

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

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5 Introduction

6 Climate change impacts on tree phenology

7 Research from the past decades has shown convincing evidence that human activity is increasingly affecting
8 many worldwide environmental processes ([Ceballos et al., 2017; ?; Laurance, 2007; Parmesan & Yohe, 2003](#))
9 ([Ceballos et al., 2017; Intergovernmental Panel On Climate Change, 2023; Laurance, 2007; Parmesan & Yohe, 2003](#))
10 . This can be through land use change and loss, pollution, invasive species, resource overexploitation and
11 climate change (Driscoll *et al.*, 2018; Parmesan *et al.*, 1999; Wu, 2013). Though some immediate actions
12 can mitigate these impacts (e.g. ([Campbell et al., 2014](#)))[\(e.g. Campbell et al., 2014\)](#), reversing 150 years of
13 human-induced greenhouse gas emissions is harder. These emissions have affected Earth's climate and are
14 projected to keep changing it for many centuries ([?; Intergovernmental Panel On Climate Change, 2023](#)).
15 Yet, the extent of the consequences that a warming climate will have on biological processes is still debated
16 (Huey *et al.*, 2012), in part because it requires accurate predictions of current and future trends in some of
17 the most reported and direct biological impacts of climate change, as I review below. And also because it
18 requires understanding the complex additional effects of these impacts, which I propose to study for my thesis.
19

20 Trends and drivers of spring and autumn phenological events

21 The most frequently observed biological impact of climate change over the past decades is major changes
22 in [spring and autumn phenology](#)—the timing of recurring life history events (Parmesan & Yohe, 2003; Cle-
23 land *et al.*, 2007; Lieth *et al.*, 1974; Woolway *et al.*, 2021; Menzel *et al.*, 2006). [Together, shifts Shifts](#) in
24 spring and autumn phenology modify when the growing season starts and when it ends. [Understanding](#)
25 [the consequences of changing](#) [These shifts in](#) growing season length [on ecosystems could have impacts on](#)
26 [ecosystems and anticipating these consequences](#) requires understanding how much, and why it has changed
27 (Duputié *et al.*, 2015).

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

36
37 *Drivers of autumn phenology:* In contrast, autumn phenology (e.g. budset and leaf senescence) has delayed
38 with climate change—though shifts in the autumn have been much smaller than those in the spring (Gallin-
39 nat *et al.*, 2015; Jeong & Medvigy, 2014)—and its drivers are also far less understood. [Lesser Two realities](#)
40 [could explain these differences: lesser](#) attention is paid to autumn phenology (Piao *et al.*, 2019) and the
41 data is often noisier (Wu *et al.*, 2024), [two realities that could explain these differences](#). However, some of
42 these disparities are likely due to different factors driving autumn phenology, as these phenophases appear

44 to be caused by shortening photoperiod and colder temperatures (Cooke *et al.*, 2012; Flynn & Wolkovich,
 45 2018; Körner & Basler, 2010; Delpierre *et al.*, 2016). Given that low temperatures can accelerate senescence,
 46 warmer autumns may delay ~~these autumn~~ phenophases, possibly by extending the activity of photosynthetic
 47 enzymes, which decreases the degradation rate of chlorophyll (Yan *et al.*, 2021). Additionally, summer
 48 droughts could pause the activity schedule of trees and delay senescence to increase carbon assimilation (Dox
 49 *et al.*, 2022). Finally, there could be other factors affecting senescence delays that we do not consider here,
 50 such an antagonistic effect of warming and atmospheric brightening (Sanchez-Lorenzo *et al.*, 2015; Wu *et al.*,
 51 2021).

52 **How shifts in spring and autumn phenology will affect trees and forests are not clear**
 53 Shifts in spring and autumn phenology in trees support a long-lasting and intuitive assumption that earlier
 54 spring and delayed autumn events extend ~~seasons and seasons and~~ thus increase growth (Keenan *et al.*,
 55 2014; Stridbeck *et al.*, 2022). However, research from recent 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)~~ ~~Dow *et al.* (2022)~~
 57 showed that despite an earlier growth onset, longer seasons did not increase the growth rate nor overall annual
 58 increment in trees. This could substantially affect forest carbon-cycle model projections on and thus
 59 feedbacks to future climate (Richardson *et al.*, 2013; Swidrak *et al.*, 2013). ~~Starting to grow earlier and~~
 60 ~~stopping later both have different effects on trees~~ ~~These projections are likely to be furtherly altered by the~~
 61 ~~different effects that an earlier start and a later end of season have on trees, some of which I propose to~~
 62 ~~study in this thesis~~ (Figure 1).
 63

