

¹ Does age matter in tree growth responses to longer growing season?

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³ February 5, 2026

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, 2023; Laurance, 2007; Parmesan & Yohe, 2003). This can be through land use change and loss,
⁹ 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 af-
¹² fected Earth's climate and are projected to keep changing it for many centuries (Intergovernmental Panel On
¹³ Climate Change, 2023). Yet, the extent of the consequences that a warming climate will have on biological
¹⁴ processes is still debated (Huey *et al.*, 2012), in part because it requires accurate predictions of current and
¹⁵ future trends in some of the most reported and direct biological impacts of climate change, as I review below.
¹⁶ And also because it requires understanding the complex additional effects of these impacts, which I propose
¹⁷ 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 phenology—the timing of recurring life history events (Parmesan & Yohe, 2003; Cleland *et al.*, 2007; Lieth
²¹ *et al.*, 1974; Woolway *et al.*, 2021; Menzel *et al.*, 2006). Shifts in spring and autumn phenology modify when
²² the growing season starts and when it ends. These shifts in growing season length could have impacts on
²³ ecosystems, but anticipating these consequences requires understanding how much, and why it has changed
²⁴ (Duputié *et al.*, 2015).

²⁵

²⁶ *Drivers of spring phenology:* Spring phenological events (e.g. budburst and leafout) have been advancing
²⁷ from 0.5 (Wolfe *et al.*, 2005) to 4.2 days/decade (Chmielewski & Rötzer, 2001; Fu *et al.*, 2014) and are
²⁸ mainly driven by temperature (Chuine, 2010; Cleland *et al.*, 2007; Peñuelas & Filella, 2001), especially for
²⁹ trees. In the winter, when trees are still in dormancy, they accumulate cold temperatures (chilling) for which
³⁰ a certain amount is required to be ready to accumulate heat (forcing) (Vitasse *et al.*, 2014). Then, in the
³¹ spring, a certain amount of forcing triggers budburst (Fu *et al.*, 2015). Heat requirements are met sooner
³² in warm springs, thus explaining the advancement of spring events and earlier onset of growing seasons over
³³ the last decades (Fu *et al.*, 2015, 2013; Laube *et al.*, 2014).

³⁴

³⁵

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

45 *et al.*, 2021). Additionally, summer droughts could pause the activity schedule of trees and delay senescence
46 to increase carbon assimilation (Dox *et al.*, 2022). Finally, there could be other factors affecting senescence
47 delays that we do not consider here, such an antagonistic effect of warming and atmospheric brightening
48 (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 extend seasons and thus increase growth (Keenan *et al.*, 2014; Stridbeck
53 *et al.*, 2022). However, research from recent years has cast doubt on this hypothesis (Dow *et al.*, 2022;
54 Green & Keenan, 2022; Silvestro *et al.*, 2023). For instance, Dow *et al.* (2022) showed that despite an earlier
55 growth onset, longer seasons did not increase the growth rate nor overall annual increment in trees. This could
56 substantially affect forest carbon-cycle model projections on and thus feedbacks to future climate (Richardson
57 *et al.*, 2013; Swidrak *et al.*, 2013). These projections could be impacted by the different effects that an
58 earlier start and a later end of season have on trees, some of which I propose to study in my thesis (Figure 1).

