

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

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⁴ Introduction

⁵ Climate change impacts on tree phenology

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

¹⁸ Trends and drivers of spring and autumn phenological events

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

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

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

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

49

50 **How shifts in spring and autumn phenology will affect trees and forests are not clear**

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

59

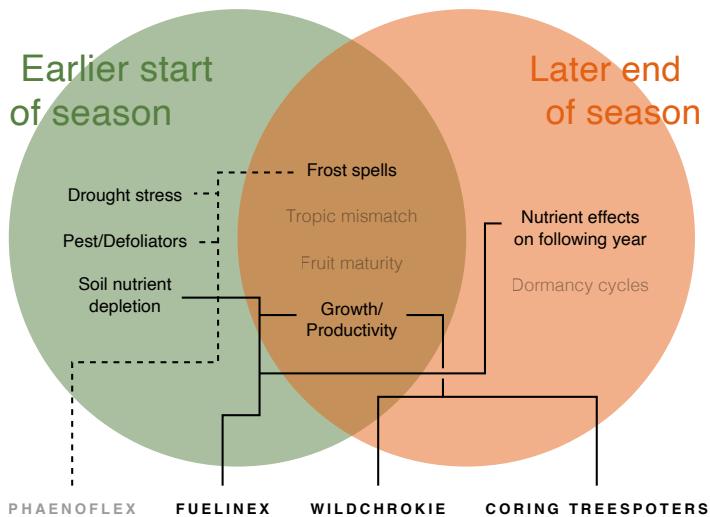


Figure 1: The effects that an earlier start and later end of season can have on trees. In bold are the effects that were studied over the course of this thesis. Phaenoflex (in grey) is a related experimental project, that is not part of this thesis, but one I collaborated on in 2023 and 2024.

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

74 and nutrient availability, and temperature (Cabon *et al.*, 2022, 2020; Muller *et al.*, 2011; Peters *et al.*, 2021).
75 Thus, this demonstrates that carbon projection models that solely rely on vegetation alone may mislead
76 carbon sequestration dynamics of our forests.

77
78 Spring and fall phenological events are shifting with debatable consequences on tree growth. The sensitivity
79 of cambial activity to water, temperature and nutrients has the potential to have far-reaching consequences
80 given the hard-to-predict nature of future climate change, where any of these variables could vary from low
81 to high amplitude (Almagro *et al.*, 2025; Cabon *et al.*, 2022). This expected asymmetry of future environ-
82 mental changes makes understanding the internal physiological constraints (via genetic and developmental
83 control), and external limits (via extreme temperatures or moisture deficit) to growth critical, which I aim
84 to investigate with experiments and observations.

85 Experiments and observations to anticipate the future of growth and season 86 length relationship

87 Past phenological trends can help (or not) predict future phenological changes

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

96 Growth drivers differences across species need to be considered

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

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

119
120 *Ground based observations:* Second, leaf phenology can provide valuable and accessible insights into the
121 growth temporality of trees that are not suitable for experimental trials. Collecting cambial phenology
122 data, which is a direct measure of wood growth, is time consuming and expensive. In contrast, leaf phe-
123 nology through ground-based observations are low-cost methods that provide direct evidence of changing
124 phenophases (Piao *et al.*, 2019). Cambial and leaf phenology are often closely synchronized, therefore, the

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

135

136 Goals of my thesis

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

145 Complexity of measuring growth and defining growing season length

146 What is a growing season?

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

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

161

162 What is growth?

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

167

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

174

Alongside the diameter-height allometric relationship, dendroecology—applications of dendrochronological techniques to problems in ecology (Fritts & Swetnam, 1989)—emerged to answer ecological problems as well as to hindcast (e.g. (Bergeron *et al.*, 2004)) and forecast ecological processes both at the regional (Gazol

178 *et al.*, 2018) and global scale (Manzanedo & Pederson, 2019; Büntgen *et al.*, 2018). Now, these methods are
179 used to understand more precise growth patterns and their relationship with different environmental factors.
180 This is why I will use tree rings as a proxy for how much trees grew in any given year.