64

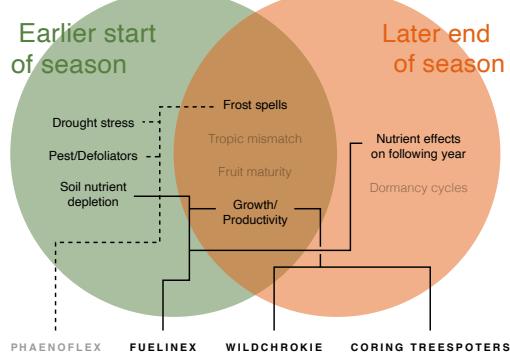


Figure 1: The effects that an earlier start and later end of season can have on trees. Solid lines connect effects studied over the course of this thesis. Phaenoflex (in grey) and its dashed lines represent other effects I investigated in a related experimental project that is not part of this thesis, but one I collaborated on in 2023 and 2024.

65 Understanding these findings requires answering why trees do not grow more despite longer growing seasons.
 66 While carbon allocation to above-ground biomass is one of the largest carbon sinks, how this carbon is
 67 allocated into wood is poorly understood. Indeed, the assumption of a linear relationship between wood
 68 growth and carbon assimilation is not well supported mechanistically and represents an important limitation
 69 of vegetation models (Cabon *et al.*, 2022). Net primary production represents the difference between
 70 photosynthesis and plant respiration, but this commonly used metric ~~completely~~ omits the representation
 71 of growth processes. This is perhaps because of a long-lasting paradigm of source-limited photosynthesis
 72 (Friend *et al.*, 2019; Parent *et al.*, 2010). Whether a tree's growth is source (photosynthetic activity de-
 73 termines sink activity) or sink (growth, respiration, and other metabolic processes determine the carbon
 74 source) controlled depends upon a closely coordinated sequence of dynamic responses and is still an active
 75 research question. However, Gessler & Zweifel (2024) recently suggested that neither source nor sink control
 76 systematically dominates. This complex dynamic enforces the importance of understanding the temperature

77 sensitivity relationship between growth activity and photosynthesis. Growing evidence suggests that cambial
78 activity may be more sensitive than photosynthesis to a range of environmental conditions, such as water
79 and nutrient availability, and temperature (Cabon *et al.*, 2022, 2020; Muller *et al.*, 2011; Peters *et al.*, 2021).
80 Thus, this demonstrates that carbon projection models that solely rely on vegetation alone may mislead
81 carbon sequestration dynamics of our forests.

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

90 Experiments and observations to anticipate the future of growth and season 91 length relationship

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

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

101 Growth drivers differences across species need to be considered

102 Recent work emphasizing the need to understand the drivers regulating growth across biomes highlights
103 strong species-level variation that may be critical to accurate projections. Phenology varies greatly across
104 species (~~e.g., closely related species tend to budburst at similar times under similar conditions~~) (Wolkovich *et al.*, 2014)
105 (e.g., closely related species tend to budburst at similar times under similar conditions Wolkovich *et al.*, 2014)
106 , but so does the relationship between growth and season length, which may explain the wide variation of this
107 relationship within communities (Buckley & Kingsolver, 2012). This points out another weakness of current
108 carbon sequestration models that pool species together, likely ~~overpassing missing~~ important nuances in the
109 growth responses plausibly explained by species differences. Excluding species differences in models may
110 mislead future carbon dynamic models (Green & Keenan, 2022; Cabon *et al.*, 2022; Wolkovich *et al.*, 2025).
111 ~~Different strategies can help understand how different species respond to warming and thus We propose to~~
112 ~~address this issue by using experiments and ground-based observations to better understand the responses~~
113 ~~of different species to warming. While both of these strategies have downsides, they are likely to leverage~~
114 ~~valuable insights which are necessary to improve carbon sequestration projections~~ (Wolkovich *et al.*, 2025).