59

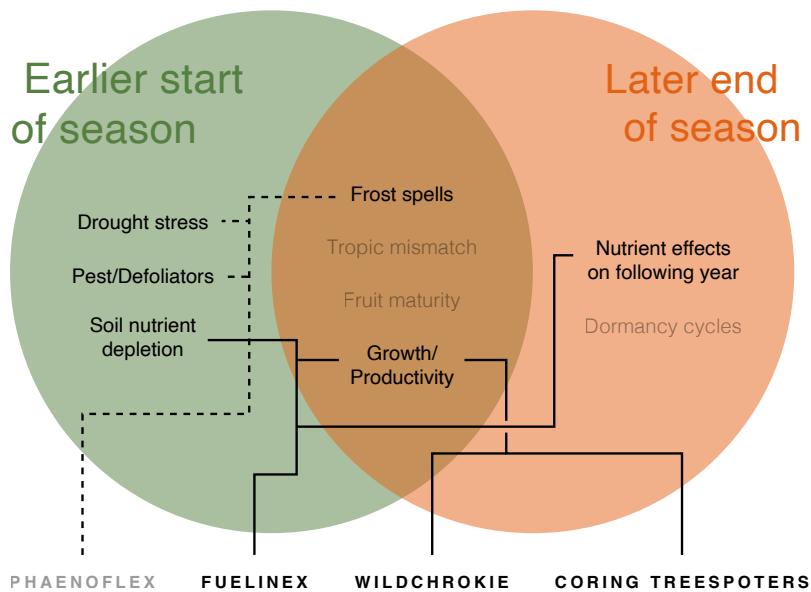


Figure 1: The effects that an earlier start and later end of season can have on trees. Solid lines connect effects studied over the course of this thesis. Phaenoflex (in grey) and its dashed lines represent other effects I investigated in a related experimental project that is not part of this thesis,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

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 allo-
62 cated into wood is poorly understood. Indeed, the assumption of a linear relationship between wood growth
63 and carbon assimilation is not well supported mechanistically and represents an important limitation of
64 vegetation models (Cabon *et al.*, 2022). Net primary production represents the difference between photosyn-
65 thesis and plant respiration, but this commonly used metric omits the representation of growth processes.
66 This is perhaps because of a long-lasting paradigm of source-limited photosynthesis (Friend *et al.*, 2019;
67 Parent *et al.*, 2010). Whether a tree's growth is source (photosynthetic activity determines sink activity) or
68 sink (growth, respiration, and other metabolic processes determine the carbon source) controlled depends
69 upon a closely coordinated sequence of dynamic responses and is still an active research question. However,

70 Gessler & Zweifel (2024) recently suggested that neither source nor sink control systematically dominates.
71 This complex dynamic enforces the importance of understanding the temperature sensitivity relationship
72 between growth activity and photosynthesis. Growing evidence suggests that cambial activity may be more
73 sensitive than photosynthesis to a range of environmental conditions, such as water and nutrient availability,
74 and temperature (Cabon *et al.*, 2022, 2020; Muller *et al.*, 2011; Peters *et al.*, 2021). Thus, this demonstrates
75 that carbon projection models that solely rely on vegetation may mislead carbon sequestration dynamics of
76 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 to
90 warming are very likely to be non-linear (Ettinger *et al.*, 2020; Fu *et al.*, 2013). Indeed, accurate predic-
91 tions require an in-depth mechanistic understanding of phenophases and their sensitivities to environmental
92 drivers, especially to temperature and photoperiod (Fu *et al.*, 2013). Therefore, the very foundation of the
93 assumption that longer seasons increase growth may shift with future climate change. The well-observed
94 advance in spring phenology may decelerate, and delayed fall phenology may shift towards earlier leaf senes-
95 cence (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 missing important nu-
103ANCES in the growth responses plausibly explained by species differences. Excluding species differences in
104 models may mislead future carbon dynamic models (Green & Keenan, 2022; Cabon *et al.*, 2022; Wolkovich
105 *et al.*, 2025). We propose to address this issue by using experiments and ground-based observations to better
106 understand the responses of different species to warming. While both of these strategies have downsides,
107 they are likely to leverage valuable insights which are necessary to improve carbon sequestration projections
108 (Wolkovich *et al.*, 2025).

