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Thesis Proposal

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3

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1 Introduction

5

1.1 Climate change impacts on tree phenology

6

Research from the past decades has shown convincing evidence that human activity is increasingly affecting many worldwide environmental processes (Ceballos *et al.*, 2017; Intergovernmental Panel On Climate Change (Ipcc), 2023; Laurance, 2007; Parmesan & Yohe, 2003). This can be through land use change and loss, pollution, invasive species, resource overexploitation and climate change (Driscoll *et al.*, 2018; Parmesan *et al.*, 1999; Wu, 2013). Though some immediate actions can mitigate these impacts (e.g. (Campbell *et al.*, 2014)), reversing 150 years of human-induced greenhouse gas emissions is harder. These emissions have affected Earth's climate and are projected to keep changing it for many centuries (Intergovernmental Panel On Climate Change (Ipcc), 2023). Yet, the extent of the consequences that a warming climate will have on biological processes is still debated (Huey *et al.*, 2012), in part because it requires accurate predictions of current and future trends in some of the most reported and direct biological impacts of climate change, as I review below. And also because it requires understanding the complex additional effects of these impacts, 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 spring and autumn phenology—the timing of recurring life history events (Parmesan & Yohe, 2003; Cleland *et al.*, 2007; Lieth *et al.*, 1974; Woolway *et al.*, 2021; Menzel *et al.*, 2006). Together, shifts in spring and autumn phenology modify when the growing season starts and when it ends. Understanding the consequences of changing growing season length on ecosystems requires understanding how much, and why it has changed (Duputié *et al.*, 2015).

26

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

35

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

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

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

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

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

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

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

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

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

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

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

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

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

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

122
123 **1.2.2.2. Ground based observations:** Second, leaf phenology through ground-based observations can
124 provide valuable and accessible insights into the growth temporality of trees that are not suitable for experi-
125 mental trials. Since cambial and leaf phenology are closely linked, having the more accessible leaf phenology
126 data can act as a reliable proxy for the onset and end of tree growth. It is to say that knowing when leaves
127 elongate and colour can guide when trees start and stop growing—fundamental metrics to determine the
128 growing season length. Ground observations have the advantage of providing accurate data on phenological
129 events for specific sites and species. Recently, the widespread use of smartphones has opened a whole new
130 world of possible phenological monitoring through citizen scientists' records of data over much larger areas
131 and for a wider range of species (Dickinson *et al.*, 2012; Hufkens *et al.*, 2019; Piao *et al.*, 2019). While there
132 are drawbacks to these observations (e.g. non-standard protocols, highly uneven spatiotemporal distribution
133 of these observations), these methods have a huge potential to diversify the phenology data.

134
135 **1.2.3. Goals of my thesis**

136 Using citizen science data, a common garden study and a large-scale experiment, I aim to better understand
137 how different tree species, at different lifespan stages, vary in their growth responses to different season
138 length. Answering these patterns requires specifying the definitions of growth and the growing season.

139 **1.3 Complexity of measuring growth and defining growing season length**

140 **1.3.1.1. What is a growing season?**

141
142 The definition of the growing season itself is not a well-defined concept and an array of definitions are
143 used differently accross studies. Recently, Körner *et al.* (2023) proposed four definitions addressing this issue:
144 (1) true growing season, based on measurable growth; (2) phenological season, based on visible phenological
145 markers; (3) the productive season, based on primary production and (4) meteorological season, based on
146 environmental conditions.

147 Here, I will focus on how definition (2), incorporating (4), affects definition (1) as the data collected
148 for this thesis can't address (3). I will use definition (2) to infer a "window of opportunity", to calculate

149 growing degree days (GDD)—a measure of heat accumulation—using meteorological conditions. I am using
150 the meteorological season within a constrained window, instead of simply using it irrespective of phenology
151 because of the illusion that an absolute increase in GDD over the last decades—irrespective of the timing of
152 phenophases—also increases growth. Springs are warmer, falls are also sometimes warmer, and summers are
153 warmer, which together increase the number of GDD, which may appear to be a reliable proxy for better
154 environmental conditions. However, models that accumulate GDD before and/or after trees grow could
155 mislead about how this variable drives growth.

