Thesis Proposal

Christophe Rouleau-Desrochers

December 18, 2025

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 destruction, pollution, invasive species, resource overexploitation and climate change (Driscoll *et al.*, 2018; Parmesan *et al.*, 1999; Wu, 2013). Though some immediate actions can be deployed to 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). While there is a scientific consensus that observed climate change is human-caused (Change, 2014; Lynas *et al.*, 2021; Oreskes, 2004), the magnitude and the extent of the consequences that a warming climate will have on biological processes are still debatable (Huey *et al.*, 2012).

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

1.1.1.1. Changes in phenology: 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).

1.1.1.2. 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 requirement is met sooner in warm springs, thus explaining the advancement of spring events and earlier onset of growing season over the last decades (Fu *et al.*, 2015, 2013; Laube *et al.*, 2014).

1.1.1.3. Drivers of autumn phenology: In contrast, autumn phenology (e.g. budset and leaf senescence) is delayed, though to a much lesser extent than spring (Gallinat *et al.*, 2015; Jeong & Medvigy, 2014), and its drivers are also far less understood than those of spring. These ambiguities are caused by the lesser attention payed to autumn phenology (Piao *et al.*, 2019) and because the data is often noisier (Wu *et al.*, 2024). However, there is a general belief that autumn phenophases are 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. 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 linear relationship assumption 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 depend 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)—is critical and empirical data coming from experiments, but also from ground observations are paramount to predict the changes of forest carbon offset from human GHG emissions (Wolkovich *et al.*, 2025).

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 aren't 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
Recent work shows an absence of increased growth despite apparent better environmental conditions, thus casting doubt on a simple and intuitive positive relationship between growing season length and growth. This paradox further emphasizes the need to better understand the drivers regulating growth across biomes, but also how these drivers vary across the species within these biomes. 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-occuring realities in natural environmentals. For example, warm springs, and severe droughts later in the summer often happen together within a single year and manipulative experiments have the capacity to separate the relative effect of each phenomenon(Morin *et al.*, 2010; Primack *et al.*, 2015). Experiments are most often performed on juvenile trees because of logistical constraints, and while saplings are critical for their role in forest regeneration projections, their responses hardly translate to mature trees, which hold the overwhelming carbon biomass proportion of forests (Augspurger & Bartlett, 2003; Silvestro *et al.*, 2023; Vitasse, 2013). 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 to the other, 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 are not suitable for interpreting a relationship 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?

Earlier start of season

Drought stress

Pest/Defoliators

Soil nutrient depletion

Frost spells

Trophic mismatch

Fruit maturity

Growth/Productivity

Nutrient effects on following year

Dormancy cycles

Later end of season

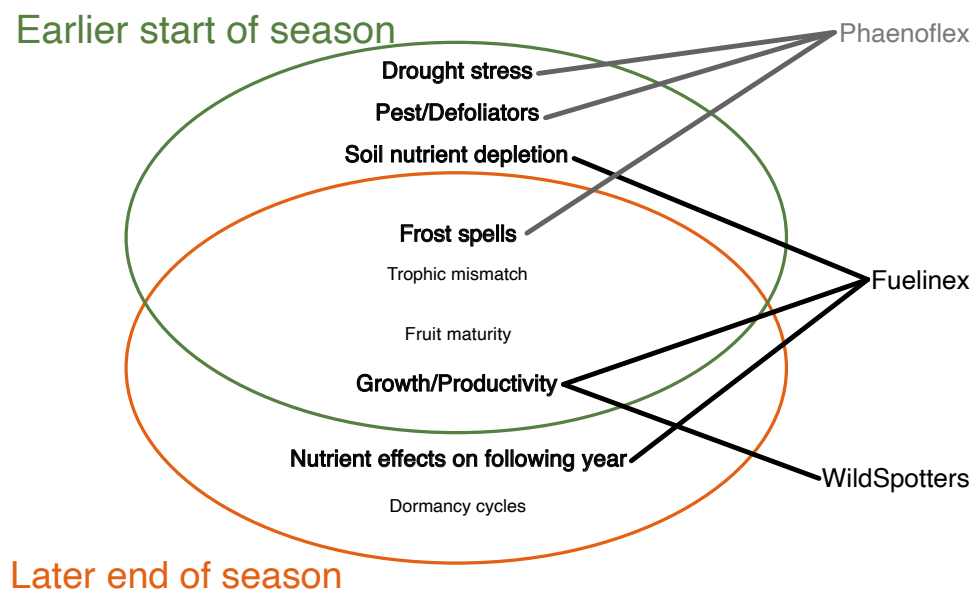Phaenoflex

Fuelinex

WildSpotters

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.

