

1 Thesis Proposal

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4 **1 Introduction**

5 **1.1 Climate change impacts on tree phenology**

6 Research from the past decades has shown convincing evidence that human activity is increasingly affecting  
7 many worldwide environmental processes (Ceballos *et al.*, 2017; Intergovernmental Panel On Climate  
8 Change (Ipcc), 2023; Laurance, 2007; Parmesan & Yohe, 2003). This can be through land use change and  
9 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  
34 delayed with climate change—though shifts in the autumn have been much smaller than those in the spring  
35 (Gallinat *et al.*, 2015; Jeong & Medvigy, 2014)—and its drivers are also far less understood. These differences  
36 may be caused in part by the lesser attention payed to autumn phenology (Piao *et al.*, 2019) and because  
37 the data is often noisier (Wu *et al.*, 2024). However, some of these differences are likely due to different  
38 drivers of autumn phenology, as these phenophases appear to be driven by shortening photoperiod and  
39 colder temperatures (Cooke *et al.*, 2012; Flynn & Wolkovich, 2018; Körner & Basler, 2010; Delpierre *et al.*,  
40 2016). Given that colder temperatures can lead to senescence, warmer autumns may delay leaf senescence,  
41 possibly by extending the activity of photosynthetic enzymes which causes decreases the degradation rate of  
42

45 chlorophyll (Yan *et al.*, 2021). Additionally, summer droughts could pause the activity schedule of trees and  
46 delay senescence to increase carbon assimilation (Dox *et al.*, 2022). Finally, there could be an antagonistic  
47 effect of warming and brightening—caused by reductions in atmospheric pollution and cloud cover (Sanchez-  
48 Lorenzo *et al.*, 2015)—on leaf senescence (Wu *et al.*, 2021). Brightening accelerates the leaf senescence  
49 processes and reduces the temperature sensitivity during that period, counteracting the expected warming-  
50 induced delays in leaf senescence (Wu *et al.*, 2021).

#### 51 **1.1.2. How these shifts translate into effects on trees/forests is not clear - Pros and cons of 52 early/late start/end of season**

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

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

#### 78 79 **1.1.3. Growing season shifts and consequences on forest ecosystems and services**

80 Spring and fall phenological events are shifting with debatable consequences on tree growth. The sensitivity  
81 of cambial activity to water, temperature and nutrients has the potential to have far-reaching consequences  
82 given the hard-to-predict nature of future climate change, where any of these variables could vary from low  
83 to high amplitude (Almagro *et al.*, 2025; Cabon *et al.*, 2022). This expected asymmetry of future environ-  
84 mental changes makes understanding the internal physiological constraints (via genetic and developmental  
85 control), and external limits (via extreme temperatures or moisture deficit) to growth critical, which I aim  
86 to investigate with experiments and observations.

### 87 **1.2 Experiments and observations to understand the future of growth and sea- 88 son length relationship**

#### 89 **1.2.1. Past phenological trends can help (or not) predict future phenological changes**

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

97 earlier leaf senescence (through summer drought-induced growth cessation).

98  
99 **1.2.2. The assumption that longer seasons lead to increased growth is called into question**  
100 Recent work emphasizing the need to understand the drivers regulating growth across biomes has highlighted  
101 strong species-level variation that may be critical to accurate projections.

102 Phenology varies greatly across species (e.g. closely related species tend to budburst at similar times  
103 under similar conditions) (Wolkovich *et al.*, 2014), but so does the relationship between growth and season  
104 length, which may explain the wide variation of this relationship within communities (Buckley & Kingsolver,  
105 2012). This highlights another weakness of current carbon sequestration models that pool species together,  
106 likely overpassing important nuances in the growth responses that could be explained by species differences.  
107 Excluding species differences in models may mislead future carbon dynamic models (Green & Keenan, 2022;  
108 Cabon *et al.*, 2022; Wolkovich *et al.*, 2025). Different strategies can help understanding how different species  
109 respond to warming and thus improve carbon sequestration projections.

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

122  
123 **1.2.2.2. Ground based observations:** Second, leaf phenology can provide valuable and accessible insights  
124 into the growth temporality of trees that are not suitable for experimental trials. Cambial phenology, which  
125 is a direct measure of wood growth, is very hard data to gather and requires expensive equipment (REF).  
126 In contrast, leaf phenology through ground-based observations are low-cost methods that provide direct  
127 evidence of changing phenophases (Piao *et al.*, 2019). Cambial and leaf phenology are often closely syn-  
128 chronized, therefore, the more accessible leaf phenology data can act as a reliable proxy for the onset and  
129 end of tree growth. In other words, knowing when leaves elongate and colour can guide as to when trees  
130 start and stop growing, which is a fundamental metric to determine the growing season length. Additionally,  
131 unlike other methods, ground observations have the advantage of providing accurate measurements of phe-  
132 nological events for specific sites and species. Recently, the widespread use of smartphones has considerably  
133 simplified the phenological monitoring by citizen scientists which has the potential to vastly increase the  
134 range of studied species and areas. (Dickinson *et al.*, 2012; Hufkens *et al.*, 2019; Piao *et al.*, 2019). While  
135 there are drawbacks to observations by citizen science programs (e.g. non-standard protocols, highly uneven  
136 spatiotemporal distribution of these observations), they have a great potential to diversify the phenology  
137 data.

138  
139 **1.2.3. Goals of my thesis**  
140 I aim to understand how different tree species, at different lifespan stages, vary in their growth responses  
141 to different season length. To achieve this, I worked across different methods. First, for my large-scale  
142 experiment named Fuelinex, I artificially controlled the growing season length for seven species of tree  
143 saplings (2-3 years old). Under Wildchrokie, I leveraged leaf phenology data from a common garden project  
144 of four species of juvenile trees (5-8 years old). Then, with coringTreespotters I used the phenology data  
145 collected by citizen scientists on eleven species of fully mature trees (>30 years old). Answering the growth  
146 patterns of the trees across these three projects requires specifying the definitions of growth and the growing  
147 season.

148 **1.3 Complexity of measuring growth and defining growing season length**

149 *1.3.1.1. What is a growing season?*

150

151 The definition of the growing season itself is not a well-defined concept and an array of definitions are  
152 used differently across studies. Recently, Körner *et al.* (2023) proposed four definitions addressing this issue:  
153 (1) true growing season, based on measurable growth; (2) phenological season, based on visible phenological  
154 markers; (3) the productive season, based on primary production and (4) meteorological season, based on  
155 environmental conditions.