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

122
123 *Ground-based observations:* Second, leaf phenology can provide valuable and accessible insights into the
124 growth temporality of trees that are not suitable for experimental trials. Collecting cambial phenology
125 data, which is a direct measure of wood growth, is time-consuming and expensive. In contrast, leaf phenology
126 through ground-based observations are low-cost methods that provide direct evidence of changing
127 phenophases (Piao *et al.*, 2019). Cambial and leaf phenology are often closely synchronized (Stridbeck *et al.*,
128 2022); therefore, the more accessible leaf phenology data can act as a reliable proxy for the onset and end of
129 tree growth. In other words, knowing when leaves elongate and colour can guide as to when trees start and
130 stop growing, which is a fundamental metric to determine the growing season length. Additionally, unlike
131 other methods, ground observations have the advantage of providing accurate measurements of phenological
132 events for specific sites and species. Recently, the widespread use of smartphones has considerably simplified
133 the phenological monitoring by citizen scientists (Dickinson *et al.*, 2012; Hufkens *et al.*, 2019; Piao *et al.*,
134 2019). While there are drawbacks to observations by citizen science programs (e.g. non-standard protocols,
135 highly uneven spatiotemporal distribution of these observations), they have the potential to vastly increase
136 the range of studied species and areas (Chandler *et al.*, 2017; Feldman *et al.*, 2018).

137
138 **Goals of my thesis**

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

149 **Complexity of measuring growth and defining growing season length**

150 **What is a growing season?**

151 The definition of the growing season itself is not well-defined, and studies use an array of definitions. Recently,
152 Körner *et al.* (2023) proposed four definitions addressing this issue: (1) true growing season, based on
153 measurable growth; (2) phenological season, based on visible phenological markers; (3) the productive season,
154 based on primary production and (4) meteorological season, based on environmental conditions.
155 Here, I will focus on how the phenological season (2), incorporating the meteorological season (4), affects the
156 true growing season (1), as our data cannot address the productive season (3). I will use the phenological
157 season (2) to infer a “window of opportunity”, to calculate growing degree days (GDD)—a measure of heat
158 accumulation—using meteorological conditions.

159
160 **What is growth?**

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

165
166 Foresters have measured tree diameter and height for decades, but these measurements may not be suitable
167 for determining relationships between growth and environmental conditions. The widely used method in
168 forestry is to measure diameter at breast height at punctual time intervals. Combined with height, these
169 data help develop allometries foresters can use to estimate how much wood they can harvest in a forest (e.g.,
170 Meyer, 1940; Saunders & Wagner, 2008). These metrics work to determine wood in forests, but their coarse
171 temporal scale—measuring every 5 or more years—is likely to miss extreme events affecting growth.

172
173 Alongside the diameter-height allometric relationship, dendroecology—applications of dendrochronological