181

182 Objectives

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

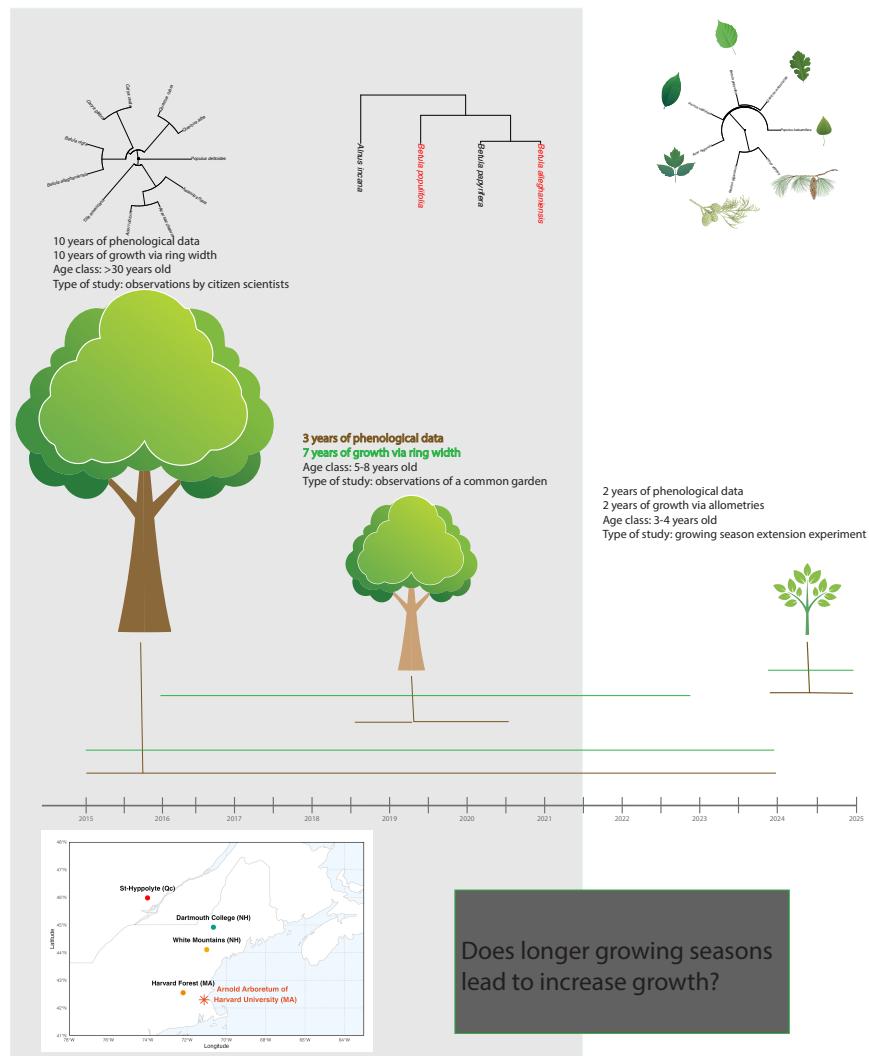


Figure 2: Overview of the age class, species, provenance of the trees used in each study along with the type of study each project consist of.

