

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

² Christophe Rouleau-Desrochers

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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 leaves (Körner & Basler, 2010; Delpierre *et al.*, 2016).

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.

¹⁹⁸ **1.5 Research questions**

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

²⁰²

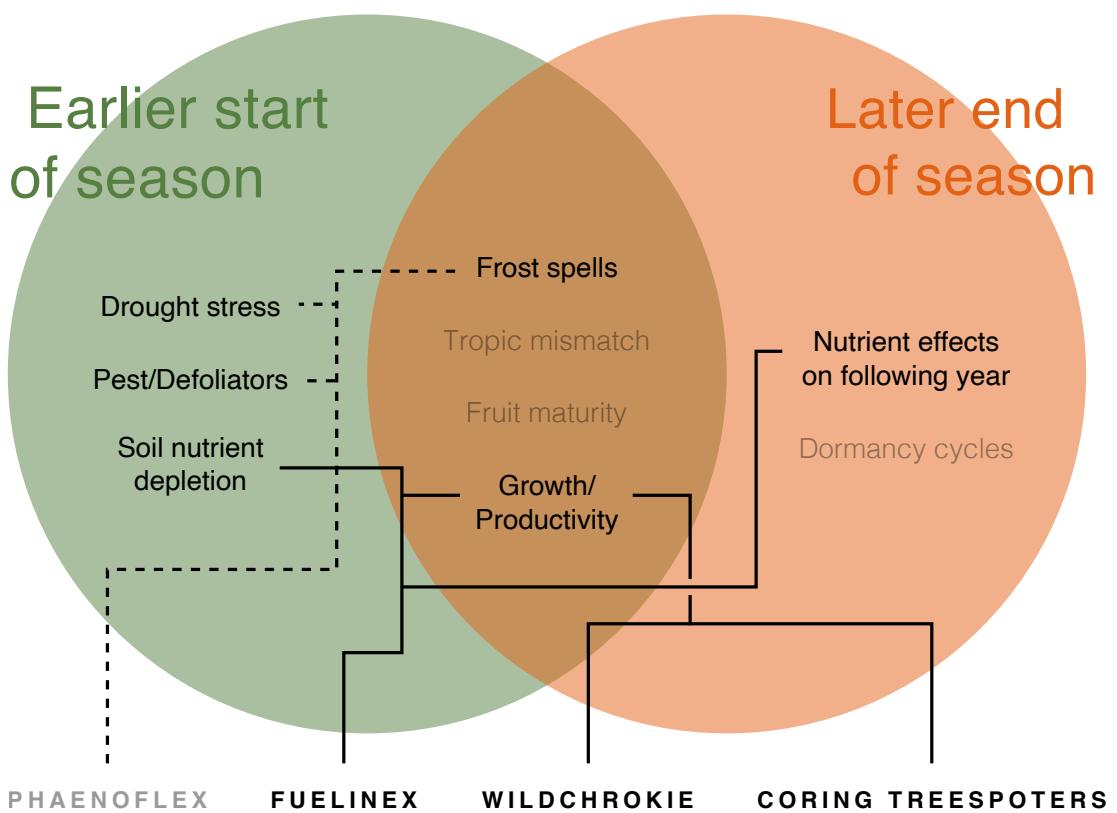


Figure 1: The effects that an earlier start and later end of season can have on trees. In bold are the effects that were studied over the course of this thesis. Phaenoflex (in grey) is a related experimental project, that is not part of this thesis, but one I collaborated on in XX years.

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
227 in the fall using NPN phenophases (DENNY2014): Leaves (483), Colored leaves (498), Fruits (516), Ripe
228 Fruits (390), Falling leaves(471), Recent fruit or seed drop (504), Increasing leaf size (467), Breaking leaf
229 buds (371), Flowers or flower buds (500), Open flowers (501), Pollen release (502). Not all phenophases were
230 recorded for every tree, for every year, and some trees miss several several years of data.

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

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

244 **Statistical analyses**

245

246 **2.2 Fuelinex**

247 **2.3 Species selection**

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

253 2023 Phaenoflex's experiment but were watered weekly and remained at ambient condition for the 2023
254 growing season. We randomly selected 90 individuals among them.

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

264 **2.4 Tree measurements**

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, and from that point to the bottom
267 of the highest apical we measured height with a metal ruler (precision of 0.1 mm). We measured those two
268 same points in the winter (2024 growing season) and in the fall (2025 growing season) of 2025. For those
269 two subsequent measurements, if the measured shoot died (because of insects, accidentally broken it, etc.), we
270 noted the previous measurement as invalid and measured the highest lateral shoot.

271 **2.5 Phenology and shoot elongation monitoring**

272 : We started monitoring phenology of all the trees on 11 April 2024, missing the initial leaf phenology
273 for most individuals, but we monitored subsequent phenophases twice a week until the leaves have fully
274 elongated. Phenophases are described in table XXX.

Table 1: Phenological stages and their descriptions for deciduous species and pine.

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

275 Before shoot elongation onset, we marked a reference point with red pain for the measurement at the
276 base of either the new-year the apical or highest lateral shoot. To facilitate and improve the quality of the
277 shoot elongation measurements, we attached paper rulers on the following species A. negundo, B. papyfera,
278 P. balsamifera and Q. macrocarpa. For species on which we couldn't install the paper rulers, we took those
279 same measurements, but with a metal ruler.

