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Thesis Proposal

2

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3

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4 1 Introduction

5 1.1 Climate change impacts on tree phenology

6 Research from the past decades has shown convincing evidence that human activity is increasingly affecting
7 many worldwide environmental processes (Ceballos *et al.*, 2017; Intergovernmental Panel On Climate
8 Change (Ipcc), 2023; Laurance, 2007; Parmesan & Yohe, 2003). This can be through land use change and
9 destruction, pollution, invasive species, resource overexploitation and climate change (Driscoll *et al.*, 2018;
10 Parmesan *et al.*, 1999; Wu, 2013). Though some immediate actions can be deployed to mitigate these impacts
11 (e.g. (Campbell *et al.*, 2014)), reversing 150 years of human-induced greenhouse gas emissions is harder.
12 These emissions have affected Earth's climate and are projected to keep changing it for many centuries (Intergovernmental Panel On Climate Change (Ipcc), 2023). While there is a scientific consensus that observed
13 climate change is human-caused (Change, 2014; Lynas *et al.*, 2021; Oreskes, 2004), the magnitude and the
14 extent of the consequences that a warming climate will have on biological processes are still debatable (Huey
15 *et al.*, 2012).

17

18 1.1.1. Trends of spring and autumn phenological events and their drivers

19

20 *1.1.1.1. Changes in phenology:* The most frequently observed biological impact of climate change over
21 the past decades is major changes in spring and autumn phenology —the timing of recurring life history
22 events (Parmesan & Yohe, 2003; Cleland *et al.*, 2007; Lieth *et al.*, 1974; Woolway *et al.*, 2021; Menzel *et al.*,
23 2006). Together, shifts in spring and autumn phenology modify when the growing season starts and when
24 it ends. Understanding the consequences of changing growing season length on ecosystems requires under-
25 standing how much, and why it has changed (Duputié *et al.*, 2015).

26

27 *1.1.1.2. Drivers of spring phenology:* Spring phenological events (e.g. budburst and leafout) have been
28 advancing from 0.5 (Wolfe *et al.*, 2005) to 4.2 days/decade (Chmielewski & Rötzer, 2001; Fu *et al.*, 2014)
29 and are mainly driven by temperature (Chuine, 2010; Cleland *et al.*, 2007; Peñuelas & Filella, 2001). In the
30 winter, when trees are still in dormancy, they accumulate cold temperatures (chilling) for which a certain
31 amount is required to be ready to accumulate heat (forcing) (Vitasse *et al.*, 2014). Then, in the spring,
32 a certain amount of forcing triggers budburst (Fu *et al.*, 2015). Heat requirement is met sooner in warm
33 springs, thus explaining the advancement of spring events and earlier onset of growing season over the last
34 decades (Fu *et al.*, 2015, 2013; Laube *et al.*, 2014).

35

36 *1.1.1.3. Drivers of autumn phenology:* In contrast, autumn phenology (e.g. budset and leaf senescence)
37 is delayed, though to a much lesser extent than spring (Gallinat *et al.*, 2015; Jeong & Medvigy, 2014), and
38 its drivers are also far less understood than those of spring. These ambiguities are caused by the lesser atten-
39 tion payed to autumn phenology (Piao *et al.*, 2019) and because the data is often noisier (Wu *et al.*, 2024).
40 However, there is a general belief that autumn phenophases are driven by shortening photoperiod and colder
41 temperatures (Cooke *et al.*, 2012; Flynn & Wolkovich, 2018; Körner & Basler, 2010; Delpierre *et al.*, 2016).
42 Several hypotheses can explain delayed autumn phenophases. First, warmer autumn temperatures may ex-
43 tend the activity of photosynthetic enzymes which causes decreases the degradation rate of chlorophyll, thus
44 delaying the timing of leaf senescence (Yan *et al.*, 2021). Second, summer droughts could pause the activity