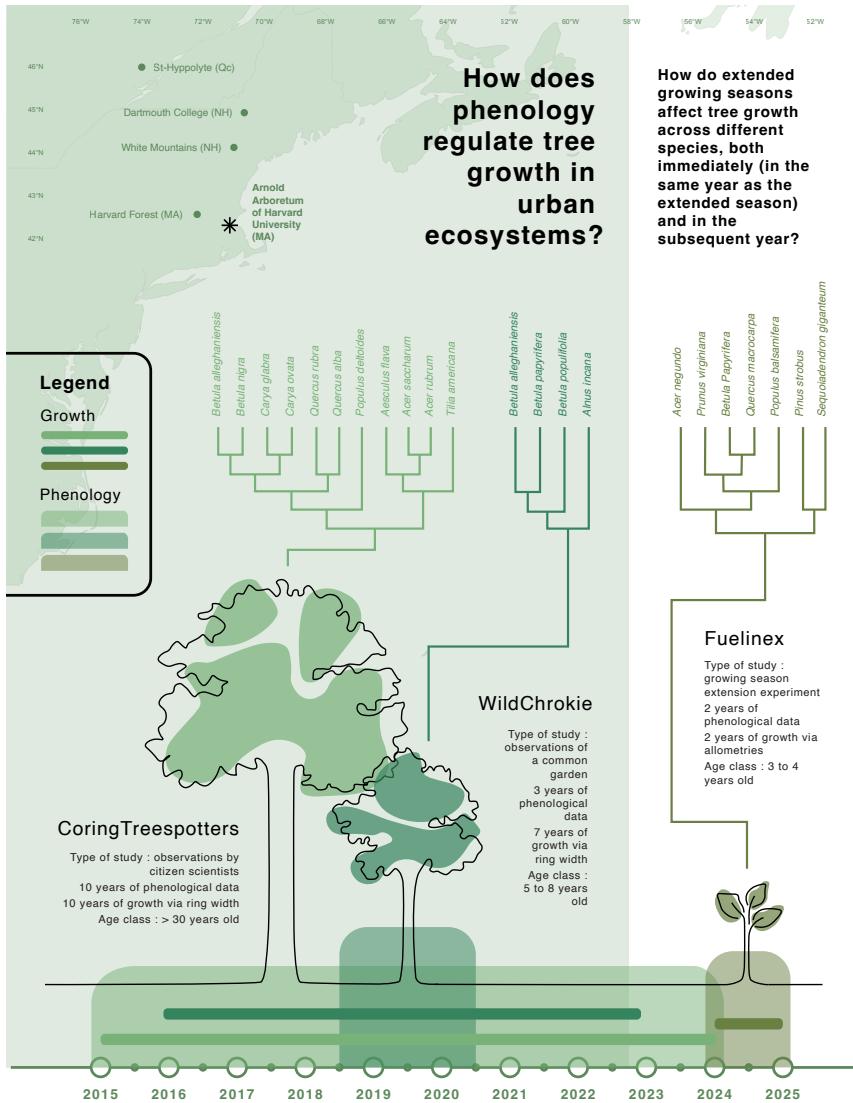


Figure 2: Overview of the age class, species, provenance of the trees used in each study along with the type of study each project consists of. The colored lines represent the period of the growth data and the shaded areas are the phenological data. Both are colour-coded by project. Each phylogram illustrates the species used in each project. The map illustrates the four different provenances used in Wildchrokie, and the star represents the location of Wildchrokie and coringTreespotters.

174 techniques to problems in ecology (Fritts & Swetnam, 1989)—emerged to answer ecological problems as well
 175 as to hindcast (e.g., Bergeron *et al.*, 2004)) and forecast ecological processes both at the regional (Gazol
 176 *et al.*, 2018) and global scale (Manzanedo & Pederson, 2019; Büntgen *et al.*, 2018). Now, these methods can
 177 unveil more precise growth patterns and their relationship with different environmental factors. This is why
 178 I will use tree rings as a proxy for how much trees grew in any given year.
 179

180 Objectives

181 The objectives for my experiment (Fuelinex) are to assess tree species' potential to prolong or stretch their
 182 activity schedule by artificially manipulating growing season length and analyze how this translates (or not)
 183 into growth, during the current year (2024) and in the following year (2025). I will also conduct a secondary

184 experiment to examine whether trees can absorb nutrients late in the season and if that translates into growth
185 during the following season. For the observational data projects (Wildchrokic and coringTreespotters), I will
186 investigate how the timing of phenological events affects growth across years for juvenile and mature trees,
187 using observational phenology data and tree rings. The duration and type of study, the age classes and species
188 used in each project are presented in Figure 2). Together, my two chapters will allow me to investigate the
189 decoupling between growth increment in response to longer growing seasons.