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

127
128

129 ~~Ground-based~~ Ground-based observations: Second, leaf phenology can provide valuable and accessible in-
130 sights into the growth temporality of trees that are not suitable for experimental trials. Collecting cambial
131 phenology data, which is a direct measure of wood growth, is time-consuming and expensive. In con-
132 trast, leaf phenology through ground-based observations are low-cost methods that provide direct evidence
133 of changing phenophases (Piao *et al.*, 2019). Cambial and leaf phenology are often closely synchronized
134 ([Stridbeck *et al.*, 2022](#)); therefore, the more accessible leaf phenology data can act as a reliable proxy for
135 the onset and end of tree growth. In other words, knowing when leaves elongate and colour can guide as to
136 when trees start and stop growing, which is a fundamental metric to determine the growing season length.
137 Additionally, unlike other methods, ground observations have the advantage of providing accurate measure-
138 ments of phenological events for specific sites and species. Recently, the widespread use of smartphones
139 has considerably simplified the phenological monitoring by citizen scientists (Dickinson *et al.*, 2012; Hufkens
140 *et al.*, 2019; Piao *et al.*, 2019). While there are drawbacks to observations by citizen science programs (e.g.
141 non-standard protocols, highly uneven spatiotemporal distribution of these observations), they have the po-
142 tential to vastly increase the range of studied species and areas ([Chandler *et al.*, 2017](#); [Feldman *et al.*, 2018](#)).
143

144 Goals of my thesis

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

156 Complexity of measuring growth and defining growing season length

157 What is a growing season?

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

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

172 What is growth?

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

177
178 Foresters have measured tree diameter and height for decades, but these measurements may not be suitable
179 for determining relationships between growth and environmental conditions. The widely used method in

181 forestry is to measure diameter at breast height at punctual time intervals. Combined with height, these
182 data help develop allometries foresters can use to estimate how much wood they can harvest in a forest
183 (e.g., Meyer, 1940; Saunders & Wagner, 2008) (e.g., Meyer, 1940; Saunders & Wagner, 2008). These met-
184 rics work to determine wood in forests, but their coarse temporal scale—measuring every 5 or more years—is
185 likely to miss extreme events affecting growth.

186 Alongside the diameter-height allometric relationship, dendroecology—applications of dendrochronological
187 techniques to problems in ecology (Fritts & Swetnam, 1989)—emerged to answer ecological problems as well
188 as to hindcast (e.g., Bergeron et al., 2004) (e.g., Bergeron et al., 2004) and forecast ecological processes
189 both at the regional (Gazol et al., 2018) and global scale (Manzanedo & Pederson, 2019; Büntgen et al.,
190 2018). Now, these methods can unveil more precise growth patterns and their relationship with different
191 environmental factors. This is why I will use tree rings as a proxy for how much trees grew in any given
192 year.
193

194

195 Objectives

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

205 Research questions

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

209

210 Methodology

211 Chapter 1: Fuelinex

212 **Species selection and growing conditions** We used seven species of tree saplings for our experiment (Fuel-
213 inex). We purchased Paper birch (*Betula papyfera*), Choke Cherry (*Prunus virginiana*), Bur oak (*Quercus*
214 *macrocarpa*) from Peel's nursery in November 2023 and the trees arrived at Totem Field studios (49.26
215 °N, -123.25 °W), where the other four species were stored until the spring of 2023. Manitoba maple
216 (*Acer negundo*), Eastern white pine (*Pinus strobus*), Balsam poplar (*Populus balsamifera*) and Giant se-
217 quoia (*Sequoiadendron giganteum*) leftover trees that we purchased in 2022 for 2023 for a previous
218 experiment. We watered them weekly, and they remained at ambient condition ambient conditions for
219 the 2023 growing season. We randomly selected 90 individuals of each species among them. We propa-
220 gated B. poplar *P. balsamifera* from 30 cm whips while the trees were still dormant (McCarthy et al. (2018)
221 (McCarthy et al., 2018)). In May 2024, we repotted all the trees in 2-gallon plastic pots with a medium for
222 perennials consisting of 50 % peat, 25% crushed pumice and 25% crushed bark (purchased from www.westcreekfarm.com).
223 In February 2025, we repotted the trees with the same medium in 3-gallon pots. We arranged the trees in
224 three blocks, each containing all 6 treatments and 7 species, with two of these blocks placed under an open-
225 walled and well-ventilated polytunnel greenhouse. All saplings were connected to a drip irrigation system
226 (40 PVC frame from Netafilm 54 with a Toro controller) to maintain constant irrigation across the sea-
227 son. Using fertilizer premix, we fertilized the trees twice during the growing season of 2024 (except for the