192 **Research questions**

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

196

197 **Methodology**

198 **Chapter 1: Fuelinex**

199 **Species selection and growing conditions** We used seven species of tree sapling for our experiment
200 (Fuelinex). We purchased Paper birch (*Betula papyfera*), Choke Cherry (*Prunus virginiana*), Bur oak (*Quer-*
201 *cus macrocarpa*) from Peel's nursery in November 2023 and the trees arrived at Totem Field studios 49.26
202 °N, -123.25 °W where the other four species were stored until the spring of 2023. Manitoba maple (*Acer*
203 *negundo*), Eastern white pine (*Pinus strobus*), Balsam poplar (*Populus balsamifera*) and Giant sequoia (*Se-*
204 *quoiaadendron giganteum*) are leftover trees that we purchased in 2022 for 2023 for a previous experiment.
205 We watered them weekly and they remained at ambient condition for the 2023 growing season. We randomly
206 selected 90 individuals of each species among them. We propagated B. poplar from 30 cm whips while the
207 trees were still dormant (McCartyEARLY2017). In May 2024, we repotted all the trees in 2-gallon plastic
208 pots with a medium for perennials consisting of 50 % peat, 25% crushed pumice and 25% crushed bark
209 (www.westcreekfarm.com). In February 2025, we repotted the trees with the same medium in 3-gallon pots.
210 We arranged the trees in three blocs, each containing all 6 treatments and 7 species, with two of these blocs
211 placed under an open-walled and well ventilled polytunnel greenhouse. All saplings were connected to a drip
212 irrigation system (40 PVC frame from Netafilm 54 with a Toro controller) to maintain constant irrigation
213 across the season. Using fertilizer premix from XXX, we fertilized the trees twice during the growing season
214 of 2024 (except for the nutrient boosted trees) and three times during 2025, just enough to keep the trees
215 alive (Table XXX).

216

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

227

228 **Phenology and shoot elongation monitoring:**

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

233

234 *Shoot elongation:* Before shoot elongation onset, we marked a reference point with red pain at the base of
235 either the new-year apical or highest lateral shoot. To facilitate and improve the quality of the shoot elonga-
236 tion measurements, we attached paper rulers (accuracy \pm 0.1cm) on *A. negundo*, *B. papyfera*, *P. balsamifera*
237 and *Q. macrocarpa*. For species not suitable for those paper rulers, we took those same measurements, but
238 with a metal ruler (accuracy \pm 0.1cm). We measured shoot elongation weekly from the red mark to the base
239 of the bud (for deciduous species) and at the top of the apical meristem for conifers. For determinate growth
240 species ((*A. negundo*, *P. virginiana* and *Q. macrocarpa*), after two weeks of little or no change in elongation,
241 we started monitoring them every other week until September 1st for both growing seasons.

²⁴²
²⁴³ **Senescence:** Every week, starting on 4 September 2024, we monitored senescence by a visual assessment of
²⁴⁴ the remaining green leaf cover in percentage and by measuring the chlorophyll content meter with a chloro-
²⁴⁵ phyll content meter. We also recorded the date of loss of green leaf cover and leaf drop.

²⁴⁶

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

Group	Scale	Phenostage	Description
<i>Deciduous species</i>			
0	dormant	no bud development visible	
1	bud swelling	swollen and/or elongating buds	
2	budburst	bud scales open and leaves partially visible	
3	leaf-out	leaves fully emerged from bud but still folded, crinkled or pendant	
4	leaf unfolding	leaves fully unfolded	
<i>Pine</i>			
0	dormant	no signs of activity	
1	swelling	swelling or elongation of shoot visible	
2	budburst	green needle tips along the shoot visible	
3	leaf-out	scales open along the shoot and first needles become visible	
4	leaf-unfolding	green needles emerging away from the shoot	