280 Every week, starting on 4 September 2024, we monitored senescence by a visual assessment of the
281 remaining green leaf cover in percentage and by measuring the chlorophyll content meter with a chlorophyll

282 content meter.

283 **2.6 Fertilizer**

284 : Using fertilizer premix from UBC's garden, we fertilized the trees twice during the growing season of 2024
285 (except for the nutrient boosted trees) and three times during 2025, just enough to keep the trees alive.

286 **2.7 Spring and Fall treatments**

287 For the treatments, we placed the Cool Spring individuals in climate chambers to delay the start of their
288 growing season on March 6 2024 while the Warm Spring replicates remained at ambient conditions. Once all
289 Warm Spring individuals have fully leaf out, we removed the Cool Spring replicates from the chambers and
290 placed them back at ambient conditions for the whole summer. Then, we placed the trees for the Warm Fall
291 treatments in the climate chambers on 4 September 2024. The photoperiod was set every week on Wednesday
292 to fit the local sunrise and sunset and was ramped until it reached full light. The temperature was set to
293 fit the mean 30-year weekly maximum temperature of the previous month (e.g. 1st week of September set
294 to averaged 1st week of August). The Cool Fall treatment trees remained at ambient conditions. For both
295 climate chamber treatment, we rotated and watered the trees weekly to minimize the effects the climate
296 chambers could have on the trees. We also set the photoperiod regime to the corresponding sunrise and
297 sunset of the ongoing week and was ramped until it reached full light

298 **2.8 Shoot elongation measurements**

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

305 In 2025, we preferably chose the continuous shoot that was measured the previous year. If that shoot died,
306 we chose another shoot according to the previous criterias.

307 Two methods:

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

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

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

319 **2.9 Leaf count**

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

324 **2.10 Biomass collection**

325 In the fall of 2025, when all the individuals from a species have lost all their leaves, we proceeded to remove
326 the trees from their pots, remove the dirt by shaking them first and washing off the dirt off the roots gently

327 with regular water gun. Then, we moved the trees, 1 bloc at a time in the drying ovens where they were
328 left to dry for 72 hours at 70C. Not in paper bags. Then below and above ground biomass were separated
329 by cutting the tree at 1cm above the highest root. We weighted biomass at a precision of 0.01gr

330 3 Supplemental material

331 3.1 Wildchrokie

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

336 3.2 Treespotters

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

341 3.1. Spring frosts

Definition:	Late spring frosts are below-freezing temperatures in late spring (Zohner <i>et al.</i> , 2020)
Mechanisms	Early warm spells → early leaf out → hard frost (<-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)
Global trend of occurrence	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)
Consequences (Individual and Ecosystem level consequences)	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)
Differences across species/provenance	

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

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

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3.2. Drought

	<p>Definition: "Drought is a prolonged absence or marked deficiency of precipitation that results in water shortage or a period of abnormally dry weather sufficiently prolonged for the lack of precipitation to cause a serious hydrological imbalance (Trenberth <i>et al.</i>, 2014; Intergovernmental panel on climate change, 2007).</p>
	<p>Mechanisms</p> <ul style="list-style-type: none"> — Hot temperature + low precipitation (aka global-change-type drought (Tyree & Zimmermann, 2002)) = ↑ evapotranspiration → less water in soil → cavitation → embolism → hydraulic failure (Tyree & Zimmermann, 2002) = tissue death (Choat <i>et al.</i>, 2018); — Earlier spring phenology = longer GS → increases vegetative growth → increases evapotranspiration → increases drawdown of soil moisture = progressive water stress (Li <i>et al.</i>, 2023) — Long-term vs short-term stomatal responses and consequences on tissue death (Choat <i>et al.</i>, 2018); — Recovery and its determinants (Choat <i>et al.</i>, 2018; Li <i>et al.</i>, 2023)
344	<p>Global trend of occurrence</p> <ul style="list-style-type: none"> — ↑ precipitation anomalies since 1990 (Trenberth <i>et al.</i>, 2014); — Models often exclude PDO/ENSO which limit the capacity to attribute increasing droughts to CC (Trenberth <i>et al.</i>, 2014); — Weak evidence of detection and attribution of changes in meteorological drought since the mid-20th century (Change, 2014); — 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)
345	<p>Consequences (Individual and Ecosystem level consequences)</p> <ul style="list-style-type: none"> — Recurring droughts may limit trees' ability to recover from other types of stress. — Tree mortality (e.g. Texas and California extreme droughts are estimated to have killed 300 and 102 million trees (Li <i>et al.</i>, 2023))
346	<p>Differences across species/provenance</p>

3.3. Heat waves

Definition:	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).
Mechanisms	<p>↑ atmospheric CO₂ = ↑ 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>
347 Global trend of occurrence	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).
Consequences (Individual and Ecosystem level consequences)	- Reduced photosynthesis - Increased mortality - Photosynthetic tissue loss (Gagne <i>et al.</i> , 2020).
Differences across species/provenance	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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