190 **Research questions**

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

194

195 **Methodology**

196 **Chapter 1: Fuelinex**

197 **Species selection and growing conditions** We used seven species of tree saplings for our experiment
198 (Fuelinex). We purchased Paper birch (*Betula papyfera*), Choke Cherry (*Prunus virginiana*), Bur oak (*Quer-*
199 *cus macrocarpa*) from Peel's nursery in November 2023 and the trees arrived at Totem Field studios (49.26
200 °N, -123.25 °W), where the other four species were stored until the spring of 2023. Manitoba maple (*Acer*
201 *negundo*), Eastern white pine (*Pinus strobus*), Balsam poplar (*Populus balsamifera*) and Giant sequoia (*Se-*
202 *quoiadendron giganteum*) were leftover trees that we purchased in 2022 for 2023 for a previous experiment.
203 We watered them weekly, and they remained at ambient conditions for the 2023 growing season. We ran-
204 domly selected 90 individuals of each species among them. We propagated *P. balsamifera* from 30 cm whips
205 while the trees were still dormant (Mc Carthy *et al.*, 2018). In May 2024, we repotted all the trees in
206 2-gallon plastic pots with a medium for perennials consisting of 50 % peat, 25% crushed pumice and 25%
207 crushed bark (purchased from www.westcreekfarm.com). In February 2025, we repotted the trees with the
208 same medium in 3-gallon pots. We arranged the trees in three blocks, each containing all 6 treatments and 7
209 species, with two of these blocks placed under an open-walled and well-ventilated polytunnel greenhouse. All
210 saplings were connected to a drip irrigation system (40 PVC frame from Netafilm 54 with a Toro controller)
211 to maintain constant irrigation across the season. Using fertilizer premix, we fertilized the trees twice during
212 the growing season of 2024 (except for the nutrient-boosted trees) and three times during 2025, just enough
213 to keep the trees alive (Table S4).

214

215 **Tree measurements and biomass:**

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

226

227 **Phenology and shoot elongation monitoring:**

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

232

233 *Shoot elongation*: Before shoot elongation onset, we marked a reference point with red paint at the base of ei-
 234 ther the new-year apical or the highest lateral shoot. To facilitate and improve the quality of the shoot elonga-
 235 tion measurements, we attached paper rulers (accuracy $\pm 0.1\text{cm}$) on *A. negundo*, *B. papyfera*, *P. balsamifera*
 236 and *Q. macrocarpa*. For species not suitable for those paper rulers, we took those same measurements, but
 237 with a metal ruler (accuracy $\pm 0.1\text{cm}$). We measured shoot elongation weekly from the red mark to the base
 238 of the bud for angiosperms, and at the top of the apical meristem for gymnosperms. For determinate growth
 239 species (*A. negundo*, *P. virginiana* and *Q. macrocarpa*), when the trees did not elongate for two weeks, we
 240 started monitoring them every other week until September 1st for both growing seasons.

241
 242 *Senescence*: Every week, starting on 4 September 2024, we monitored senescence by a visual assessment of
 243 the remaining green leaf cover in percentage and by measuring the chlorophyll content meter with a SPAD-
 244 502 chlorophyll meter (Minolta Camera Co. Japan). We also recorded the date of loss of green leaf cover
 245 and leaf drop.

246

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, crin- kled 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 (Figure S1) with two additional treatments to test nutrient effects in the
 249 fall (Figure 3), for a total of 15 replicates/treatment/species. On 6 March 2024, we placed the Cool Spring
 250 individuals in climate chambers to delay the start of their growing season, while the Warm Spring replicates
 251 remained at ambient conditions. Once all Warm Spring individuals had fully leafed out, we removed the
 252 Cool Spring replicates from the chambers and placed them back at ambient conditions for the whole sum-
 253 mer. On 4 September 2024, we placed the trees for the Warm Fall treatments in the climate chambers. The
 254 temperature was set to fit the mean 30-year weekly maximum temperature of the previous month (e.g. 1st
 255 week of September set to the average of the 1st week of August). The Cool Fall treatment trees remained
 256 at ambient conditions. For both climate chamber treatments, we rotated and watered the trees weekly to
 257 minimize the climate chamber's effect. We also set the photoperiod regime to the corresponding sunrise and
 258 sunset of the ongoing week and ramped it until it reached full light. To test for nutrient limitation at the
 259 end of the season, we added a supplemental dose of nutrients (Table S4) to two treatments (Figure 3). In
 260 2025, all the trees were kept at ambient conditions together at Totem field during which we recorded the
 261 same phenophases.

262

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

265 *P. virginiana* and *Q. macrocarpa*).