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

165 *1.3.1.2. What is growth?*

166 Wood formation (xylogenesis) consists of allocating carbon for long-term storage in woody plants. Xylogenesis  
167 starts with cambial activation and cell production which produces xylem and phloem cells (Etzold *et al.*,  
168 2022; Silvestro *et al.*, 2025). The rate and duration of these phases lead to irreversible radial growth increments  
169 usually represented through tree rings. In these, secondary xylem cells account disproportionately to  
170 the number of cells produced because they divide more than phloem cells (Plomion *et al.*, 2001; Rathgeber  
171 *et al.*, 2016).

172

173 **1.3.2. Traditional diameter measurements miss the resolution of annual growth increment**

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

180 **1.3.3. Dendroecology to analyses growth responses to changing growing season length**

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

187

188 **1.4 Objectives**

189 The objectives for my experiment (Fuelinex) are to assess tree species' potential to prolong or stretch their  
190 activity schedule by artificially manipulating growing season length and analyze how this translates (or not)  
191 into growth, during the current year (2024) and in the following year (2025). I will also conduct a secondary  
192 experiment to examine whether trees can absorb nutrients late in the season and if that translates into growth  
193 during the following season. For the observational data projects (Wildchrokie and coringTreespotters), I will  
194 investigate how the timing of phenological events affects growth across years for juvenile and mature trees,  
195 using observational phenology data and tree ring.

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

<sup>198</sup> **1.5 Research questions**

<sup>199</sup> Fuelinex: How do extended growing seasons affect tree growth across different species, both immediately (in  
<sup>200</sup> the same year as the extended season) and in subsequent years? WildSpotters: How does phenology regulate  
<sup>201</sup> tree growth in urban ecosystems?

<sup>202</sup>

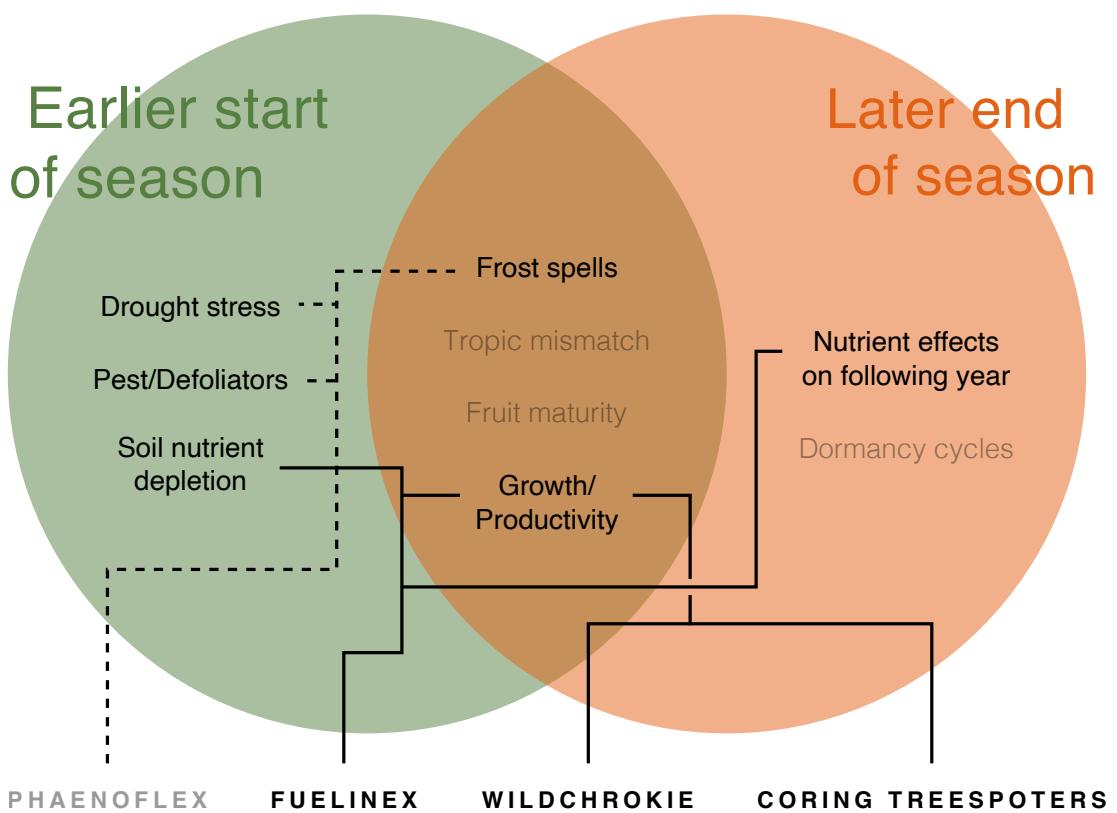


Figure 1: The effects that an earlier start and later end of season can have on trees. In bold are the effects that were studied over the course of this thesis. Phaenoflex (in grey) is a related experimental project, that is not part of this thesis, but one I collaborated on in XX years.

203 **2 Methodology**

204 **2.1 Wildchrokic**

205 **2.1. Studies locations**

206 **Common garden** \*\*\* what follows are the methods from the wildhell repo In 2014-2015, we collected seeds  
207 from four field sites in northeastern North America spanning approximately a 3.5° latitudinal gradient.  
208 The four field sites included Harvard Forest (42.55 °N, 72.20°W), the White Mountains (44.11 °N, 71.40  
209 °W), Second College Grant, (44.79 °N, 71.15 °W), and St. Hippolyte, QC, CAN (45.98 °N, 74.01 °W).  
210 We transported all seeds back to the Weld Hill Research Building at the Arnold Arboretum in Boston  
211 Massachusetts (42.30 °N, 71.13 °W) where we germinated seeds following standard germination protocols,  
212 and grew them to seedling stages in the research greenhouse. In the spring of 2017 we out-planted seedlings  
213 to establish the garden. Plots were regularly weeded and watered throughout the duration of the study and  
214 were pruned in the fall of 2020.

215 In the spring of 2023, we collected cross-sections for most trees and 1 tree core on a few individuals. Both  
216 the cores and cross-sections were left to dry at ambient temperature for three months.

217 *Phenological monitoring* For the years of 2018-2019, we made phenological observations of all individuals  
218 in the common garden twice per week from February to December. In 2020 due to the COVID 19 pandemic,  
219 we monitored once per week from March to November. We describe phenological stages using a modified  
220 BBCH scale (?) a common metrics for quantify woody plant phenological progression. We observed all major  
221 vegetative stages (budburst BBCH 07, leafout BBCH 15, end of leaf expansion BBCH 19, leaf coloration/drop  
222 BBCH 97, reproductive phases flowering BBCH 60-65, fruiting BBCH 72-79 and fruit/cones fully ripe BBCH  
223 89). We added additional phases for budset and labelled full budset as BBCH 102.