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

50

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 support a long-lasting and intuitive assumption that earlier spring
54 and delayed autumn events lead to longer seasons—and thus increased growth (Keenan *et al.*, 2014; Stridbeck
55 *et al.*, 2022). However, research from the past three years has cast doubt on this hypothesis (Dow *et al.*,
56 2022; Green & Keenan, 2022; Silvestro *et al.*, 2023b). For instance, (Dow *et al.*, 2022) showed that despite an
57 earlier growth onset, longer seasons did not increase the growth rate nor overall annual increment. This could
58 substantially affect carbon-cycle model projections and thus feedbacks to future climate (Richardson *et al.*,
59 2013; Swidrak *et al.*, 2013). Starting to grow earlier and stopping later both have different consequences
60 (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 is
63 allocated into wood is poorly understood. Indeed, the linear relationship assumption between wood growth
64 and carbon assimilation is not well supported mechanistically and represents an important limitation of
65 vegetation models (Cabon *et al.*, 2022). Net primary production represents the difference between photosyn-
66 thesis and plant respiration, but this commonly used metric completely omits the representation of growth
67 processes. This is perhaps because of a long-lasting paradigm of source-limited photosynthesis (Friend *et al.*,
68 2019; Parent *et al.*, 2010). Whether a tree's growth is source (photosynthetic activity determines sink ac-
69 tivity) or sink (growth, respiration, and other metabolic processes determine the carbon source) controlled
70 depend upon a closely coordinated sequence of dynamic responses and is still an area of active debate. How-
71 ever, (Gessler2024Beyond) recently suggested that neither source or sink control systematically dominate.
72 This complex dynamic enforces the importance of understanding the temperature sensitivity relationship
73 between growth activity and photosynthesis. Growing evidence suggests that cambial activity may be more
74 sensitive than photosynthesis to a range of environmental conditions, such as water and nutrient availability,
75 and temperature (Cabon *et al.*, 2022, 2020; Muller *et al.*, 2011; Peters *et al.*, 2021). Thus, this demonstrates
76 that carbon projection models that solely rely on vegetation alone may mislead carbon sequestration dy-
77 namics 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 to
83 high amplitude (Almagro *et al.*, 2025; Cabon *et al.*, 2022). This expected asymmetry of future environmental
84 changes makes understanding the internal physiological constraints (via genetic and developmental control),
85 and external limits (via extreme temperatures or moisture deficit) to growth critical. Moreover, the capacity
86 to tease apart different biomes—as for example boreal vs tropical forests are expected to react differently
87 (REF)—is critical and empirical data coming from experiments, but also from ground observations are
88 paramount to predict the changes of forest carbon offset from human GHG emissions (Wolkovich *et al.*,
89 2025).

90

1.2 Nature of the problem, and how to address it

91 **1.2.1. Past phenological trends can help (or not) predict future phenological changes**

92 We cannot directly use observed phenological trends in the last decades to extrapolate future phenological
93 changes because: (1) the mechanisms guiding them aren't clear, and (2) phenological responses of trees
94 to warming are very likely to be non-linear (Ettinger *et al.*, 2020; Fu *et al.*, 2013). Indeed, accurate pre-
95 dictions require an in-depth, accurate mechanistic understanding of phenophases and their sensitivities to
96 environmental drivers, especially to temperature and photoperiod (Fu *et al.*, 2013). Therefore, the very

97 foundation of the assumption that longer seasons increase growth may shift with future climate change. The
98 well-observed advance in spring phenology may decelerate, and delayed fall phenology may shift towards
99 earlier leaf senescence (through summer drought-induced growth cessation).

100
101 **1.2.2. The assumption that longer seasons lead to increased growth is called into question**
102 Recent work shows an absence of increased growth despite apparent better environmental conditions, thus
103 casting doubt on a simple and intuitive positive relationship between growing season length and growth.
104 This paradox further emphasizes the need to better understand the drivers regulating growth across biomes,
105 but also how these drivers vary across the species within these biomes. Phenology varies greatly across
106 species (e.g. closely related species tend to budburst at similar times under similar conditions) (Wolkovich
107 *et al.*, 2014), but so does the relationship between growth and season length, which may explain the wide
108 variation of this relationship within communities (Buckley & Kingsolver, 2012). This highlights another
109 weakness of current carbon sequestration models that pool species together, likely overpassing important
110 nuances in the growth responses that could be explained by species differences. Excluding species differences
111 in models may mislead future carbon dynamic models (Green & Keenan, 2022; Cabon *et al.*, 2022; Wolkovich
112 *et al.*, 2025). Different strategies can help understanding how different species respond to warming and thus
113 improve carbon sequestration projections.