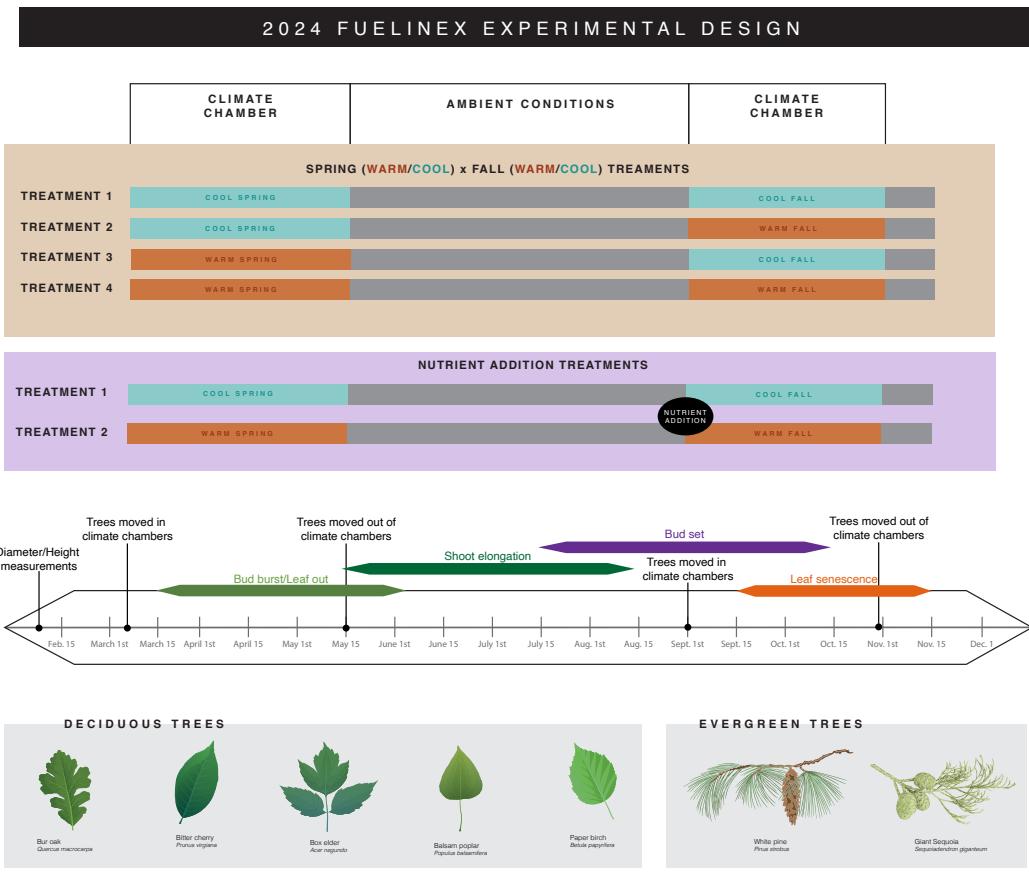


Figure 3: Experimental design during the 2024 growing season. Cooling treatments are represented in blue, and warming treatments are in orange. The grey zone in the middle represents an approximate period during the growing season where all treatments were together at ambient conditions. The colored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

266 Chapter 2: Wildchrokie and coringTreespotters

267 Wildchrokie

268 *Common garden setup (direct quote from Buonaiuto, in review)*

269 “In 2014-2015, we collected seeds from four field sites in northeastern North America spanning approximately
270 a 3.5° latitudinal gradient. The four field sites included Harvard Forest (42.55 °N, 72.20°W), the White
271 Mountains (44.11 °N, 71.40 °W), Second College Grant, (44.79 °N, 71.15 °W), and St. Hippolyte, QC, CAN
272 (45.98 °N, 74.01 °W) (Figure 4). We transported all seeds back to the Weld Hill Research Building at the
273 Arnold Arboretum in Boston Massachusetts (42.30 °N, 71.13 °W) where we germinated seeds following stan-
274 dard germination protocols, and grew them to seedling stages in the research greenhouse. In the spring of
275 2017, we out-planted seedlings to establish the garden. Plots were regularly weeded and watered throughout
276 the duration of the study and were pruned in the fall of 2020.”