224 **Coringtreespotters** The Treespotters is a citizen science program that started in 2015 and aimed to  
225 train citizen scientist for accurate and rigorous phenological monitoring. From 2015 to 2024, hundreds of  
226 citizen scientists monitored 50 trees of 11 species regularly from budburst in the spring to leaf colouring in  
227 the fall using NPN phenophases (DENNY2014). Not all phenophases were recorded for every tree, for every  
228 year, and some trees miss several several years of data.

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

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

242 **Statistical analyses**

243 **2.2 Fuelinex**

244 **2.3 Species selection**

245 We used seven species of tree sapling for our experiment (Fuelinex). Paper birch (*Betula papyfera*), Choke  
246 Cherry (*Prunus virginiana*), Bur oak (*Quercus macrocarpa*) were purchased from Peel's nursery in November  
247 2023 and arrived at Totem Field studios 49.26 °N, -123.25 °W where the other four species were stored  
248 until the spring of 2023. Manitoba maple (*Acer negundo*), Eastern white pine (*Pinus strobus*), Balsam  
249 poplar (*Populus balsamifera*) and Giant sequoia (*Sequoiadendron giganteum*) were purchased in 2022 for  
250 2023 Phaenoflex's experiment but were watered weekly and remained at ambiant condition for the 2023  
251 growing season. We randomly selected 90 individuals among them.

Because Pobas were too large, that they are fast-growing and that Fuelinex is a two-year experiment, we took cuttings from Poba and replanted them in soil with the following methodology. The cuttings were stored in climate chambers with the corresponding temperature (see Hobo loggers) from February 13, 2024 to Feb 20, 2024. The tree cuttings were planted at that time. 30 cm long shoot tip cuttings of balsam poplar were soaked at the cut wound for 15 minutes in a solution of 20 mL indole-butyric acid 0.4% (Wilson Liquid root stimulator) diluted in 2 litres of warm tap water. (0.004% concentration). 180 1-gallon pots were filled up to 1 inch from the lip with pre-moistened peat-based potting mix containing large pumice chunks. Soil was pressed firmly to compact. Cuttings were placed into the soil at the depth such that pre-drawn paint lines could still be visible just above the soil surface.

## 2.4 Tree measurements

The following measurements were performed from Feb 7, 2024 to Feb 11, 2024. Using red paint, we marked the trees on their trunk at 3 cm from the soil. Then we measured the diameter at the top of that mark using a digital caliper and from that point to the bottom of the highest apical we measured height with a metal ruler (precision of 0.1 mm). We measured those two same points in the winter (2024 growing season) and in the fall (2025 growing season) of 2025. For those two subsequent measurements, if the measured shoot died, we noted the previous measurement as invalid (because of insects, accidentally broken it, etc.) and measured the highest lateral shoot.

## 2.5 Shoot elongation

: To facilitate and improve the quality of the shoot elongation monitoring, we attached paper rulers on the following species A. negundo, B. papyfera, P. balsamifera and Q. macrocarpa. We used A3 RiteIntheRain paper so they remain in good condition under the rain. We also taped the end of each ruler with packaging tape for 2 reasons: 1. Increase the the fusion of the tape with the ruler and 2. Increase the durability of the fixation to the tree. We used Band Aid medical tape to fix the paper rulers to the trees in order for the trunk to be able to breath.

Prior to the installation, using red pain, we marked where the reference point for the measurement. This was the bottom of the new-year apical shoot. For species on which we couldn't install the paper rulers, we took those same measurements, but with a metal ruler.

## 2.6 Fertilizer

Using fertilizer premix from UBC's garden, we fertilized the trees twice during the growing season of 2024 and three times during 2025, just enough to keep the trees alive.

**2025 :** On Friday 11 April 2025, 125mL of undiluted liquid fertilizer (same as 2024) was added to all trees, excluding the nitro boost treatment replicates. The latter didn't get any nutrients in spring and will get some only later on in the summer. Since we dropped the nitro treatments for the segi, all of these replicates got fertilizer. See note

## 2.7 Hobo loggers

Hobo loggers (Temp/humidity) were set up in the climate chambers at the beginning of the Cool Spring treatments. They were then transferred to Totem Field at different locations and hidden behind a white sheet of paper to avoid the sun from hitting them directly.

On June 7, 2024, Hobo loggers (Temp/light) were placed in 3 different blocks at Totem Field. They were placed at the top of PVC pipes at a height of 1m from the ground. They were placed in a position where the foliage covers of the trees would not shade them. I set 6/block. This was performed after I notice that there will be a big light difference. The plants that are the farthest from the greenhouse door receive far less light than the one closest to the door. They were configured on Sunday June 9, 2024. I also installed 4 loggers on the greenhouse roof in case the ones positioned at 1m above the soil don't record the light properly.

296 **2.8 Spring and Fall treatments**

297 The Cool Spring treatment consisted of placing the CS replicates in climate chambers to delay the start of  
298 their growing season on March 6 2024. The WS replicates remained at Totem Field studios

299 The Warm Fall treatment consisted of placing WS/WF, CS/WF and WSWF\_nitro treatments in the  
300 climate chambers on 4 September 2024. The photoperiod was set every week on Wednesday to fit the local  
301 sunrise and sunset and was ramped until it reached full light. The temperature was set to fit the mean  
302 30 years daily maximum temperature of one prior month. E.g. the the temperature for the first week of  
303 September was set to the temperature regime of the first week of August. The CF treatments remained at  
304 Totem Field Studios.

305 For both climate chamber treatment, the trees were rotated and watered weekly to minimize the effects  
306 the climate chambers could have on the trees.

307 **2.9 Senescence monitoring**

308 Every week, starting on September \*\*\*, senescence was monitored by two methods. The first being a visual  
309 assessment of the remaining green leaf cover. We used a systemic aproach to estimate what percentage of  
310 green leaf cover was remaining by comparing to what would be 100% of cover.. From September \*\*\*\* to  
311 September 25, we used a chlorophyll content meter \*\*\*. On October 2, because of device failure, we switched  
312 to SPAD-502DL Plus (Konica Minolta) from Loren Rieseberg's lab. To calibrate the two instruments to val-  
313 ues that are comparable, we used\*\*\*\*. check: <https://nph.onlinelibrary.wiley.com/doi/full/10.1046/j.0028-646X.2001.00289.x>

315 **2.10 Shoot elongation measurements**

316 In 2024 and 2025, shoot elongation measurements were conducted using two distinct methods. But for both  
317 methods, the following were conducted: in 2024, we selected the shoot coming off the apical meristem when  
318 possible. If the bud died or if the shoot snapped off, we selected the closest lateral shoot. In the case of Prvi  
319 on which there are no obvious apical shoot (sometimes there will be 2 branches of equal height) we selected  
320 the highest one and if that one died, we selected the other. Then we went on the lateral shoot if both died.  
321 Then using rain paint, we marked the base of the chosen bud.