²⁴⁷ **Experimental design** Individuals from each species were randomly selected for a full factorial design of
²⁴⁸ Warm/Cool, Spring/Fall treatments (Suppl Figure XXX) with two addditional treatments to test nutrient
²⁴⁹ effects in the fall (Figure XXX exp design). On 6 March 2024, we placed the Cool Spring individuals in
²⁵⁰ climate chambers to delay the start of their growing season, while the Warm Spring replicates remained at
²⁵¹ ambient conditions. Once all Warm Spring individuals have fully leaf out, we removed the Cool Spring repli-
²⁵² cates from the chambers and placed them back at ambient conditions for the whole summer. On 4 September
²⁵³ 2024, we placed the trees for the Warm Fall treatments in the climate chambers. The temperature was set
²⁵⁴ to fit the mean 30-year weekly maximum temperature of the previous month (e.g. 1st week of September
²⁵⁵ set to averaged 1st week of August). The Cool Fall treatment trees remained at ambient conditions. For
²⁵⁶ both climate chamber treatment, we rotated and watered the trees weekly to minimize the climate chambers
²⁵⁷ effect. We also set the photoperiod regime to the corresponding sunrise and sunset of the ongoing week and
²⁵⁸ was ramped until it reached full light. To test for nutrient limitation at the end of the season, we added a
²⁵⁹ supplemental dose of nutrient (Supple Table XXX) to two treatments (Figure XXX).

²⁶⁰

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

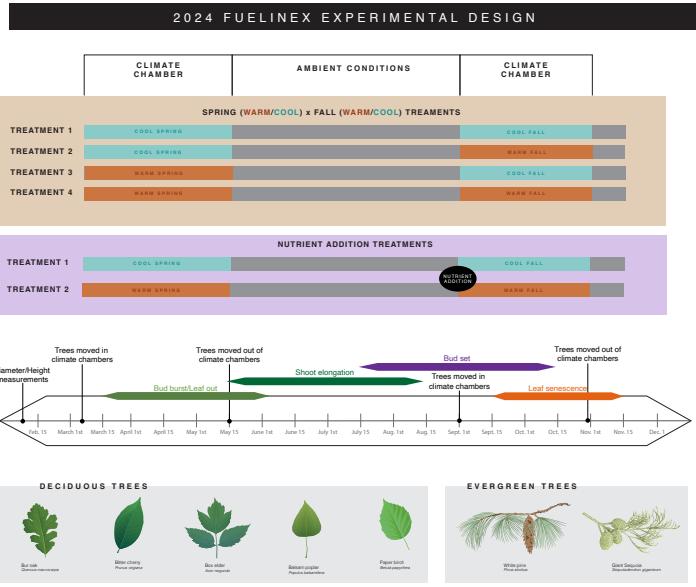


Figure 3: Experimental design during the 2024 growing season. Cooling treatments are represented in blue and warming treatments are in orange. The grey zone in the middle represents an approximate period during the growing season where all treatments were together at ambient conditions.

264 Chapter 2: Wildchrokie and coringTreespotters

265 Wildchrokie

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

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

275

276 Phenological monitoring and sample collection

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

286

287 Coringtreespotters

288 Citizen science program

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

291 50 trees of 11 species regularly from budburst in the spring to leaf colouring in the fall using NPN phenophases
 292 (DENNY2014): Leaves (483), Colored leaves (498), Fruits (516), Ripe Fruits (390), Falling leaves(471),
 293 Recent fruit or seed drop (504), Increasing leaf size (467), Breaking leaf buds (371), Flowers or flower buds
 294 (500), Open flowers (501), Pollen release (502). Not all phenophases were recorded for every tree, for every
 295 year, and some trees miss several several years of data.

296 *Phenological monitoring and sample collection*

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

304

305 **Sample processing, imaging and measuring**

306 We mounted the cores on wooden mounts, and sanded the cores and cross-sections using progressively fine
 307 grit (150, 300, 400, 600, 800, 1000). We scanned the cores and cross-sections at a resolution of ***dpi using
 308 a homemade great scanner (Tina2026?) We used the digitalized images to measure the tree ring widths with
 309 Fiji ImageJ. Then, we performed visual crossdating using Dplr, we did not performed statistical crossdating
 310 because of the short chronologies that limit the capacity of these analyses.