277

278 *Phenological monitoring and sample collection (direct quote from Buonaiuto, in review)*

279 “For the years 2018-2019, we made phenological observations of all individuals in the common garden twice
280 per week from February to December. In 2020 due to the COVID 19 pandemic, we monitored them once per
281 week from March to November. We describe phenological stages using a modified BBCH scale, a common

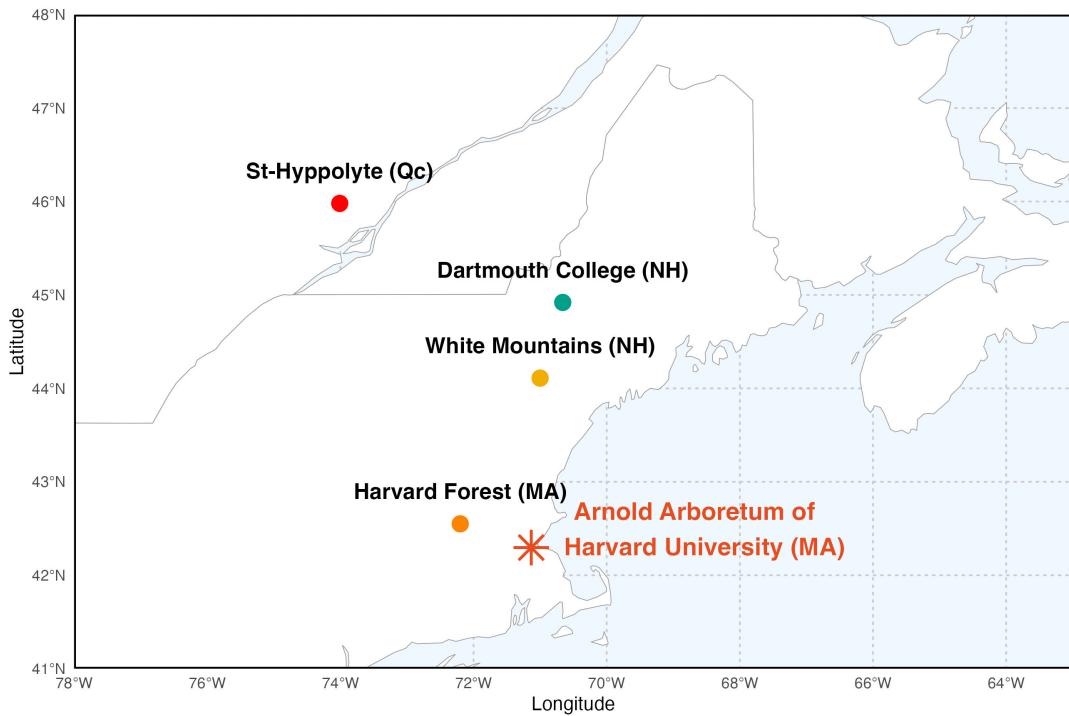


Figure 4: Locations of the provenance study for the common garden study (Wildchrokie). The common garden and the citizen science project (coringTreespotters) took place at the Arnold Arboretum of Harvard University, represented by the orange star.

metric for quantifying woody plant phenological progression (Finn *et al.*, 2007). We observed all major vegetative stages (budburst BBCH 07, leafout BBCH 15, end of leaf expansion BBCH 19, leaf coloration/drop BBCH 97, reproductive phases flowering BBCH 60-65, fruiting BBCH 72-79 and fruit/cones fully ripe BBCH 89). We added additional phases for budset and labelled the full budset as BBCH 102.” In the spring of 2023, we collected cross-sections for most trees and 1 tree core on a few individuals. Both the cores and cross-sections were left to dry at ambient temperature for three months.”