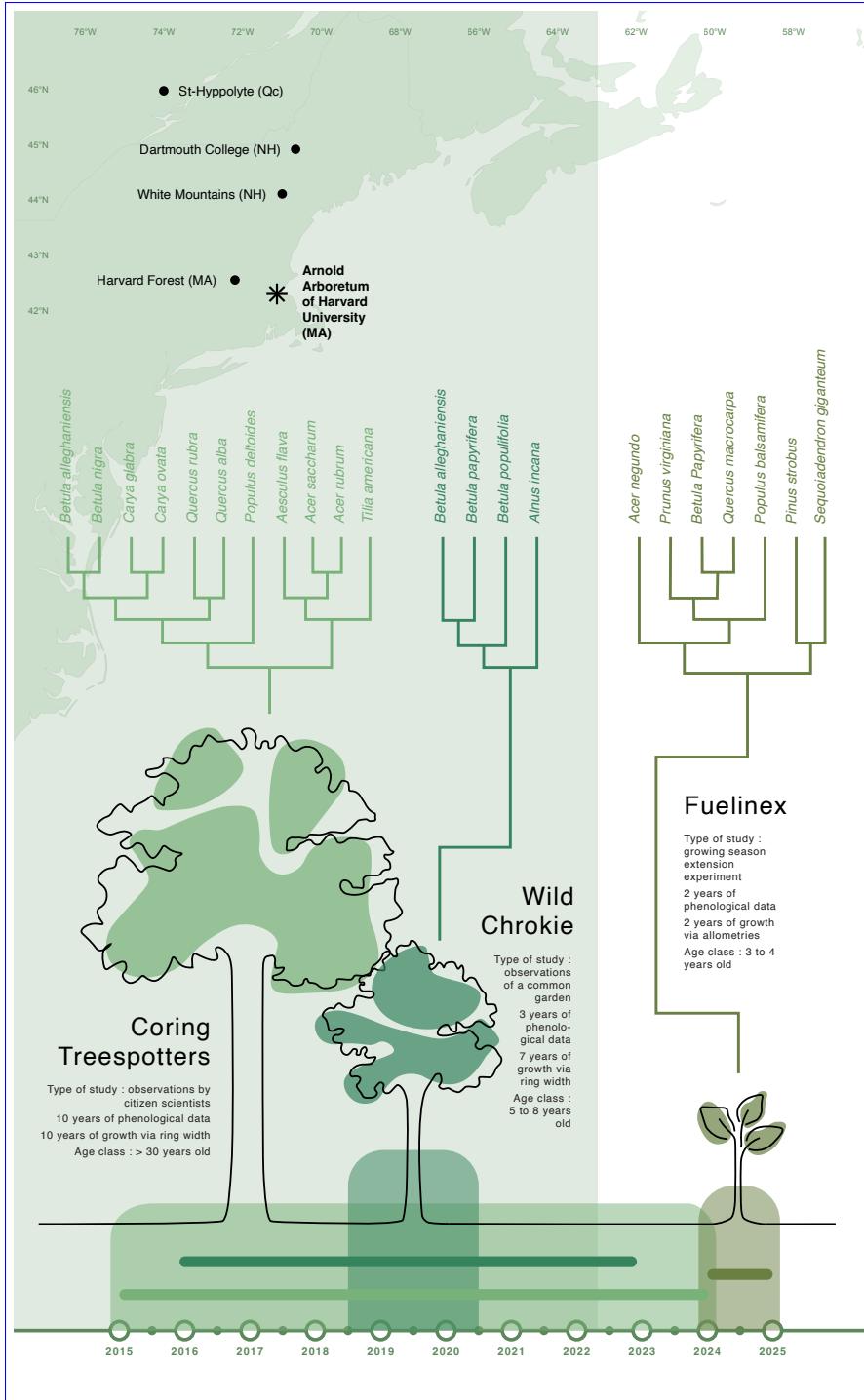


Figure 2: Overview of the age class, species, provenance of the trees used in each study along with the type of study each project consist of. The colored lines represent the period of the growth data and the shaded area, the phenological data. Each phylogenograms illustrate the species used in each project. The map illustrate the four different provenances used in Wildchrokic and the start represents the location of Wildchrokic and coringTreespotters.