156 *1.3.1.2. What is growth?*

157 Wood formation (xylogenesis) consists of allocating carbon for long-term storage in woody plants. Xylogenesis
158 starts with cambial activation and cell production which produces xylem and phloem cells (Etzold *et al.*,
159 2022; Silvestro *et al.*, 2025). The rate and duration of these phases lead to irreversible radial growth incre-
160 ments usually represented through tree rings. In these, secondary xylem cells account disproportionately to
161 the number of cells produced because they divide more than phloem cells (Plomion *et al.*, 2001; Rathgeber
162 *et al.*, 2016).

163
164 **1.3.2. Traditional diameter measurements miss the resolution of annual growth increment**
165 Foresters have measured tree diameter and height for decades, but these measurements may not be suitable
166 for determining relationships between growth and environmental conditions. Diameter and—sometimes—
167 height are used infer allometries that could provide an estimate in how much wood could be harvested in a
168 forest (e.g. (Meyer, 1940; Saunders & Wagner, 2008)). The widely used method in forestry is to measure
169 diameter at breast height at punctual time intervals (Yuancai & Parresol, 2001). However, these measure-
170 ments don't provide short-term indicators of growth, and are likely to miss extreme events affecting growth.
171 This growth data lacks the temporal resolution necessary to properly infer a robust relationship between
172 growth and environmental conditions.

173
174 **1.3.3. Dendroecology to analyses growth responses to changing growing season length**
175 Alongside the diameter-height allometric relationship, dendroecology—applications of dendrochronological
176 techniques to problems in ecology (Fritts & Swetnam, 1989)—emerged to answer ecological problems as well
177 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
179 can be used to understand more precise growth patterns and their relationship with different environmental
180 factors. This is why I will use tree rings as a proxy for how much trees grew in any given year.

181

182 **1.4 Objectives**

183 My objectives for Fuelinex are to assess tree species' potential to prolong or stretch their activity schedule
184 by artificially manipulating growing season length and analyze how this translates (or not) into growth,
185 during the current year (2024) and in the following year (2025). I will also conduct a secondary experiment
186 to examine whether trees can absorb nutrients late in the season and if that translates into growth during
187 the following season. For the WildSpotters projects, I will investigate how the timing of phenological events
188 affects growth across years for juvenile and mature trees, using observational phenology data and tree ring.

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

191 **1.5 Research questions**

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

195

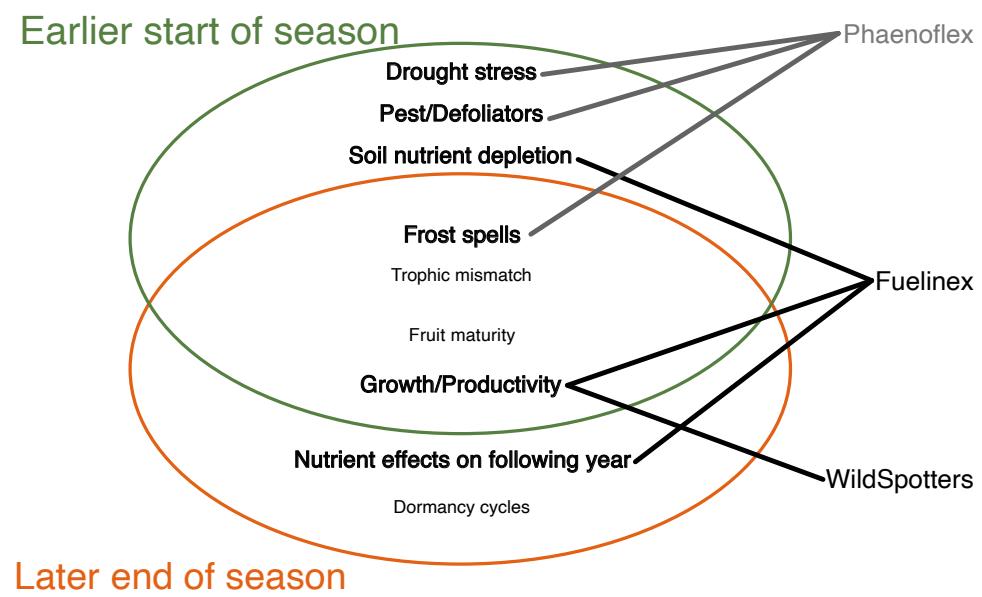


Figure 1: The effects that an earlier start and later end of season can have on trees. In bold are the effects that were studied over the course of this thesis. Phaenoflex (in grey) is a related experimental project, that is not part of this thesis, but one I collaborated on in XX years.