114
115 **1.2.2.1. Experiments:** First, experiments are extremely useful in teasing apart co-occurring realities in
116 natural environments. For example, warm springs, and severe droughts later in the summer often happen
117 together within a single year and manipulative experiments have the capacity to separate the relative effect
118 of each phenomenon (Morin *et al.*, 2010; Primack *et al.*, 2015). Experiments are most often performed on
119 juvenile trees because of logistical constraints, and while saplings are critical for their role in forest regen-
120 eration projections, their responses hardly translate to mature trees, which hold the overwhelming carbon
121 biomass proportion of forests (Augspurger & Bartlett, 2003; Silvestro *et al.*, 2023b; Vitasse, 2013). Even if
122 young trees are often more plastic than adult forms, their responses can still provide valuable insights in
123 differences across species and populations (Wolkovich *et al.*, 2025).

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

136
137 **1.2.3. Goals of my thesis**

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

141 **1.3 Complexity of measuring growth and defining growing season length**

142 **1.3.1.1. What is a growing season?**

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

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

158 1.3.1.2. *What is growth?*

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

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

175
176 **1.3.3. Dendroecology to analyses growth responses to changing growing season length**
177 Alongside the diameter-height allometric relationship, dendroecology—applications of dendrochronological
178 techniques to problems in ecology (Fritts & Swetnam, 1989)—emerged to answer ecological problems as well
179 as to hindcast (e.g. (Bergeron *et al.*, 2004)) and forecast ecological processes both at the regional (Gazol
180 *et al.*, 2018) and global scale (Manzanedo & Pederson, 2019; Büntgen *et al.*, 2018). Now, these methods
181 can be used to understand more precise growth patterns and their relationship with different environmental
182 factors. This is why I will use tree rings as a proxy for how much trees grew in any given year.

183 184 **1.3.4. Asynchrony between primary and secondary growth**

I argue that internal growth control in trees may shape their growth responses to growing season length, and
these can be split into two categories: primary and secondary growth synchronicity and growth determinancy.

Primary (shoot elongation) and secondary (xylem and phloem formation) growth both contribute to how
much carbon is stored in plant tissue, but how much they differ in their responses to environmental drivers
is poorly understood. After a dormancy period, trees will start growing, both vertically (primary) and
horizontally (secondary), but there is high variation among species as to when each growth starts, for how
long it lasts and when it stops. For instance, ring-porous species initiate primary growth early in the season,
sometimes even before budburst (e.g. oaks) (Stridbeck *et al.*, 2022), whereas xylogenesis in diffuse-porous
species is usually more synchronized with budburst. These two examples highlight how more complicated
it might be to infer general conclusions as to how growing season shifts may also shift growth, where some
species may extend their primary growth, but restrict their secondary growth and vice versa.

In addition to differences in primary and secondary growth synchronicity, the role of internal growth
control—often overlooked—may misshape our understanding of growth responses to growing season length
(Baumgarten *et al.*, 2025). In perennial plants, two dichotomous growth strategies are commonly mentioned:
determinate and indeterminate growth, though it appears that species exist along a gradient of these
(Baumgarten *et al.*, 2025). Indeterminate growth is usually associated with short-lived and fast growth
species, where these life-history strategies may give them a competing advantage as tissue growth can be
produced quickly in response to changing environmental conditions. However, this comes with a higher risk

203 of late spring and early fall frost as well as late droughts (Baumgarten *et al.*, 2025; Brienen *et al.*, 2020).
204 At the opposite side of the spectrum, determinate species are usually long-lived and slow-growing and are
205 mainly constrained by conditions during bud formation; this may increase bud survival at the detriment of
206 opportunistic growth in face of better-than-expected conditions (Baumgarten *et al.*, 2025).

207 Thus, primary versus secondary growth allocation, coupled with growth determinancy, are variables often
208 overlooked, but which greatly vary across species and that are likely to affect how trees respond to shifting
209 season length.

210

211 1.4 Objectives

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

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

220 1.5 Research questions

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

224

225 2 Methodology

226 2.1 Wildchrokie

227 2.1. Studies locations **Common garden** In 2014-2015, we collected seeds from four field sites in northeastern
228 North America spanning approximately a 3.5° latitudinal gradient. The four field sites included Harvard
229 Forest (42.55°N, 72.20°W), the White Mountains (44.11°N, 71.40°W), Second College Grant, (44.79°N,
230 71.15°W), and St. Hippolyte, QC, CAN (45.98°N, 74.01°W). We transported all seeds back to the Weld
231 Hill Research Building at the Arnold Arboretum in Boston Massachusetts (42.30°N, 71.13°W) where we
232 germinated seeds following standard germination protocols, and grew them to seedling stages in the research
233 greenhouse. In the spring of 2017 we out-planted seedlings to establish the garden. Plots were regularly
234 weeded and watered throughout the duration of the study and were pruned in the fall of 2020.