228 nutrient-boosted trees) and three times during 2025, just enough to keep the trees alive (Table S4).

229

230 **Tree measurements and biomass:**

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

241

242 **Phenology and shoot elongation monitoring:**

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

247

248 *Shoot elongation:* Before shoot elongation onset, we marked a reference point with red paint at the base of
 249 either the new-year apical or the highest lateral shoot. To facilitate and improve the quality of the shoot
 250 elongation measurements, we attached paper rulers (accuracy \pm 0.1cm) on ~~A. negundo, B. papyfera, P.~~
~~balsamifera and Q. macrocarpa~~ *A. negundo, B. papyfera, P. balsamifera and Q. macrocarpa*. For species
 251 not suitable for those paper rulers, we took those same measurements, but with a metal ruler (accuracy \pm
 252 0.1cm). We measured shoot elongation weekly from the red mark to the base of the bud for angiosperms,
 253 and at the top of the apical meristem for gymnosperms. For determinate growth species (~~(A. negundo, P.~~
~~virgiana and Q. macrocarpa)~~ *A. negundo, P. virgiana and Q. macrocarpa*), when the trees did not elongate
 255 for two weeks, we started monitoring them every other week until September 1st for both growing seasons.

256

257 *Senescence:* Every week, starting on 4 September 2024, we monitored senescence by a visual assessment
 258 of the remaining green leaf cover in percentage and by measuring the chlorophyll content meter with a
~~chlorophyll content meter~~ *SPAD-502 chlorophyll meter (Minolta Camera Co. Japan)*. We also recorded
 260 the date of loss of green leaf cover and leaf drop.

261

262 **Experimental design** Individuals from each species were randomly selected for a full factorial design of
 263 Warm/Cool, Spring/Fall treatments (Figure S1) with two additional treatments to test nutrient effects in the
 264 fall (Figure 3), for a total of 15 replicates/treatment/species. On 6 March 2024, we placed the Cool Spring
 265 individuals in climate chambers to delay the start of their growing season, while the Warm Spring replicates
 266 remained at ambient conditions. Once all Warm Spring individuals ~~have had~~ fully leafed out, we removed
 267 the Cool Spring replicates from the chambers and placed them back at ambient conditions for the whole
 268 summer. On 4 September 2024, we placed the trees for the Warm Fall treatments in the climate chambers.
 269 The temperature was set to fit the mean 30-year weekly maximum temperature of the previous month (e.g.
 270 1st week of September set to the average of the 1st week of August). The Cool Fall treatment trees remained
 271 at ambient conditions. For both climate chamber treatments, we rotated and watered the trees weekly to
 272 minimize the climate chamber's effect. We also set the photoperiod regime to the corresponding sunrise and
 273 sunset of the ongoing week and ramped it until it reached full light. To test for nutrient limitation at the end
 274 of the season, we added a supplemental dose of nutrients (Table S4) to two treatments (Figure 3). In 2025,
 275 all the trees were kept at ambient conditions together at Totem field during which we ~~reorder recorded~~ the
 276 same phenophases.

