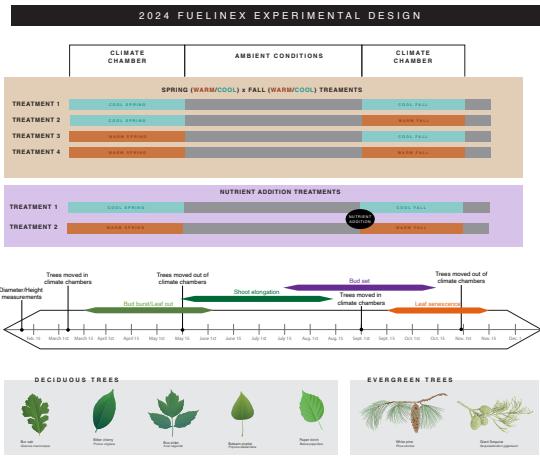


Figure 3

Table 2: 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

Table 3: 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

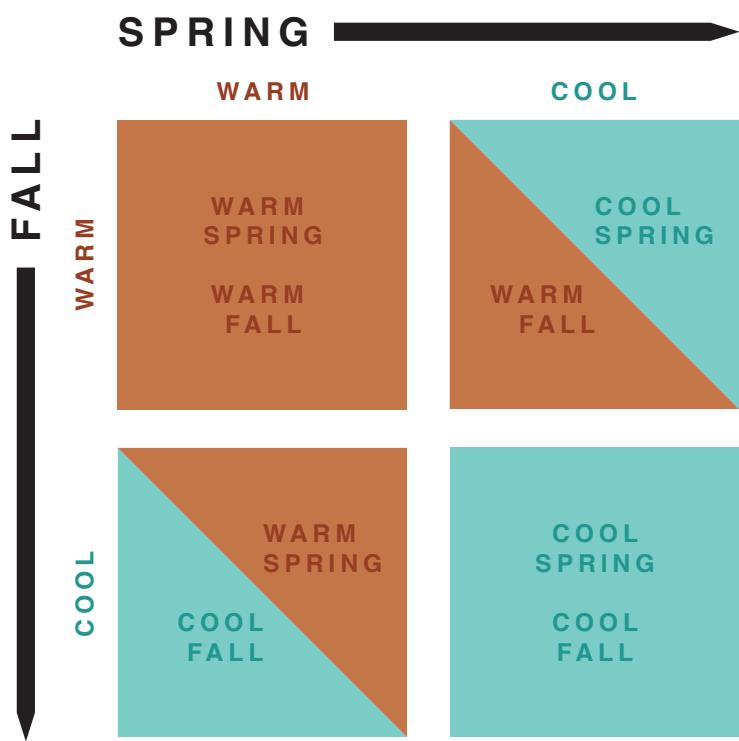


Figure 4

Table 4: 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 5: 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>

## 308 2 Supplemental material

### 309 3.1. Spring frosts

<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 (<-2Celsius) → tissue death = loss of photosynthetic capacity (Polgar & Primack, 2011); Response: second cohort of leaves are more efficient and mitigate carbon sequestration loss (Reinmann <i>et al.</i> , 2023)
<b>Global trend of occurrence</b>	Most vulnerable regions are the ones with no past risk of occurrence (); ↑ in Europe and East Asia, but ↓ North America; Global trend is controversial (Reinmann <i>et al.</i> , 2023)
<b>Consequences (Individual and Ecosystem level consequences)</b>	Loss of vegetative tissue = ↓ photosynthesis = ↓ and remobilization of NSC to repair damaged tissues = ↓ secondary growth (Meyer <i>et al.</i> , 2024); Loss of reproductive tissue (higher flower mortality) (Sgubin <i>et al.</i> , 2018); Costs for orchards and stuff (Reinmann <i>et al.</i> , 2023)
<b>Differences across species/provenance</b>	