322 In 2025, we preferably chose the continuous shoot that was measured the previous year. If that shoot died,  
323 we chose another shoot acording to the previous criterias.

324 Two methods:

325 1. Paper rulers using rite in the rain paper and printed a 38cm ruler. For the species on which there was  
326 trunk/branch space on which we could safely install a paper ruler, we installed one. The species were: Acne,  
327 Bepa, Poba, Quma. Since the ruler was positioned at the bottom of the red mark, we didn't have to adjust  
328 it every time we measured shoot elongation. Then the shoot elongation was measured at the botttom of the  
329 apical bud.

330 2. Metal rulers: using a metal scientific ruler, we measured the shoot from the bottom of the red mark to  
331 the bottom of the apical bud for deciduous species. We measured until the top of the apical meristem for  
332 Pist.

333 Shoot elongation was measured weekly for all species. For determinate growth species, after two weeks of  
334 little or no change in elongation, we started monitoring them every second week. For indeterminate growth  
335 species, they kept on being monitored every week.

336 **2.11 Leaf count**

337 In order to determine whether nutrient addition treatments in the fall affected leaf primordia formation,  
338 we counted the leaves on 27 May for the determinate growth species only i.e. Acne, Prvi and Quma. We  
339 counted the leaves only for the shoot coming out of the apical meristem. We always counted all the leaves  
340 on the current-year shoot measured for shoot elongation measurements.

341 **2.12 Biomass collection**

342 In the fall of 2025, when all the individuals from a species have lost all their leaves, we proceeded to remove  
343 the trees from their pots, remove the dirt by shaking them first and washing off the dirt off the roots gently  
344 with regular water gun. Then, we moved the trees, 1 bloc at a time in the drying ovens where they were  
345 left to dry for 72 hours at 70C. Not in paper bags. Then below and above ground biomass were separated  
346 by cutting the tree at 1cm above the highest root. We weighted biomass at a precision of 0.01gr

347 **3 Supplemental material**

348 **3.1 Wildchrokie**

- 349 1. Common garden from 2015 to 2023
- 350 2. Four species within the Betulacea family (Table 2)
- 351 3. Data: phenology, height, tree rings
- 352 4. Analysis: Hierarchical model to understand how tree ring width relates to GDD

353 **3.2 Treespotters**

- 354 1. Citizen science project from 2015 to today (Table 3)
- 355 2. Tree coring
- 356 3. Data: phenology, tree rings
- 357 4. Analysis: Hierarchical model to understand how tree ring width relates to GDD

358 **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>	

Table 1: 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		89
Giant Sequoia ( <i>Sequoiadendron giganteum</i> )	Slow-growth, long life		54

Table 2: 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 3: 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

### 3.2. Drought

<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 (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>
<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>— 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>
<b>Consequences (Individual and Ecosystem level consequences)</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 (Li <i>et al.</i>, 2023))</li> </ul>
<b>Differences across species/provenance</b>	

### 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>
364 <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)

## 365 References

- 366 Almagro, D., Martin-Benito, D., Rossi, S., Conde, M., Fernández-de-Uña, L. & Gea-Izquierdo, G. (2025).  
367 Long-Term Cambial Phenology Reveals Diverging Growth Responses of Two Tree Species in a Mixed  
368 Forest Under Climate Change. *Global Change Biology*, 31, e70503.
- 369 Augspurger, C.K. & Bartlett, E.A. (2003). Differences in leaf phenology between juvenile and adult trees in  
370 a temperate deciduous forest. *Tree Physiology*, 23, 517–525.
- 371 Bergeron, Y., Gauthier, S., Flannigan, M. & Kafka, V. (2004). Fire regimes at the transition between  
372 mixedwood and coniferous boreal forest in northwestern Quebec. *Ecology*, 85, 1916–1932.
- 373 Buckley, L.B. & Kingsolver, J.G. (2012). Functional and Phylogenetic Approaches to Forecasting Species'  
374 Responses to Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, 43, 205–226.
- 375 Büntgen, U., Wacker, L., Galván, J.D., Arnold, S., Arseneault, D., Baillie, M., Beer, J., Bernabei, M.,  
376 Bleicher, N., Boswijk, G., Bräuning, A., Carrer, M., Ljungqvist, F.C., Cherubini, P., Christl, M., Christie,  
377 D.A., Clark, P.W., Cook, E.R., Esper, J., Fowler, A.M., Gennaretti, F., Grießinger, J., Grissino-Mayer,  
378 H., Grudd, H., Gunnarson, B.E., Hantemirov, R., Herzig, F., Hessl, A., Heussner, K.U., Jull, A.J.T.,  
379 Kukarskikh, V., Kirdyanov, A., Krusic, P.J., Kyncl, T., Lara, A., LeQuesne, C., Linderholm, H.W., Loader,  
380 N.J., Luckman, B., Miyake, F., Myglan, V.S., Nicolussi, K., Oppenheimer, C., Palmer, J., Panyushkina, I.,  
381 Pederson, N., Rybníček, M., Schweingruber, F.H., Seim, A., Sigl, M., Churakova, O., Speer, J.H., Synal,  
382 H.A., Tegel, W., Treydte, K., Villalba, R., Wiles, G., Wilson, R., Winship, L.J., Wunder, J., Yang, B. &