311

312 **Statistical analyses**

313 For both projects, we used Bayesian hierarchical modeld coded in Stan with the rstan package version 2.32.7
 314 (CarpenterSTAN2044??)) to run the Stan code in R. With these models we estimated ringwidth as a function
 315 of growing degree days, accumulated from the leafout date to the budset date. We had three grouping
 316 factors for Wildchrokie (species, site and treeid) and two for coringTreespotters (species and treeid). We
 317 ran four chains with each 2000 warmup, that we discarded and 2000 sampling iterations, that we kept for
 318 posterior distribution estimates. The models did not have any divergent transitions and Rhat was below 1.01.

319

320 *Wildchrokie model structure*

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

321 *coringTreespotters model structure*

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

322 References

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580 **Supplemental material**

Table 2: Fuelinex species grouped by tree type, life history, and wood anatomy.

Deciduous Trees			
Common Name (Latin)	Life History Strategy	Wood Anatomy	n (ap- prox)
Bur oak (<i>Quercus macrocarpa</i>)	Slow-growth, long life	Ring-porous	87
Bitter cherry (<i>Prunus virginiana</i>)	Fast-growth, short life	Diffuse-porous	78
Box elder (<i>Acer negundo</i>)	Fast-growth, short life	Diffuse-porous	90
Balsam poplar (<i>Populus balsamifera</i>)	Fast-growth, short life	Diffuse-porous	84
Paper birch (<i>Betula papyrifera</i>)	Fast-growth, short life	Diffuse-porous	90
Evergreen Trees			
White pine (<i>Pinus strobus</i>)	Slow-growth, long life	Non-porous	89
Giant Sequoia (<i>Sequoiaadendron giganteum</i>)	Slow-growth, long life	Non-porous	54

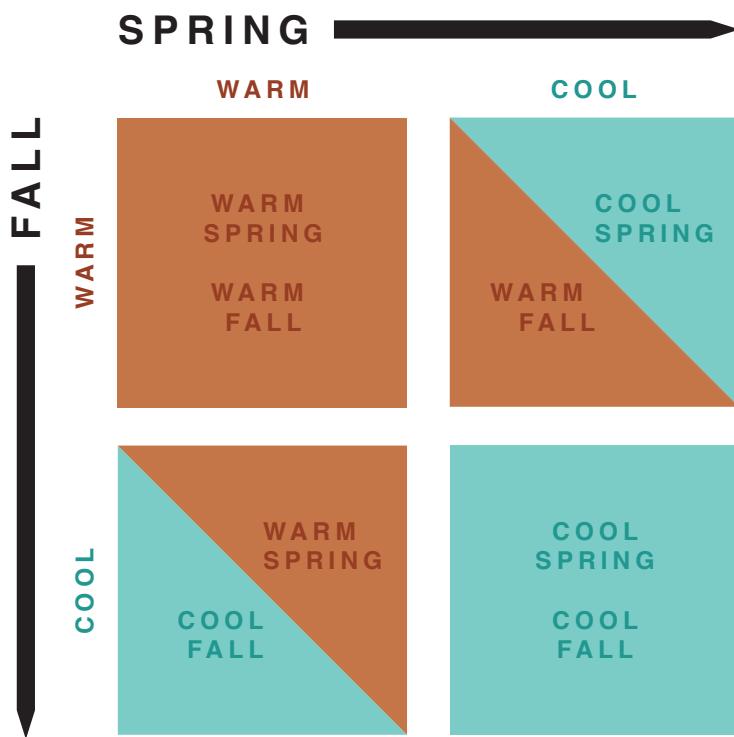


Figure 4

Table 3: Wilchrokie 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

Table 5: Nutrient addition over the two growing seasons for the nutrient addition treatment and the other treatments. The fertilizer is from Evergro (Delta, BC V4G 1B6), ID: Pepper Feed Main.