311 **3.2. Drought**

	<p><b>Definition:</b></p> <p>"Drought is a prolonged absence or marked deficiency of precipitation that results in water shortage or a period of abnormally dry weather sufficiently prolonged for the lack of precipitation to cause a serious hydrological imbalance (Trenberth <i>et al.</i>, 2014; Intergovernmental panel on climate change, 2007).</p>
	<p><b>Mechanisms</b></p> <ul style="list-style-type: none"> <li>— Hot temperature + low precipitation (aka 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 → increases vegetative growth → increases evapotranspiration → increases 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>
312	<p><b>Global trend of occurrence</b></p> <ul style="list-style-type: none"> <li>— ↑ precipitation anomalies since 1990 (Trenberth <i>et al.</i>, 2014);</li> <li>— Models often exclude PDO/ENSO which limit the capacity to attribute increasing droughts to CC (Trenberth <i>et al.</i>, 2014);</li> <li>— Weak evidence of detection and attribution of changes in meteorological drought since the mid-20th century (Change, 2014);</li> <li>— Using a spacial, model-based perspective, anthropogenic forcing increased the frequency, duration and intensity of SPI-based droughts for North America (Hidalgo <i>et al.</i>, 2009), Europe and the Mediterranean (Spinoni <i>et al.</i>, 2018), (Kurnik <i>et al.</i>, 2011) and E Asia (Chiang <i>et al.</i>, 2021; Marvel <i>et al.</i>, 2019; Spinoni <i>et al.</i>, 2014)</li> </ul>
	<p><b>Consequences (Individual and Ecosystem level consequences)</b></p> <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 (Li <i>et al.</i>, 2023))</li> </ul>
313	<p><b>Differences across species/provenance</b></p>

314 **3.3. Heat waves**

<b>Definition:</b>	Heat wave is a period of excessively hot weather (5 or more consecutive days of prolonged heat in which the daily maximum temperature is higher than the average maximum temperature by 5 °C ), which may be accompanied by high humidity (Marx <i>et al.</i> , 2021).
<b>Mechanisms</b>	<p>↑ atmospheric CO<sub>2</sub> = ↑ temperature → ↑ heat waves... More specifically: A mechanism for the increase occurrence of heat waves is a weakeking of the polar jet stream (important weather factor for middle latitude regions of North America, Europe and Asia) caused by global warming which increases the occurence of stationnary weather, resulting in heavy rain falls or heat waves (Marx <i>et al.</i>, 2021). Extreme heat → growth either through (1) Directly via cell processes disruption or (2) indirectly via effects of rising leaf-to-air vaport deficit (VPD) (Gagne <i>et al.</i>, 2020).</p> <p>Increased temperature leads to reduced photosynthesis which can be attributed to: 1. Damage to photosynthetic machinery 2. Inactivation of RUBISCO 3. Reduction to RuBP regeneration 4. Membrane stability 5. Increased mitochondrial respiration and photorespiration (Hauck <i>et al.</i>, 2025)</p>
315 <b>Global trend of occurrence</b>	Heat waves have increased (Gagne <i>et al.</i> , 2020; Meehl & Tebaldi, 2004; Teskey <i>et al.</i> , 2015) and are expected to increase under future climate change (Dosio <i>et al.</i> , 2018; Change, 2014; Teskey <i>et al.</i> , 2015). Summertime extreme temperatures associated with prolonged heat waves, lasting for several weeks, now impact approximately 10% of land surfaces, up from only 1% in the 1960s. (Teskey <i>et al.</i> , 2015). The more intense and more frequently occurring heat waves cannot be explained solely by natural climate variations and without human-made climate change (Marx <i>et al.</i> , 2021).
<b>Consequences (Individual and Ecosystem level consequences)</b>	- Reduced photosynthesis - Increased mortality - Photosynthetic tissue loss (Gagne <i>et al.</i> , 2020).
<b>Differences across species/provenance</b>	Some species have thermal photosynthetic/respiratory acclimatation while others don't. Growth and survival will change depending on species to thermally acclimate to both photosynthesis and respiration - This is explained by growth strategies of gymnosperms vs angiosperms (which are usually better)

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