- 383 Young, G.H.F. (2018). Tree rings reveal globally coherent signature of cosmogenic radiocarbon events in  
384 774 and 993 CE. *Nature Communications*, 9, 3605.
- 385 Cabon, A., Fernández-de-Uña, L., Gea-Izquierdo, G., Meinzer, F.C., Woodruff, D.R., Martínez-Vilalta, J. &  
386 De Cáceres, M. (2020). Water potential control of turgor-driven tracheid enlargement in Scots pine at its  
387 xeric distribution edge. *New Phytologist*, 225, 209–221.
- 388 Cabon, A., Kannenberg, S.A., Arain, A., Babst, F., Baldocchi, D., Belmecheri, S., Delpierre, N., Guerrieri,  
389 R., Maxwell, J.T., McKenzie, S., Meinzer, F.C., Moore, D.J.P., Pappas, C., Rocha, A.V., Szejner, P.,  
390 Ueyama, M., Ulrich, D., Vincke, C., Voelker, S.L., Wei, J., Woodruff, D. & Anderegg, W.R.L. (2022).  
391 Cross-biome synthesis of source versus sink limits to tree growth. *Science*, 376, 758–761.
- 392 Campbell, L.M., Hagerman, S. & Gray, N.J. (2014). Producing Targets for Conservation: Science and Politics  
393 at the Tenth Conference of the Parties to the Convention on Biological Diversity. *Global Environmental  
394 Politics*, 14, 41–63.
- 395 Ceballos, G., Ehrlich, P.R. & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction  
396 signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*,  
397 114.
- 398 Change, I.P.O.C. (2014). Detection and Attribution of Climate Change: from Global to Regional. In:  
399 *Climate Change 2013 – The Physical Science Basis*. Cambridge University Press, pp. 867–952. 1st edn.
- 400 Chiang, F., Mazdiyasni, O. & AghaKouchak, A. (2021). Evidence of anthropogenic impacts on global drought  
401 frequency, duration, and intensity. *Nature Communications*, 12, 2754.
- 402 Chmielewski, F.M. & Rötzer, T. (2001). Response of tree phenology to climate change across Europe.  
403 *Agricultural and Forest Meteorology*, 108, 101–112.
- 404 Choat, B., Brodribb, T.J., Brodersen, C.R., Duursma, R.A., López, R. & Medlyn, B.E. (2018). Triggers of  
405 tree mortality under drought. *Nature*, 558, 531–539.
- 406 Chuine, I. (2010). Why does phenology drive species distribution? *Philosophical Transactions of the Royal  
407 Society B: Biological Sciences*, 365, 3149–3160.
- 408 Cleland, E., Chuine, I., Menzel, A., Mooney, H. & Schwartz, M. (2007). Shifting plant phenology in response  
409 to global change. *Trends in Ecology & Evolution*, 22, 357–365.
- 410 Cooke, J.E.K., Eriksson, M.E. & Junntila, O. (2012). The dynamic nature of bud dormancy in trees:  
411 environmental control and molecular mechanisms. *Plant, Cell & Environment*, 35, 1707–1728.
- 412 Delpierre, N., Vitasse, Y., Chuine, I., Guillemot, J., Bazot, S., Rutishauser, T. & Rathgeber, C.B.K. (2016).  
413 Temperate and boreal forest tree phenology: from organ-scale processes to terrestrial ecosystem models.  
414 *Annals of Forest Science*, 73, 5–25.
- 415 Dickinson, J.L., Shirk, J., Bonter, D., Bonney, R., Crain, R.L., Martin, J., Phillips, T. & Purcell, K. (2012).  
416 The current state of citizen science as a tool for ecological research and public engagement. *Frontiers in  
417 Ecology and the Environment*, 10, 291–297.
- 418 Dosio, A., Mentaschi, L., Fischer, E.M. & Wyser, K. (2018). Extreme heat waves under 1.5 °C and 2 °C  
419 global warming. *Environmental Research Letters*, 13, 054006.
- 420 Dow, C., Kim, A.Y., D'Orangeville, L., Gonzalez-Akre, E.B., Helcoski, R., Herrmann, V., Harley, G.L.,  
421 Maxwell, J.T., McGregor, I.R., McShea, W.J., McMahon, S.M., Pederson, N., Tepley, A.J. & Anderson-  
422 Teixeira, K.J. (2022). Warm springs alter timing but not total growth of temperate deciduous trees.  
423 *Nature*, 608, 552–557.
- 424 Dox, I., Skrøppa, T., Decoster, M., Prislan, P., Gascó, A., Gričar, J., Lange, H. & Campioli, M. (2022).  
425 Severe drought can delay autumn senescence of silver birch in the current year but advance it in the next  
426 year. *Agricultural and Forest Meteorology*, 316, 108879.