196 **2 Methodology**

197 **2.1 Wildchrokic**

198 **2.1. Studies locations**

199 **Common garden** *** what follows are the methods from the wildhell repo In 2014-2015, we collected seeds
200 from four field sites in northeastern North America spanning approximately a 3.5° latitudinal gradient. The
201 four field sites included Harvard Forest (42.55°N, 72.20°W), the White Mountains (44.11°N, 71.40°W),
202 Second College Grant, (44.79°N, 71.15°W), and St. Hippolyte, QC, CAN (45.98°N, 74.01°W). We trans-
203 ported all seeds back to the Weld Hill Research Building at the Arnold Arboretum in Boston Massachusetts
204 (42.30°N, 71.13°W) where we germinated seeds following standard germination protocols, and grew them
205 to seedling stages in the research greenhouse. In the spring of 2017 we out-planted seedlings to establish the
206 garden. Plots were regularly weeded and watered throughout the duration of the study and were pruned in
207 the fall of 2020.

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

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

217 **Coringtreespotters** The Treespotters is a citizen science program that started in 2015 and aimed to
218 train citizen scientist for accurate and rigorous phenological monitoring. From 2015 to 2024, hundreds of
219 citizen scientists monitored 50 trees of 11 species regularly from budburst in the spring to leaf colouring in
220 the fall. The BBCH scale was used (check if that's true). Not all phenophase was recorded for every tree,
221 for every year, and some trees miss several several years of data.

222 From 20 to 22 April 2025, we collected two 5-mm diameter core, 15-cm length at 1.3 meter above
223 ground from 50 trees of the 11 species (Table XX) that were previously monitored for phenology, using
224 an increment borer (Mora Borer, Haglöfs Sweden, Bromma, Stockholm, Sweden). The cores were collected
225 perpendicularly to the slope and at 180 degrees from each other. We cleaned the increment borer with alcohol
226 (70% ethanol?) and the inside with a brush before collecting each core. We stored the cores in paper straws
227 that were previously labelled and punched to help drying. They were stored at ambient temperature for
228 three months.

229 **Sample processing, imaging and measuring for WildSpotters** We mounted the cores on wooden
230 mounts, and sanded the cores and cross-sections using progressively fine grit (150, 300, 400, 600, 800,
231 1000). We scanned the cores and cross-sections at a resolution of ***dpi using a homemade great scanner
232 (Tina2026?) We used the digitalized images to measure the tree ring widths with Fiji Image J. Then, we
233 performed visual crossdating using Dpl, but no statistical crossdating was performed because of the short
234 chronologies that limit the capacity for these analyses.

235 **Statistical analyses**

236 **2.2 Fuelinex**

237 The experimental design of fuelinex is described in the figure.

238 **3 Supplemental material**

239 **3.1 Wildchrokic**

- 240 1. Common garden from 2015 to 2023
241 2. Four species within the Betulacea family (Table 2)

- 242 3. Data: phenology, height, tree rings
- 243 4. Analysis: Hierarchical model to understand how tree ring width relates to GDD

244 **3.2 Treespotters**

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

249 **3.1. Spring frosts**

Definition:	Late spring frosts are below-freezing temperatures in late spring (Zohner <i>et al.</i> , 2020)
Mechanisms	Early warm spells → early leaf out → hard frost (<-2Celsius) → tissue death = loss of photosynthetic capacity (Polgar & Primack, 2011); Response: second cohort of leaves are more efficient and mitigate carbon sequestration loss (Reinmann <i>et al.</i> , 2023)
Global trend of occurrence	Most vulnerable regions are the ones with no past risk of occurrence (); ↑ in Europe and East Asia, but ↓ North America; Global trend is controversial (Reinmann <i>et al.</i> , 2023)
Consequences (Individual and Ecosystem level consequences)	Loss of vegetative tissue = ↓ photosynthesis = ↓ and remobilization of NSC to repair damaged tissues = ↓ secondary growth (Meyer <i>et al.</i> , 2024); Loss of reproductive tissue (higher flower mortality) (Sgubin <i>et al.</i> , 2018); Costs for orchards and stuff (Reinmann <i>et al.</i> , 2023)
Differences across species/provenance	

Table 1: Fuelinex species grouped by tree type, life history, and wood anatomy.