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)

244   3. Data: phenology, height, tree rings

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

3.2   Treespotters

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

248   2. Tree coring

249   3. Data: phenology, tree rings

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

251   **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

9

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)

References

Almagro, D., Martin-Benito, D., Rossi, S., Conde, M., Fernández-de-Uña, L. & Gea-Izquierdo, G. (2025). Long-Term Cambial Phenology Reveals Diverging Growth Responses of Two Tree Species in a Mixed Forest Under Climate Change. *Global Change Biology*, 31, e70503.

Augspurger, C.K. & Bartlett, E.A. (2003). Differences in leaf phenology between juvenile and adult trees in a temperate deciduous forest. *Tree Physiology*, 23, 517–525.

Bergeron, Y., Gauthier, S., Flannigan, M. & Kafka, V. (2004). Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. *Ecology*, 85, 1916–1932.

Buckley, L.B. & Kingsolver, J.G. (2012). Functional and Phylogenetic Approaches to Forecasting Species' Responses to Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, 43, 205–226.

Büntgen, U., Wacker, L., Galván, J.D., Arnold, S., Arseneault, D., Baillie, M., Beer, J., Bernabei, M., Bleicher, N., Boswijk, G., Bräuning, A., Carrer, M., Ljungqvist, F.C., Cherubini, P., Christl, M., Christie, D.A., Clark, P.W., Cook, E.R., Esper, J., Fowler, A.M., Gennaretti, F., Grießinger, J., Grissino-Mayer, H., Grudd, H., Gunnarson, B.E., Hantemirov, R., Herzig, F., Hessl, A., Heussner, K.U., Jull, A.J.T., Kukarskih, V., Kirdyanov, A., Krusic, P.J., Kyncl, T., Lara, A., LeQuesne, C., Linderholm, H.W., Loader, N.J., Luckman, B., Miyake, F., Myglan, V.S., Nicolussi, K., Oppenheimer, C., Palmer, J., Panyushkina, I., Pederson, N., Rybníček, M., Schweingruber, F.H., Seim, A., Sigl, M., Churakova, O., Speer, J.H., Synal, H.A., Tegel, W., Treydte, K., Villalba, R., Wiles, G., Wilson, R., Winship, L.J., Wunder, J., Yang, B. &

Young, G.H.F. (2018). Tree rings reveal globally coherent signature of cosmogenic radiocarbon events in 774 and 993 CE. *Nature Communications*, 9, 3605.

Cabon, A., Fernández-de-Uña, L., Gea-Izquierdo, G., Meinzer, F.C., Woodruff, D.R., Martínez-Vilalta, J. & De Cáceres, M. (2020). Water potential control of turgor-driven tracheid enlargement in Scots pine at its xeric distribution edge. *New Phytologist*, 225, 209–221.

Cabon, A., Kannenberg, S.A., Arain, A., Babst, F., Baldocchi, D., Belmecheri, S., Delpierre, N., Guerrieri, R., Maxwell, J.T., McKenzie, S., Meinzer, F.C., Moore, D.J.P., Pappas, C., Rocha, A.V., Szejner, P., Ueyama, M., Ulrich, D., Vincke, C., Voelker, S.L., Wei, J., Woodruff, D. & Anderegg, W.R.L. (2022). Cross-biome synthesis of source versus sink limits to tree growth. *Science*, 376, 758–761.

Campbell, L.M., Hagerman, S. & Gray, N.J. (2014). Producing Targets for Conservation: Science and Politics at the Tenth Conference of the Parties to the Convention on Biological Diversity. *Global Environmental Politics*, 14, 41–63.

Ceballos, G., Ehrlich, P.R. & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*, 114.

Change, I.P.O.C. (2014). Detection and Attribution of Climate Change: from Global to Regional. In: *Climate Change 2013 – The Physical Science Basis*. Cambridge University Press, pp. 867–952. 1st edn.

Chiang, F., Mazdiyasni, O. & AghaKouchak, A. (2021). Evidence of anthropogenic impacts on global drought frequency, duration, and intensity. *Nature Communications*, 12, 2754.

Chmielewski, F.M. & Rötzer, T. (2001). Response of tree phenology to climate change across Europe. *Agricultural and Forest Meteorology*, 108, 101–112.

Choat, B., Brodribb, T.J., Brodersen, C.R., Duursma, R.A., López, R. & Medlyn, B.E. (2018). Triggers of tree mortality under drought. *Nature*, 558, 531–539.

Chuine, I. (2010). Why does phenology drive species distribution? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 3149–3160.

Cleland, E., Chuine, I., Menzel, A., Mooney, H. & Schwartz, M. (2007). Shifting plant phenology in response to global change. *Trends in Ecology & Evolution*, 22, 357–365.

Cooke, J.E.K., Eriksson, M.E. & Junttila, O. (2012). The dynamic nature of bud dormancy in trees: environmental control and molecular mechanisms. *Plant, Cell & Environment*, 35, 1707–1728.