- 427 Driscoll, D.A., Bland, L.M., Bryan, B.A., Newsome, T.M., Nicholson, E., Ritchie, E.G. & Doherty, T.S.  
428 (2018). A biodiversity-crisis hierarchy to evaluate and refine conservation indicators. *Nature Ecology &*  
429 *Evolution*, 2, 775–781.
- 430 Duputié, A., Rutschmann, A., Ronce, O. & Chuine, I. (2015). Phenological plasticity will not help all species  
431 adapt to climate change. *Global Change Biology*, 21, 3062–3073.
- 432 Ettinger, A.K., Chamberlain, C.J., Morales-Castilla, I., Buonaiuto, D.M., Flynn, D.F.B., Savas, T., Samaha,  
433 J.A. & Wolkovich, E.M. (2020). Winter temperatures predominate in spring phenological responses to  
434 warming. *Nature Climate Change*, 10, 1137–1142.
- 435 Etzold, S., Sterck, F., Bose, A.K., Braun, S., Buchmann, N., Eugster, W., Gessler, A., Kahmen, A., Peters,  
436 R.L., Vitasse, Y., Walther, L., Ziemińska, K. & Zweifel, R. (2022). Number of growth days and not length  
437 of the growth period determines radial stem growth of temperate trees. *Ecology Letters*, 25, 427–439.
- 438 Flynn, D.F.B. & Wolkovich, E.M. (2018). Temperature and photoperiod drive spring phenology across all  
439 species in a temperate forest community. *New Phytologist*, 219, 1353–1362.
- 440 Friend, A.D., Eckes-Shephard, A.H., Fonti, P., Rademacher, T.T., Rathgeber, C.B.K., Richardson, A.D. &  
441 Turton, R.H. (2019). On the need to consider wood formation processes in global vegetation models and  
442 a suggested approach. *Annals of Forest Science*, 76, 49.
- 443 Fritts, H. & Swetnam, T. (1989). Dendroecology: A Tool for Evaluating Variations in Past and Present  
444 Forest Environments. In: *Advances in Ecological Research*. Elsevier, vol. 19, pp. 111–188.
- 445 Fu, Y.H., Campioli, M., Deckmyn, G. & Janssens, I.A. (2013). Sensitivity of leaf unfolding to experimental  
446 warming in three temperate tree species. *Agricultural and Forest Meteorology*, 181, 125–132.
- 447 Fu, Y.H., Piao, S., Op De Beeck, M., Cong, N., Zhao, H., Zhang, Y., Menzel, A. & Janssens, I.A. (2014).  
448 Recent spring phenology shifts in western Central Europe based on multiscale observations. *Global Ecology  
449 and Biogeography*, 23, 1255–1263.
- 450 Fu, Y.H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., Ciais, P., Huang, M., Menzel, A., Peñuelas,  
451 J., Song, Y., Vitasse, Y., Zeng, Z. & Janssens, I.A. (2015). Declining global warming effects on the  
452 phenology of spring leaf unfolding. *Nature*, 526, 104–107. Publisher: Nature Publishing Group.
- 453 Gagne, M.A., Smith, D.D. & McCulloh, K.A. (2020). Limited physiological acclimation to recurrent heat-  
454 waves in two boreal tree species. *Tree Physiology*, 40, 1680–1696.
- 455 Gallinat, A.S., Primack, R.B. & Wagner, D.L. (2015). Autumn, the neglected season in climate change  
456 research. *Trends in Ecology & Evolution*, 30, 169–176.
- 457 Gazol, A., Camarero, J.J., Vicente-Serrano, S.M., Sánchez-Salguero, R., Gutiérrez, E., De Luis, M.,  
458 Sangüesa-Barreda, G., Novak, K., Rozas, V., Tíscar, P.A., Linares, J.C., Martín-Hernández, N., Martínez  
459 Del Castillo, E., Ribas, M., García-González, I., Silla, F., Camisón, A., Génova, M., Olano, J.M., Longares,  
460 L.A., Hevia, A., Tomás-Burguera, M. & Galván, J.D. (2018). Forest resilience to drought varies across  
461 biomes. *Global Change Biology*, 24, 2143–2158.
- 462 Gessler, A. & Zweifel, R. (2024). Beyond source and sink control – toward an integrated approach to  
463 understand the carbon balance in plants. *New Phytologist*, 242, 858–869.
- 464 Green, J.K. & Keenan, T.F. (2022). The limits of forest carbon sequestration. *Science*, 376, 692–693.
- 465 Hauck, M., Schneider, T., Bahlinger, S., Fischbach, J., Oswald, G., Csapek, G. & Dulamsuren, C. (2025).  
466 Heat tolerance of temperate tree species from Central Europe. *Forest Ecology and Management*, 580,  
467 122541.
- 468 Hidalgo, H.G., Das, T., Dettinger, M.D., Cayan, D.R., Pierce, D.W., Barnett, T.P., Bala, G., Mirin, A.,  
469 Wood, A.W., Bonfils, C., Santer, B.D. & Nozawa, T. (2009). Detection and Attribution of Streamflow  
470 Timing Changes to Climate Change in the Western United States. *Journal of Climate*, 22, 3838–3855.

- 471 Huey, R.B., Kearney, M.R., Krockenberger, A., Holtum, J.A.M., Jess, M. & Williams, S.E. (2012). Predicting  
472 organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philosophical  
473 Transactions of the Royal Society B: Biological Sciences*, 367, 1665–1679.
- 474 Hufkens, K., Melaas, E.K., Mann, M.L., Foster, T., Ceballos, F., Robles, M. & Kramer, B. (2019). Monitoring  
475 crop phenology using a smartphone based near-surface remote sensing approach. *Agricultural and Forest  
476 Meteorology*, 265, 327–337.
- 477 Intergouvernemental panel on climate change (ed.) (2007). *Climate change 2007: the physical science basis*.  
478 Cambridge university press, Cambridge.
- 479 Intergovernmental Panel On Climate Change (Ipcc) (2023). *Climate Change 2022 – Impacts, Adaptation and  
480 Vulnerability: Working Group II Contribution to the Sixth Assessment Report of the Intergovernmental  
481 Panel on Climate Change*. 1st edn. Cambridge University Press.
- 482 Jeong, S. & Medvigy, D. (2014). Macroscale prediction of autumn leaf coloration throughout the continental  
483 United States. *Global Ecology and Biogeography*, 23, 1245–1254.
- 484 Keenan, T.F., Gray, J., Friedl, M.A., Toomey, M., Bohrer, G., Hollinger, D.Y., Munger, J.W., O'Keefe, J.,  
485 Schmid, H.P., Wing, I.S., Yang, B. & Richardson, A.D. (2014). Net carbon uptake has increased through  
486 warming-induced changes in temperate forest phenology. *Nature Climate Change*, 4, 598–604.
- 487 Kurnik, B., Barbosa, P. & Vogt, J. (2011). Testing two different precipitation datasets to compute the  
488 standardized precipitation index over the Horn of Africa. *International Journal of Remote Sensing*, 32,  
489 5947–5964.
- 490 Körner, C. & Basler, D. (2010). Phenology Under Global Warming. *Science*, 327, 1461–1462. Publisher:  
491 American Association for the Advancement of Science.
- 492 Körner, C., Möhl, P. & Hiltbrunner, E. (2023). Four ways to define the growing season. *Ecology Letters*, 26,  
493 1277–1292.
- 494 Laube, J., Sparks, T.H., Estrella, N., Höfler, J., Ankerst, D.P. & Menzel, A. (2014). Chilling outweighs  
495 photoperiod in preventing precocious spring development. *Global Change Biology*, 20, 170–182.
- 496 Laurance, W.F. (2007). Have we overstated the tropical biodiversity crisis? *Trends in Ecology & Evolution*,  
497 22, 65–70.
- 498 Li, Y., Zhang, W., Schwalm, C.R., Gentine, P., Smith, W.K., Ciais, P., Kimball, J.S., Gazol, A., Kannenberg,  
499 S.A., Chen, A., Piao, S., Liu, H., Chen, D. & Wu, X. (2023). Widespread spring phenology effects on  
500 drought recovery of Northern Hemisphere ecosystems. *Nature Climate Change*, 13, 182–188.
- 501 Lieth, H., Jacobs, J., Lange, O.L., Olson, J.S. & Wieser, W. (eds.) (1974). *Phenology and Seasonality  
502 Modeling*. vol. 8 of *Ecological Studies*. Springer Berlin Heidelberg, Berlin, Heidelberg.
- 503 Lynas, M., Houlton, B.Z. & Perry, S. (2021). Greater than 99% consensus on human caused climate change  
504 in the peer-reviewed scientific literature. *Environmental Research Letters*, 16, 114005.
- 505 Manzanedo, R.D. & Pederson, N. (2019). Towards a More Ecological Dendroecology. *Tree-Ring Research*,  
506 75, 152.
- 507 Marvel, K., Cook, B.I., Bonfils, C.J.W., Durack, P.J., Smerdon, J.E. & Williams, A.P. (2019). Twentieth-  
508 century hydroclimate changes consistent with human influence. *Nature*, 569, 59–65.
- 509 Marx, W., Haunschmid, R. & Bornmann, L. (2021). Heat waves: a hot topic in climate change research.  
510 *Theoretical and Applied Climatology*, 146, 781–800.
- 511 Meehl, G.A. & Tebaldi, C. (2004). More Intense, More Frequent, and Longer Lasting Heat Waves in the  
512 21st Century. *Science*, 305, 994–997.