277

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

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

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

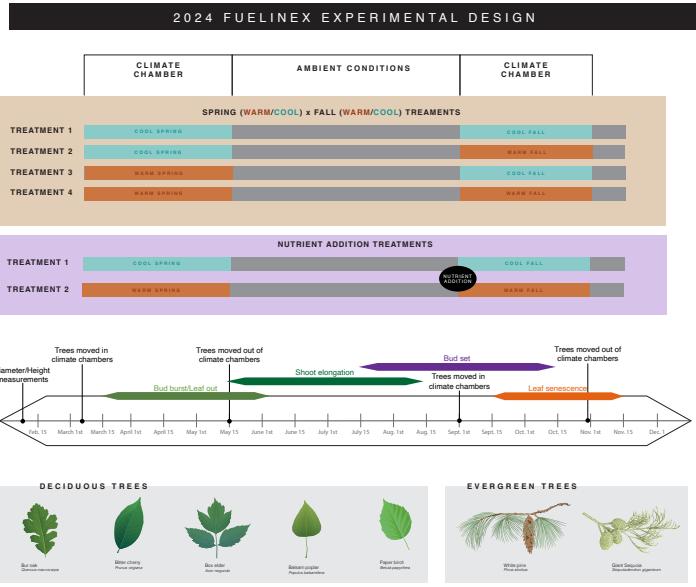


Figure 3: Experimental design during the 2024 growing season. Cooling treatments are represented in blue, and warming treatments are in orange. The grey zone in the middle represents an approximate period during the growing season where all treatments were together at ambient conditions. The colored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

282 Chapter 2: Wildchrokie and coringTreespotters

283 Wildchrokie

284 Common garden setup ([direct quote from](#) Buonaiuto, in review)

285 "In 2014-2015, we collected seeds from four field sites in northeastern North America spanning approximately
286 a 3.5° latitudinal gradient. The four field sites included Harvard Forest (42.55 °N, 72.20°W), the White
287 Mountains (44.11 °N, 71.40 °W), Second College Grant, (44.79 °N, 71.15 °W), and St. Hippolyte, QC, CAN
288 (45.98 °N, 74.01 °W) (Figure 4). We transported all seeds back to the Weld Hill Research Building at the
289 Arnold Arboretum in Boston Massachusetts (42.30 °N, 71.13 °W) where we germinated seeds following stan-
290 dard germination protocols, and grew them to seedling stages in the research greenhouse. In the spring of
291 2017, we out-planted seedlings to establish the garden. Plots were regularly weeded and watered throughout
292 the duration of the study and were pruned in the fall of 2020."
293

294 Phenological monitoring and sample collection ([direct quote from](#) Buonaiuto, in review)

295 "For the years 2018-2019, we made phenological observations of all individuals in the common garden twice
296 per week from February to December. In 2020 due to the COVID 19 pandemic, we monitored them once per
297 week from March to November. We describe phenological stages using a modified BBCH scale, a common
298 metric for quantifying woody plant phenological progression (Finn *et al.*, 2007). We observed all major veg-
299 etative stages (budburst BBCH 07, leafout BBCH 15, end of leaf expansion BBCH 19, leaf coloration/drop
300 BBCH 97, reproductive phases flowering BBCH 60-65, fruiting BBCH 72-79 and fruit/cones fully ripe BBCH
301 89). We added additional phases for budset and labelled the full budset as BBCH 102."
302 In the spring of
303 2023, we collected cross-sections for most trees and 1 tree core on a few individuals. Both the cores and
304 cross-sections were left to dry at ambient temperature for three months.
305