288

289 Coringtreespotters

290 Citizen science program

291 The Treespotters was a citizen science program that started in 2015 and aimed to train citizen scientists for
 292 accurate and rigorous phenological monitoring at the Arnold Arboretum of Harvard University (42.30 °N,
 293 -71.12 °W) (Figure 4). From 2015 to 2024, hundreds of citizen scientists monitored 50 trees of 11 species.
 294 They regularly followed those individuals from budburst in the spring to leaf colouring in the fall using the
 295 National Phenology Network (NPN) phenophases (Denny *et al.*, 2014): Leaves (483), Colored leaves (498),
 296 Fruits (516), Ripe Fruits (390), Falling leaves(471), Recent fruit or seed drop (504), Increasing leaf size (467),
 297 Breaking leaf buds (371), Flowers or flower buds (500), Open flowers (501), Pollen release (502). Not all
 298 phenophases were recorded for every tree, for every year, and some trees miss several years of data.

299

300 Phenological monitoring and sample collection

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

307

308 Sample processing, imaging and measuring

309 We mounted the cores on wooden mounts, and sanded the cores and cross-sections using progressively finer
 310 sandpaper grits: 150, 300, 400, 600, 800, 1000. We scanned the cores and cross-sections at a resolution
 311 of 6250 dpi, with a high-resolution treering scanner (Fong, unpublished). We used the digitized images to
 312 measure the tree ring widths with ImageJ (Schneider *et al.*, 2012). Then, we performed visual crossdating
 313 using DplR (Bunn, 2010), we did not perform statistical crossdating because of the short chronologies that
 314 limit the capacity of these analyses (Raden *et al.*, 2020).

315

316 Statistical analyses

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

323

324 Wildchrokie model structure

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

325 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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604 **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>Sequoiadendron giganteum</i>)	Slow-growth, long life	Non-porous	54

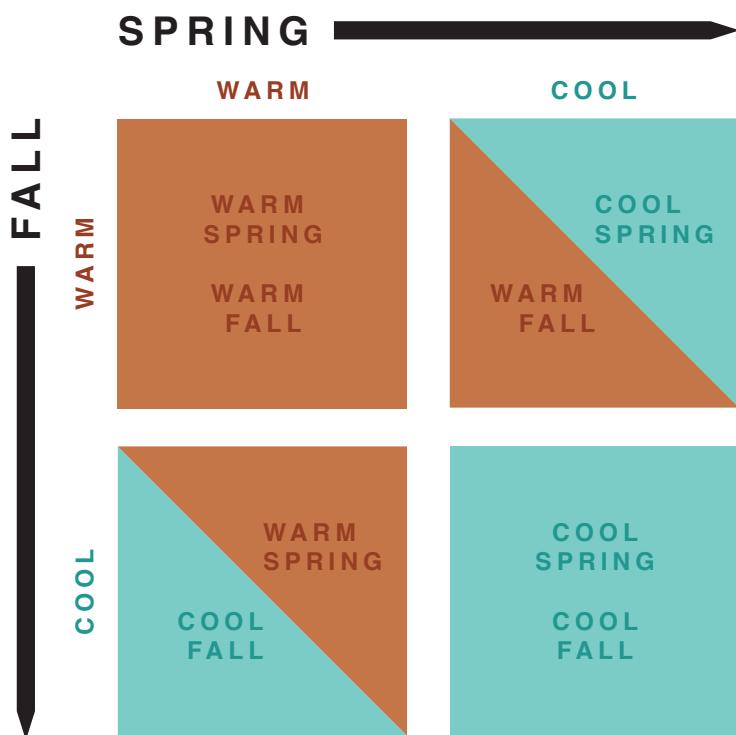


Figure S1: Arrangement of the Fuelinex four main treatments in a full factorial design

Table S2: 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 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 mL	62.5 mL
6 July 2024	62.5 mL	62.5 mL
1 Sept 2024	250 mL	0 mL
Subtotal (2024)	375	125
10 April 2025	0 mL	125 mL
9 May 2025	0 mL	125 mL
June 2025	62.5 mL	62.5 mL
July 2025	62.5 mL	62.5 mL
Subtotal (2025)	125 mL	375 mL
2-year total	500 mL	500 mL

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).