- 513 Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská,  
514 O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Defila, C., Donnelly, A., Filella, Y., Jatczak,  
515 K., Mestre, A., Peñuelas, J., Pirinen, P., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wiel-  
516 golaski, F., Zach, S. & Zust, A. (2006). European phenological response to climate change matches the  
517 warming pattern. *Global Change Biology*, 12, 1969–1976.
- 518 Meyer, B.F., Buras, A., Gregor, K., Layritz, L.S., Principe, A., Kreyling, J., Rammig, A. & Zang, C.S.  
519 (2024). Frost matters: incorporating late-spring frost into a dynamic vegetation model regulates regional  
520 productivity dynamics in European beech forests. *Biogeosciences*, 21, 1355–1370.
- 521 Meyer, H.A. (1940). A Mathematical Expression for Height Curves. *Journal of Forestry*, 38, 415–420.
- 522 Morin, X., Roy, J., Sonié, L. & Chuine, I. (2010). Changes in leaf phenology of three European oak species  
523 in response to experimental climate change. *New Phytologist*, 186, 900–910.
- 524 Muller, B., Pantin, F., Génard, M., Turc, O., Freixes, S., Piques, M. & Gibon, Y. (2011). Water deficits  
525 uncouple growth from photosynthesis, increase C content, and modify the relationships between C and  
526 growth in sink organs. *Journal of Experimental Botany*, 62, 1715–1729.
- 527 Oreskes, N. (2004). The Scientific Consensus on Climate Change. *Science*, 306, 1686–1686.
- 528 Parent, B., Turc, O., Gibon, Y., Stitt, M. & Tardieu, F. (2010). Modelling temperature-compensated  
529 physiological rates, based on the co-ordination of responses to temperature of developmental processes.  
530 *Journal of Experimental Botany*, 61, 2057–2069.
- 531 Parmesan, C., Rytholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila,  
532 L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A. & Warren, M. (1999). Poleward shifts in  
533 geographical ranges of butterfly species associated with regional warming. *Nature*, 399, 579–583.
- 534 Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural  
535 systems. *Nature*, 421, 37–42.
- 536 Peters, R.L., Steppe, K., Cuny, H.E., De Pauw, D.J., Frank, D.C., Schaub, M., Rathgeber, C.B., Cabon, A.  
537 & Fonti, P. (2021). Turgor – a limiting factor for radial growth in mature conifers along an elevational  
538 gradient. *New Phytologist*, 229, 213–229.
- 539 Peñuelas, J. & Filella, I. (2001). Responses to a Warming World. *Science*, 294, 793–795. Publisher: American  
540 Association for the Advancement of Science.
- 541 Piao, S., Liu, Q., Chen, A., Janssens, I.A., Fu, Y., Dai, J., Liu, L., Lian, X., Shen, M. & Zhu, X. (2019).  
542 Plant phenology and global climate change: Current progresses and challenges. *Global Change Biology*,  
543 25, 1922–1940.
- 544 Plomion, C., Leprovost, G. & Stokes, A. (2001). Wood Formation in Trees. *Plant Physiology*, 127, 1513–1523.
- 545 Polgar, C.A. & Primack, R.B. (2011). Leaf-out phenology of temperate woody plants: from trees to ecosys-  
546 tems. *New Phytologist*, 191, 926–941.
- 547 Primack, R.B., Laube, J., Gallatin, A.S. & Menzel, A. (2015). From observations to experiments in phenology  
548 research: investigating climate change impacts on trees and shrubs using dormant twigs. *Annals of Botany*,  
549 116, 889–897.
- 550 Rathgeber, C.B.K., Cuny, H.E. & Fonti, P. (2016). Biological Basis of Tree-Ring Formation: A Crash Course.  
551 *Frontiers in Plant Science*, 7.
- 552 Reinmann, A.B., Bowers, J.T., Kaur, P. & Kohler, C. (2023). Compensatory responses of leaf physiology  
553 reduce effects of spring frost defoliation on temperate forest tree carbon uptake. *Frontiers in Forests and  
554 Global Change*, 6, 988233.