305 Coringtreespotters

306 Citizen science program

307 The Treespotters was a citizen science program that started in 2015 and aimed to train citizen scientists for

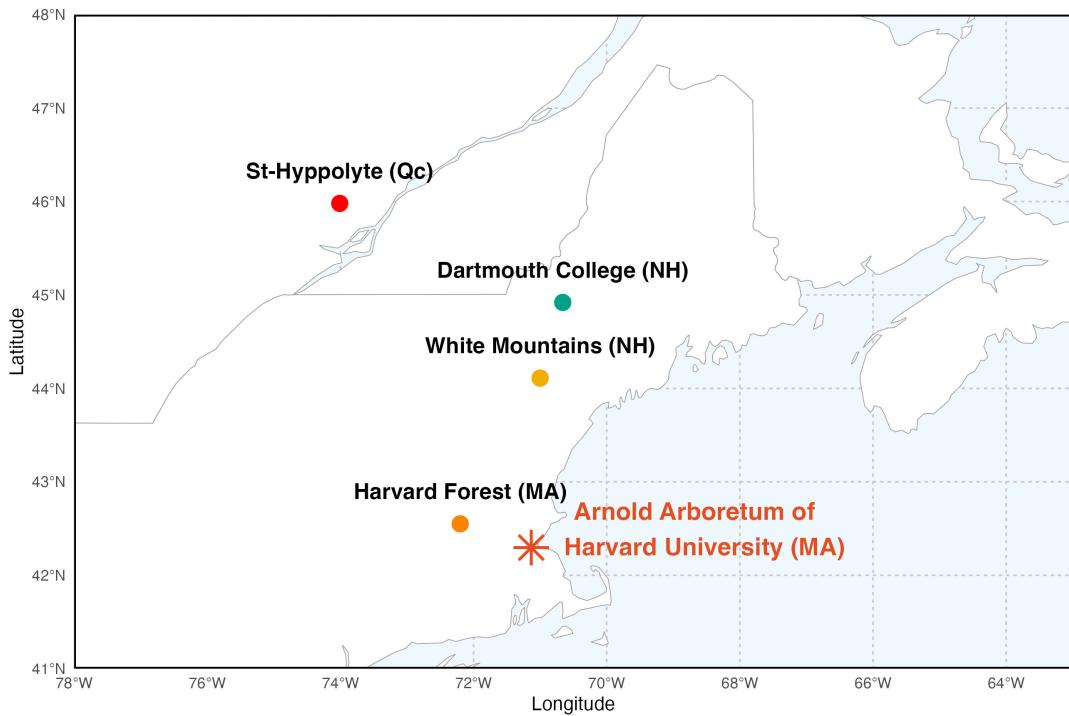


Figure 4: Locations of the provenance study for the common garden study (Wildchrokie). The common garden and the citizen science project (coringTreespotters) took place at the Arnold Arboretum of Harvard University, represented by the orange star.

308 accurate and rigorous phenological monitoring. ~~From 2015 to 2024, hundreds of citizen scientists monitored~~
 309 ~~50 trees of 11 species~~ at the Arnold Arboretum of Harvard University (42.30°N , -71.12°W) (Figure 4).
 310 ~~From 2015 to 2024, hundreds of citizen scientists monitored 50 trees of 11 species.~~ They regularly followed
 311 those individuals from budburst in the spring to leaf colouring in the fall using the National Phenology
 312 Network (NPN) phenophases (Denny *et al.*, 2014): Leaves (483), Colored leaves (498), Fruits (516), Ripe
 313 Fruits (390), Falling leaves(471), Recent fruit or seed drop (504), Increasing leaf size (467), Breaking leaf
 314 buds (371), Flowers or flower buds (500), Open flowers (501), Pollen release (502). Not all phenophases were
 315 recorded for every tree, for every year, and some trees miss several years of data.
 316

317 *Phenological monitoring and sample collection*

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

325 **326 Sample processing, imaging and measuring**

327 We mounted the cores on wooden mounts, and sanded the cores and cross-sections using ~~progressively fine~~
 328 ~~grit~~ ~~(progressively finer sandpaper (grits 150, 300, 400, 600, 800, 1000)~~. We scanned the cores and cross-
 329 sections at a resolution of 6250 dpi, with a high resolution treering scanner (Fong, unpublished). We used
 330 the digitized images to measure the tree ring widths with ~~Fiji~~ ~~ImageJ~~ ~~ImageJ (Schneider *et al.*, 2012)~~. Then,
 331 we performed visual crossdating using Dplr (Bunn, 2010), we did not perform statistical crossdating because
 332 of the short chronologies that limit the capacity of these analyses ~~(Raden *et al.*, 2020)~~.

333

334 Statistical analyses

335 For both projects, we used Bayesian hierarchical models coded in Stan with the rstan package version 2.32.7
 336 (Carpenter *et al.*, 2017) to run the Stan code in R. With these models, we estimated ringwidth as a function
 337 of growing degree days, accumulated from the leafout date to the budset date. We had three grouping
 338 factors for Wildchrokie (species, site and treeid) and two for coringTreespotters (species and treeid). We ran
 339 four chains with each 2000 warmup, which we discarded³⁴⁰ and 2000 sampling iterations, which we kept for
 340 posterior distribution estimates. The models did not have any divergent transitions and $\text{Rhat-}\hat{R}$ was below
 341 1.01.

342

343 Wildchrokie model structure

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

344 coringTreespotters model structure

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

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623 **Supplemental material**

Table S1: Fuelinex species grouped by tree type, life history, and wood anatomy.