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

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

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

Table 3: Treespotters species grouped by tree type, life history, and wood anatomy.

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

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3.2. Drought

252

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 (aka global-change-type drought (Tyree & Zimmermann, 2002)) = ↑ evapotranspiration → less water in soil → cavitation → embolism → hydraulic failure (Tyree & Zimmermann, 2002) = tissue death (Choat <i>et al.</i>, 2018); — Earlier spring phenology = longer GS → increases vegetative growth → increases evapotranspiration → increases drawdown of soil moisture = progressive water stress (Li <i>et al.</i>, 2023) — Long-term vs short-term stomatal responses and consequences on tissue death (Choat <i>et al.</i>, 2018); — Recovery and its determinants (Choat <i>et al.</i>, 2018; Li <i>et al.</i>, 2023)
Global trend of occurrence	<ul style="list-style-type: none"> — ↑ precipitation anomalies since 1990 (Trenberth <i>et al.</i>, 2014); — Models often exclude PDO/ENSO which limit the capacity to attribute increasing droughts to CC (Trenberth <i>et al.</i>, 2014); — Weak evidence of detection and attribution of changes in meteorological drought since the mid-20th century (Change, 2014); — Using a spacial, model-based perspective, anthropogenic forcing increased the frequency, duration and intensity of SPI-based droughts for North America (Hidalgo <i>et al.</i>, 2009), Europe and the Mediterranean (Spinoni <i>et al.</i>, 2018), (Kurnik <i>et al.</i>, 2011) and E Asia (Chiang <i>et al.</i>, 2021; Marvel <i>et al.</i>, 2019; Spinoni <i>et al.</i>, 2014)
Consequences (Individual and Ecosystem level consequences)	<ul style="list-style-type: none"> — Recurring droughts may limit trees' ability to recover from other types of stress. — Tree mortality (e.g. Texas and California extreme droughts are estimated to have killed 300 and 102 million trees (Li <i>et al.</i>, 2023))
Differences across species/provenance	

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3.3. Heat waves

Definition:	Heat wave is a period of excessively hot weather (5 or more consecutive days of prolonged heat in which the daily maximum temperature is higher than the average maximum temperature by 5 °C), which may be accompanied by high humidity (Marx <i>et al.</i> , 2021).
Mechanisms	<p>↑ atmospheric CO₂ = ↑ temperature → ↑ heat waves... More specifically: A mechanism for the increase occurrence of heat waves is a weakeking of the polar jet stream (important weather factor for middle latitude regions of North America, Europe and Asia) caused by global warming which increases the occurence of stationnary weather, resulting in heavy rain falls or heat waves (Marx <i>et al.</i>, 2021). Extreme heat → growth either through (1) Directly via cell processes disruption or (2) indirectly via effects of rising leaf-to-air vaport deficit (VPD) (Gagne <i>et al.</i>, 2020).</p> <p>Increased temperature leads to reduced photosynthesis which can be attributed to: 1. Damage to photosynthetic machinery 2. Inactivation of RUBISCO 3. Reduction to RuBP regeneration 4. Membrane stability 5. Increased mitochondrial respiration and photorespiration (Hauck <i>et al.</i>, 2025)</p>
255 Global trend of occurrence	Heat waves have increased (Gagne <i>et al.</i> , 2020; Meehl & Tebaldi, 2004; Teskey <i>et al.</i> , 2015) and are expected to increase under future climate change (Dosio <i>et al.</i> , 2018; Change, 2014; Teskey <i>et al.</i> , 2015). Summertime extreme temperatures associated with prolonged heat waves, lasting for several weeks, now impact approximately 10% of land surfaces, up from only 1% in the 1960s. (Teskey <i>et al.</i> , 2015). The more intense and more frequently occurring heat waves cannot be explained solely by natural climate variations and without human-made climate change (Marx <i>et al.</i> , 2021).
Consequences (Individual and Ecosystem level consequences)	- Reduced photosynthesis - Increased mortality - Photosynthetic tissue loss (Gagne <i>et al.</i> , 2020).
Differences across species/provenance	Some species have thermal photosynthetic/respiratory acclimatation while others don't. Growth and survival will change depending on species to thermally acclimate to both photosynthesis and respiration - This is explained by growth strategies of gymnosperms vs angiosperms (which are usually better)

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