Thesis Proposal

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1 Introduction

1.1 Climate change impacts on tree phenology

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.

Trends and drivers of spring and autumn phenological events
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).

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).

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 autumn 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). Several hypotheses can explain delayed autumn phenophases. First, warmer autumn temperatures may extend the activity of photosynthetic enzymes which causes decreases the degradation rate of chlorophyll, thus

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

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

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

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

1.1.3. Growing season shifts and consequences on forest ecosystems and services

Spring and fall phenological events are shifting with debatable consequences on tree growth. The sensitivity of cambial activity to water, temperature and nutrients has the potential to have far-reaching consequences given the hard-to-predict nature of future climate change, where any of these variables could vary from low to high amplitude (Almagro *et al.*, 2025; Cabon *et al.*, 2022). This expected asymmetry of future environmental changes makes understanding the internal physiological constraints (via genetic and developmental control), and external limits (via extreme temperatures or moisture deficit) to growth critical. Moreover, the capacity to tease apart different biomes—as for example boreal vs tropical forests are expected to react differently (REF)—will be critical for useful global projections of how changes of forest carbon can offset human GHG emissions.

1.2 Nature of the problem, and how to address it

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

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

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

1.2.2. The assumption that longer seasons lead to increased growth is called into question

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

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

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

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

1.3   Complexity of measuring growth and defining growing season length

1.3.1.1. What is a growing season?

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

Here, I will focus on how definition (2), incorporating (4), affects definition (1) as the data collected

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

1.3.1.2. What is growth?

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

1.3.2. Traditional diameter measurements miss the resolution of annual growth increment

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

1.3.3. Dendroecology to analyses growth responses to changing growing season length

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

1.4 Objectives

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

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

1.5 Research questions

Fuelinex: How do extended growing seasons affect tree growth across different species, both immediately (in the same year as the extended season) and in subsequent years? WildSpotters: How does phenology regulate tree growth in urban ecosystems?
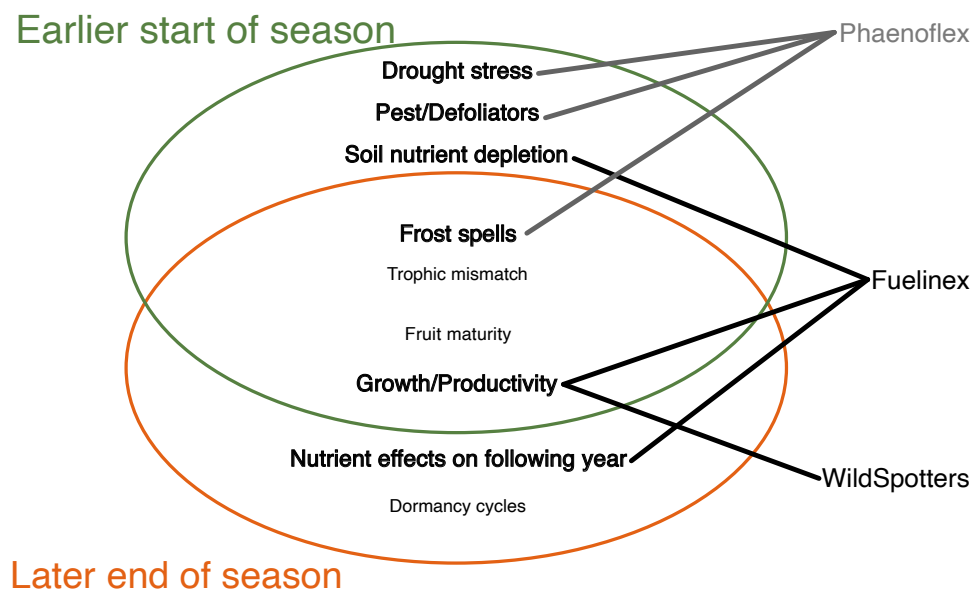
Figure 1: The effects that an earlier start and later end of season can have on trees. In bold are the effects that were studied over the course of this thesis. Phaenoflex (in grey) is a related experimental project, that is not part of this thesis, but one I collaborated on in XX years.

2 Methodology

2.1 Wildchrokie

2.1. Studies locations

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

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.

Phenological monitoring For the years of 2018-2019, we made phenological observations of all individuals in the common garden twice per week from February to December. In 2020 due to the COVID 19 pandemic, we monitored once per week from March to November. We describe phenological stages using a modified BBCH scale (**?**) a common metrics for quantify woody plant phenological progression. 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 full budset as BBCH 102.

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

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

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

Statistical analyses

2.2 Fuelinex

The experimental design of fuelinex is described in the figure.