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

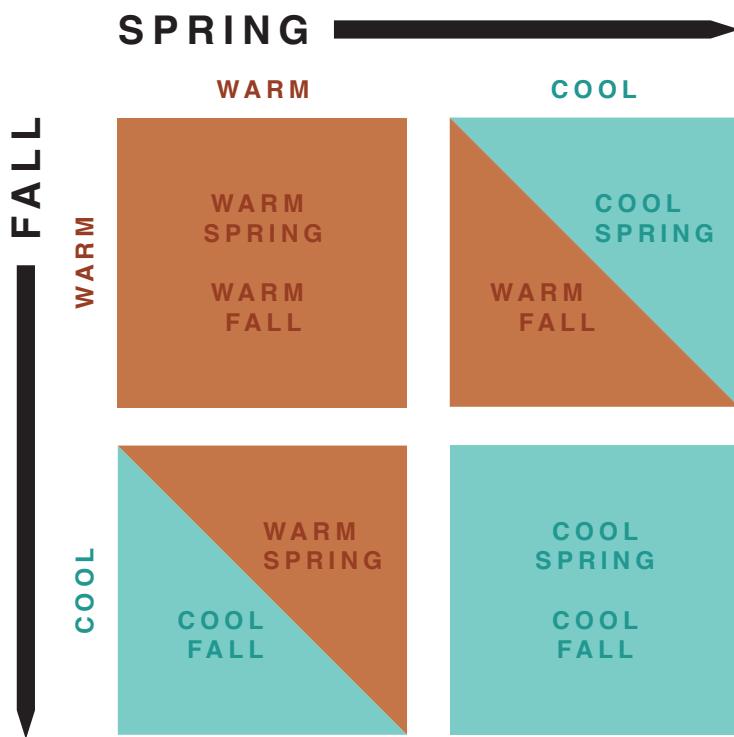


Figure S1: Arrangement of the Fuelinex four main treatments in a full factorial design

Table S2: Wilchrokic species grouped by tree type, life history, and wood anatomy.

Deciduous Trees			
Common Name (Latin)	Life History Strategy	Wood Anatomy	n
Paper birch (<i>Betula papyrifera</i>)	Fast-growth, short life	Diffuse-porous	8
Yellow birch (<i>Betula alleghaniensis</i>)	Moderate-growth, moderate life	Diffuse-porous	21
Grey birch (<i>Betula populifolia</i>)	Fast-growth, short life	Diffuse-porous	29
Grey alder (<i>Alnus incana</i>)	Fast-growth, short life	Diffuse-porous	31

Table S3: Treespotters species grouped by tree type, life history, and wood anatomy.

Deciduous Trees			
Common Name (Latin)	Life History Strategy	Wood Anatomy	n
American basswood (<i>Tilia americana</i>)	Fast-growth, moderate life	Diffuse-porous	5
Eastern cottonwood (<i>Populus deltoides</i>)	Fast-growth, short life	Diffuse-porous	4
Northern red oak (<i>Quercus rubra</i>)	Moderate-growth, long life	Ring-porous	4
White oak (<i>Quercus alba</i>)	Slow-growth, long life	Ring-porous	5
Pignut hickory (<i>Carya glabra</i>)	Slow-growth, long life	Ring-porous	4
Shagbark hickory (<i>Carya ovata</i>)	Slow-growth, long life	Ring-porous	4
River birch (<i>Betula nigra</i>)	Fast-growth, short life	Diffuse-porous	5
Yellow birch (<i>Betula alleghaniensis</i>)	Moderate-growth, moderate life	Diffuse-porous	4
Sugar maple (<i>Acer saccharum</i>)	Slow-growth, long life	Diffuse-porous	5
Red maple (<i>Acer rubrum</i>)	Slow-growth, long life	Diffuse-porous	4
Yellow buckeye (<i>Aesculus flava</i>)	Moderate-growth, moderate life	Diffuse-porous	5

Table S4: Nutrient addition over the two growing seasons for the nutrient addition treatment and the other treatments. The fertilizer is from Evergro (Delta, BC V4G 1B6), ID: Pepper Feed Main.

Date	Nutrient addition treatments	Regular treatments
7 June 2024	62.5	62.5
6 July 2024	62.5	62.5
1 Sept 2024	250	0
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 S5: 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)

Table S6: 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)).

Table S7: 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).