Date	Nutrient addition treatments	Regular treatments
7 June 2024	62.5	62.5
6 July 2024	62.5	62.5
1 Sept 2024	250	0
Subtotal (2024)	375	125
10 April 2025	0	125
9 May 2025	0	125
June 2025	62.5	62.5
July 2025	62.5	62.5
Subtotal (2025)	125	375
2-year total	500	500

Table 6: Summary of late spring frosts: definition, mechanisms, trends, and consequences

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

Table 7: Summary of drought: definition, mechanisms, global trends, and consequences

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).
Mechanisms	<ul style="list-style-type: none"> — Hot temperature + low precipitation (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 → increased vegetative growth → increased evapotranspiration → increased 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).
Global trend of occurrence	<ul style="list-style-type: none"> — ↑ precipitation anomalies since 1990 (Trenberth <i>et al.</i>, 2014); — Climate models often exclude PDO/ENSO, limiting the attribution of increasing droughts to climate change (Trenberth <i>et al.</i>, 2014); — Weak evidence for detection and attribution of changes in meteorological drought since the mid-20th century (Change, 2014); — From a spatial, model-based perspective, anthropogenic forcing increased the frequency, duration, and intensity of SPI-based droughts in North America (Hidalgo <i>et al.</i>, 2009), Europe and the Mediterranean (Spinoni <i>et al.</i>, 2018; Kurnik <i>et al.</i>, 2011), and East Asia (Chiang <i>et al.</i>, 2021; Marvel <i>et al.</i>, 2019; Spinoni <i>et al.</i>, 2014).
Consequences (Individual and ecosystem level)	<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, respectively (Li <i>et al.</i>, 2023)).
Differences across species/provenance	

Table 8: Summary of heat waves: definition, mechanisms, global trends, and consequences

Definition:	A heat wave is a period of excessively hot weather (five or more consecutive days during which the daily maximum temperature exceeds the long-term average maximum temperature by 5 °C), which may be accompanied by high humidity (Marx <i>et al.</i> , 2021).
Mechanisms	↑ atmospheric CO ₂ → ↑ temperature → ↑ frequency and intensity of heat waves. More specifically, one proposed mechanism for the increased occurrence of heat waves is a weakening of the polar jet stream (a key weather driver in mid-latitude regions of North America, Europe, and Asia) caused by global warming, which increases the persistence of stationary weather patterns, resulting in prolonged heat waves or heavy rainfall events (Marx <i>et al.</i> , 2021). Extreme heat affects growth either (1) directly via disruption of cellular processes or (2) indirectly via increased leaf-to-air vapor pressure deficit (VPD) (Gagne <i>et al.</i> , 2020). Increased temperature leads to reduced photosynthesis, which can be attributed to: 1. Damage to photosynthetic machinery; 2. Inactivation of Rubisco; 3. Reduced RuBP regeneration; 4. Loss of membrane stability; 5. Increased mitochondrial respiration and photorespiration (Hauck <i>et al.</i> , 2025).
Global trend of occurrence	Heat waves have increased in frequency and intensity (Gagne <i>et al.</i> , 2020; Meehl & Tebaldi, 2004; Teskey <i>et al.</i> , 2015) and are expected to increase further under future climate change (Dosio <i>et al.</i> , 2018; Change, 2014; Teskey <i>et al.</i> , 2015). Summertime extreme temperatures associated with prolonged heat waves lasting several weeks now impact approximately 10% of global land surfaces, compared to only 1% in the 1960s (Teskey <i>et al.</i> , 2015). These trends cannot be explained solely by natural climate variability and require anthropogenic climate change (Marx <i>et al.</i> , 2021).
Consequences (Individual and ecosystem level)	— Reduced photosynthesis; — Increased mortality; — Loss of photosynthetic tissue (Gagne <i>et al.</i> , 2020).
Differences across species/provenance	Some species exhibit thermal acclimation of photosynthesis and respiration, whereas others do not. Consequently, growth and survival responses to heat waves depend on species-specific capacity for thermal acclimation. These differences are partly explained by contrasting growth strategies of gymnosperms versus angiosperms, the latter generally showing greater acclimation potential.