3 Supplemental material

3.1 Wildchrokie

1. Common garden from 2015 to 2023

2. Four species within the Betulacea family (Table 2)

243   3. Data: phenology, height, tree rings

244   4. Analysis: Hierarchical model to understand how tree ring width relates to GDD

3.2   Treespotters

246   1. Citizen scie nce project from 2015 to today (Table 3)

247   2. Tree coring

248   3. Data: phenology, tree rings

249   4. Analysis: Hierarchical model to understand how tree ring width relates to GDD

3.1. Spring frosts

Definition:	Late spring frosts are below-freezing temperatures in late spring (Zohner *et al.*, 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 *et al.*, 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 *et al.*, 2023)
Consequences (Individual and Ecosystem level consequences)	Loss of vegetative tissue = ↓ photosynthesis = ↓ and remobilization of NSC to repair damaged tissues = ↓ secondary growth (Meyer *et al.*, 2024); Loss of reproductive tissue (higher flower mortality) (Sgubin *et al.*, 2018); Costs for orchards and stuff (Reinmann *et al.*, 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 (approx)**
Bur oak (*Quercus macrocarpa*)	Slow-growth, long life	Ring-porous	87
Bitter cherry (*Prunus virginiana*)	Fast-growth, short life	Diffuse-porous	78
Box elder (*Acer negundo*)	Fast-growth, short life	Diffuse-porous	90
Balsam poplar (*Populus balsamifera*)	Fast-growth, short life	Diffuse-porous	84
Paper birch (*Betula papyrifera*)	Fast-growth, short life	Diffuse-porous	90
Evergreen Trees			
White pine (*Pinus strobus*)	Slow-growth, long life		89
Giant Sequoia (*Sequoiadendron giganteum*)	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 (*Betula papyrifera*)	Fast-growth, short life	Diffuse-porous	8
Yellow birch (*Betula alleghaniensis*)	Moderate-growth, moderate life	Diffuse-porous	21
Grey birch (*Betula populifolia*)	Fast-growth, short life	Diffuse-porous	29
Grey alder (*Alnus incana*)	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 (*Tilia americana*)	Fast-growth, moderate life	Diffuse-porous	5
Eastern cottonwood (*Populus deltoides*)	Fast-growth, short life	Diffuse-porous	4
Northern red oak (*Quercus rubra*)	Moderate-growth, long life	Ring-porous	4
White oak (*Quercus alba*)	Slow-growth, long life	Ring-porous	5
Pignut hickory (*Carya glabra*)	Slow-growth, long life	Ring-porous	4
Shagbark hickory (*Carya ovata*)	Slow-growth, long life	Ring-porous	4
River birch (*Betula nigra*)	Fast-growth, short life	Diffuse-porous	5
Yellow birch (*Betula alleghaniensis*)	Moderate-growth, moderate life	Diffuse-porous	4
Sugar maple (*Acer saccharum*)	Slow-growth, long life	Diffuse-porous	5
Red maple (*Acer rubrum*)	Slow-growth, long life	Diffuse-porous	4
Yellow buckeye (*Aesculus flava*)	Moderate-growth, moderate life	Diffuse-porous	5

3.2. Drought

Definition:	"Drought is a prolonged absence or marked deficiency of precipitation that results in water shortage or or a period of abnormally dry weather sufficiently prolonged for the lack of precipitation to cause a serious hydrological imbalance (Trenberth *et al.*, 2014; Intergouvernemental panel on climate change, 2007).
Mechanisms	— 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 *et al.*, 2018); — Earlier spring phenology = longer GS → increases vegetative growth → increases evapotranspiration → increases drawdown of soil moisture = progressive water stress (Li *et al.*, 2023) — Long-term vs short-term stomatal responses and consequences on tissue death (Choat *et al.*, 2018); — Recovery and its determinants (Choat *et al.*, 2018; Li *et al.*, 2023)
Global trend of occurrence	— ↑ precipitation anomalies since 1990 (Trenberth *et al.*, 2014); — Models often exclude PDO/ENSO which limit the capacity to attribute increasing droughts to CC (Trenberth *et al.*, 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 *et al.*, 2009), Europe and the Mediterreanean (Spinoni *et al.*, 2018), (Kurnik *et al.*, 2011) and E Asia (Chiang *et al.*, 2021; Marvel *et al.*, 2019; Spinoni *et al.*, 2014)
Consequences (Individual and Ecosystem level consequences)	— 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 *et al.*, 2023))
Differences across species/provenance	

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 *et al.*, 2021).
Mechanisms	$\uparrow$ atmospheric CO2 $= \uparrow$ temperature $\rightarrow \uparrow$ heat waves... More specifically: A mechanism for the increase occurence 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 *et al.*, 2021). Extreme heat $\rightarrow$ growth either through (1) Directly via cell processes disruption or (2) indirectly via effects of rising leaf-to-air vapor deficit (VPD) (Gagne *et al.*, 2020). Increased temperature leads to reduced photosynthesis which can be attributed to: 1. Damage to photosynthetic machinery 2. Inactivation of RUBISCO 3. R eduction to RuBP regeneration 4. Membrane stability 5. Increased mitochondrial respiration and photorespiration (Hauck *et al.*, 2025)
Global trend of occurrence	Heat waves have increased (Gagne *et al.*, 2020; Meehl & Tebaldi, 2004; Teskey *et al.*, 2015) and are expected to increase under future climate change (Dosio *et al.*, 2018; Change, 2014; Teskey *et al.*, 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 *et al.*, 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 *et al.*, 2021).
Consequences (Individual and Ecosystem level consequences)	- Reduced photosynthesis - Increased mortality - Photosynthetic tissue loss (Gagne *et al.*, 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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