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

237 **2.1. Coringtreespotters** The citizen science programs, the Treespotters was started in 2015 and aimed
238 to train citizen scientist for accurate and rigorous phenological monitoring. From 2015 to 2024, hundreds of
239 citizen scientists monitored 50 trees of * species regularly from the early phenostage in the spring until leaf
240 colouring in the fall. The BBCH scale was used (check if that's true).

241 From 20 to 22 April 2025, we collected a 2.5-mm diameter core, 15-cm length at 1.3 meter above
242 ground from 50 trees of the 11 species (Table XX) that were previously monitored for phenology, using
243 an increment borer (Mora Borer, Haglöfs Sweden, Bromma, Stockholm, Sweden). The cores were collected
244 perpendicularly to the slope and at 180 degrees from each other. We cleaned the increment borer with alcohol
245 (70% ethanol?) and the inside with a brush before collecting each core. We stored the cores in paper straws
246 that were previously labelled and punched to help drying. They were stored at ambient temperature for
247 three months.

248 **Sample processing, imaging and measuring** Then we mounted the cores on wooden mounts, and
249 sanded the cores and cross-sections using progressively fine grit (150, 300, 400, 600, 800, 1000). We scanned

250 the cores and cross-sections at a resolution of ***dpi using a homemade great scanner (Tina2026?) We
251 used the digitalized images to measure the tree ring widths with Fiji Image J. Then, we performed visual
252 crossdating using Dplr, but no statistical crossdating was performed because of the short chronologies that
253 limit the capacity for these analyses.

254 **2.2 Fuelinex**

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

256 **3 Supplemental material**

257 **3.1 Wildchrokie**

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

262 **3.2 Treespotters**

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

267 **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	

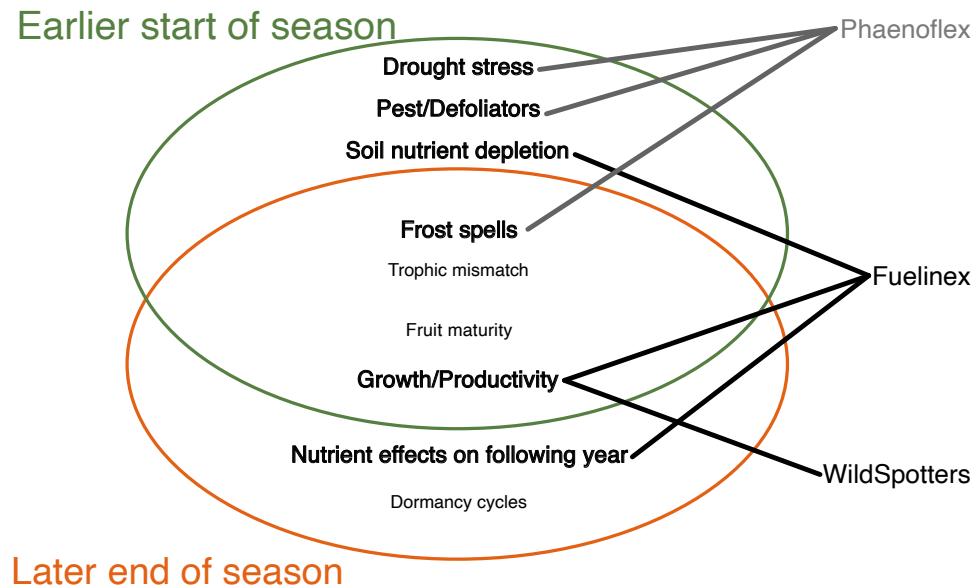


Figure 1: The effects that an earlier start and later end of season can have on trees. In bold are the effects that were studied over the course of this thesis. Phaenoflex (in grey) is a related experimental project, that is not part of this thesis.

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: 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 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

269

3.2. Drought

270

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 weakening 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 occurrence of stationary 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 vapor 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>
273 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 acclimation 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)

274 References

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