- 555 Richardson, A.D., Keenan, T.F., Migliavacca, M., Ryu, Y., Sonnentag, O. & Toomey, M. (2013). Climate  
556 change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural*  
557 and *Forest Meteorology*, 169, 156–173.
- 558 Sanchez-Lorenzo, A., Wild, M., Brunetti, M., Guijarro, J.A., Hakuba, M.Z., Calbó, J., Mystakidis, S. &  
559 Bartok, B. (2015). Reassessment and update of long-term trends in downward surface shortwave radiation  
560 over Europe (1939–2012). *Journal of Geophysical Research: Atmospheres*, 120, 9555–9569.
- 561 Saunders, M.R. & Wagner, R.G. (2008). Height-diameter models with random coefficients and site variables  
562 for tree species of Central Maine. *Annals of Forest Science*, 65, 203–203.
- 563 Sgubin, G., Swingedouw, D., Dayon, G., García De Cortázar-Atauri, I., Ollat, N., Pagé, C. & Van Leeuwen,  
564 C. (2018). The risk of tardive frost damage in French vineyards in a changing climate. *Agricultural and*  
565 *Forest Meteorology*, 250–251, 226–242.
- 566 Silvestro, R., Deslauriers, A., Prislan, P., Rademacher, T., Rezaie, N., Richardson, A.D., Vitasse, Y. &  
567 Rossi, S. (2025). From Roots to Leaves: Tree Growth Phenology in Forest Ecosystems. *Current Forestry*  
568 *Reports*, 11, 12.
- 569 Silvestro, R., Zeng, Q., Buttò, V., Sylvain, J.D., Drolet, G., Mencuccini, M., Thiffault, N., Yuan, S. & Rossi,  
570 S. (2023). A longer wood growing season does not lead to higher carbon sequestration. *Scientific Reports*,  
571 13, 4059.
- 572 Spinoni, J., Naumann, G., Carrao, H., Barbosa, P. & Vogt, J. (2014). World drought frequency, duration,  
573 and severity for 1951–2010. *International Journal of Climatology*, 34, 2792–2804.
- 574 Spinoni, J., Vogt, J.V., Naumann, G., Barbosa, P. & Dosio, A. (2018). Will drought events become more  
575 frequent and severe in Europe? *International Journal of Climatology*, 38, 1718–1736.
- 576 Stridbeck, P., Björklund, J., Fuentes, M., Gunnarson, B.E., Jönsson, A.M., Linderholm, H.W., Ljungqvist,  
577 F.C., Olsson, C., Rayner, D., Rocha, E., Zhang, P. & Seftigen, K. (2022). Partly decoupled tree-ring  
578 width and leaf phenology response to 20th century temperature change in Sweden. *Dendrochronologia*,  
579 75, 125993.
- 580 Swidrak, I., Schuster, R. & Oberhuber, W. (2013). Comparing growth phenology of co-occurring deciduous  
581 and evergreen conifers exposed to drought. *Flora: Morphology, Distribution, Functional Ecology of Plants*,  
582 208, 609–617.
- 583 Teskey, R., Werten, T., Bauweraerts, I., Ameye, M., McGuire, M.A. & Steppe, K. (2015). Responses of tree  
584 species to heat waves and extreme heat events. *Plant, Cell & Environment*, 38, 1699–1712.
- 585 Trenberth, K.E., Dai, A., Van Der Schrier, G., Jones, P.D., Barichivich, J., Briffa, K.R. & Sheffield, J.  
586 (2014). Global warming and changes in drought. *Nature Climate Change*, 4, 17–22.
- 587 Tyree, M.T. & Zimmermann, M.H. (2002). *Xylem Structure and the Ascent of Sap*. Springer Series in Wood  
588 Science. Springer Berlin Heidelberg, Berlin, Heidelberg.
- 589 Vitasse, Y. (2013). Ontogenetic changes rather than difference in temperature cause understory trees to leaf  
590 out earlier. *New Phytologist*, 198, 149–155.
- 591 Vitasse, Y., eLenz, A. & eKoerner, C. (2014). The interaction between freezing tolerance and phenology in  
592 temperate deciduous trees. *Frontiers in Plant Science*, 5. Publisher: Frontiers Media S.A.
- 593 Wolfe, D.W., Schwartz, M.D., Lakso, A.N., Otsuki, Y., Pool, R.M. & Shaulis, N.J. (2005). Climate change  
594 and shifts in spring phenology of three horticultural woody perennials in northeastern USA. *International*  
595 *Journal of Biometeorology*, 49, 303–309.
- 596 Wolkovich, E.M., Cook, B.I. & Davies, T.J. (2014). Progress towards an interdisciplinary science of plant  
597 phenology: building predictions across space, time and species diversity. *New Phytologist*, 201, 1156–1162.  
598 eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/nph.12599>.

- 599 Wolkovich, E.M., Ettinger, A.K., Chin, A.R., Chamberlain, C.J., Baumgarten, F., Pradhan, K., Manzanedo,  
600 R.D. & Hille Ris Lambers, J. (2025). Why longer seasons with climate change may not increase tree growth.  
601 *Nature Climate Change*, 15, 1283–1292.
- 602 Woolway, R.I., Sharma, S., Weyhenmeyer, G.A., Debolskiy, A., Golub, M., Mercado-Bettín, D., Perroud,  
603 M., Stepanenko, V., Tan, Z., Grant, L., Ladwig, R., Mesman, J., Moore, T.N., Shatwell, T., Vanderkelen,  
604 I., Austin, J.A., DeGasperi, C.L., Dokulil, M., La Fuente, S., Mackay, E.B., Schladow, S.G., Watanabe,  
605 S., Marcé, R., Pierson, D.C., Thiery, W. & Jennings, E. (2021). Phenological shifts in lake stratification  
606 under climate change. *Nature Communications*, 12, 2318.
- 607 Wu, J. (2013). Key concepts and research topics in landscape ecology revisited: 30 years after the Allerton  
608 Park workshop. *Landscape Ecology*, 28, 1–11.
- 609 Wu, X., Niu, C., Liu, X., Hu, T., Feng, Y., Zhao, Y., Liu, S., Liu, Z., Dai, G., Zhang, Y., Van Meerbeek, K.,  
610 Wu, J., Liu, L., Guo, Q. & Su, Y. (2024). Canopy structure regulates autumn phenology by mediating  
611 the microclimate in temperate forests. *Nature Climate Change*, 14, 1299–1305.
- 612 Wu, Z., Chen, S., De Boeck, H.J., Stenseeth, N.C., Tang, J., Vitasse, Y., Wang, S., Zohner, C. & Fu, Y.H.  
613 (2021). Atmospheric brightening counteracts warming-induced delays in autumn phenology of temperate  
614 trees in Europe. *Global Ecology and Biogeography*, 30, 2477–2487.
- 615 Yan, T., Fu, Y.H., Campioli, M., Peñuelas, J. & Wang, X. (2021). Divergent responses of phenology and  
616 growth to summer and autumnal warming. *Global Change Biology*, 27, null.
- 617 Yuancai, L. & Parresol, B.R. (2001). Remarks on Height-Diameter Modeling. Tech. Rep. SRS-RN-10, U.S.  
618 Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.
- 619 Zohner, C.M., Mo, L., Renner, S.S., Svenning, J.C., Vitasse, Y., Benito, B.M., Ordonez, A., Baumgarten,  
620 F., Bastin, J.F., Sebald, V., Reich, P.B., Liang, J., Nabuurs, G.J., de Miguel, S., Alberti, G., Antón-  
621 Fernández, C., Balazy, R., Brändli, U.B., Chen, H.Y.H., Chisholm, C., Cienciala, E., Dayanandan, S.,  
622 Fayle, T.M., Frizzera, L., Gianelle, D., Jagodzinski, A.M., Jaroszewicz, B., Jucker, T., Kepfer-Rojas, S.,  
623 Khan, M.L., Kim, H.S., Korjus, H., Johannsen, V.K., Laarmann, D., Lang, M., Zawila-Niedzwiecki, T.,  
624 Niklaus, P.A., Paquette, A., Pretzsch, H., Saikia, P., Schall, P., Šeben, V., Svoboda, M., Tikhonova, E.,  
625 Viana, H., Zhang, C., Zhao, X. & Crowther, T.W. (2020). Late-spring frost risk between 1959 and 2017  
626 decreased in North America but increased in Europe and Asia. *Proceedings of the National Academy of  
627 Sciences*, 117, 12192–12200.