Delpierre, N., Vitasse, Y., Chuine, I., Guillemot, J., Bazot, S., Rutishauser, T. & Rathgeber, C.B.K. (2016). Temperate and boreal forest tree phenology: from organ-scale processes to terrestrial ecosystem models. *Annals of Forest Science*, 73, 5–25.

Dickinson, J.L., Shirk, J., Bonter, D., Bonney, R., Crain, R.L., Martin, J., Phillips, T. & Purcell, K. (2012). The current state of citizen science as a tool for ecological research and public engagement. *Frontiers in Ecology and the Environment*, 10, 291–297.

Dosio, A., Mentaschi, L., Fischer, E.M. & Wyser, K. (2018). Extreme heat waves under 1.5 °C and 2 °C global warming. *Environmental Research Letters*, 13, 054006.

Dow, C., Kim, A.Y., D'Orangeville, L., Gonzalez-Akre, E.B., Helcoski, R., Herrmann, V., Harley, G.L., Maxwell, J.T., McGregor, I.R., McShea, W.J., McMahon, S.M., Pederson, N., Tepley, A.J. & Anderson-Teixeira, K.J. (2022). Warm springs alter timing but not total growth of temperate deciduous trees. *Nature*, 608, 552–557.

Dox, I., Skrøppa, T., Decoster, M., Prislan, P., Gascó, A., Gričar, J., Lange, H. & Campioli, M. (2022). Severe drought can delay autumn senescence of silver birch in the current year but advance it in the next year. *Agricultural and Forest Meteorology*, 316, 108879.

Driscoll, D.A., Bland, L.M., Bryan, B.A., Newsome, T.M., Nicholson, E., Ritchie, E.G. & Doherty, T.S. (2018). A biodiversity-crisis hierarchy to evaluate and refine conservation indicators. *Nature Ecology & Evolution*, 2, 775–781.

Duputié, A., Rutschmann, A., Ronce, O. & Chuine, I. (2015). Phenological plasticity will not help all species adapt to climate change. *Global Change Biology*, 21, 3062–3073.

Ettinger, A.K., Chamberlain, C.J., Morales-Castilla, I., Buonaiuto, D.M., Flynn, D.F.B., Savas, T., Samaha, J.A. & Wolkovich, E.M. (2020). Winter temperatures predominate in spring phenological responses to warming. *Nature Climate Change*, 10, 1137–1142.

Etzold, S., Sterck, F., Bose, A.K., Braun, S., Buchmann, N., Eugster, W., Gessler, A., Kahmen, A., Peters, R.L., Vitasse, Y., Walthert, L., Ziemińska, K. & Zweifel, R. (2022). Number of growth days and not length of the growth period determines radial stem growth of temperate trees. *Ecology Letters*, 25, 427–439.

Flynn, D.F.B. & Wolkovich, E.M. (2018). Temperature and photoperiod drive spring phenology across all species in a temperate forest community. *New Phytologist*, 219, 1353–1362.

Friend, A.D., Eckes-Shephard, A.H., Fonti, P., Rademacher, T.T., Rathgeber, C.B.K., Richardson, A.D. & Turton, R.H. (2019). On the need to consider wood formation processes in global vegetation models and a suggested approach. *Annals of Forest Science*, 76, 49.

Fritts, H. & Swetnam, T. (1989). Dendroecology: A Tool for Evaluating Variations in Past and Present Forest Environments. In: *Advances in Ecological Research*. Elsevier, vol. 19, pp. 111–188.

Fu, Y.H., Campioli, M., Deckmyn, G. & Janssens, I.A. (2013). Sensitivity of leaf unfolding to experimental warming in three temperate tree species. *Agricultural and Forest Meteorology*, 181, 125–132.

Fu, Y.H., Piao, S., Op De Beeck, M., Cong, N., Zhao, H., Zhang, Y., Menzel, A. & Janssens, I.A. (2014). Recent spring phenology shifts in western Central Europe based on multiscale observations. *Global Ecology and Biogeography*, 23, 1255–1263.

Fu, Y.H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., Ciais, P., Huang, M., Menzel, A., Peñuelas, J., Song, Y., Vitasse, Y., Zeng, Z. & Janssens, I.A. (2015). Declining global warming effects on the phenology of spring leaf unfolding. *Nature*, 526, 104–107. Publisher: Nature Publishing Group.

Gagne, M.A., Smith, D.D. & McCulloh, K.A. (2020). Limited physiological acclimation to recurrent heat-waves in two boreal tree species. *Tree Physiology*, 40, 1680–1696.

Gallinat, A.S., Primack, R.B. & Wagner, D.L. (2015). Autumn, the neglected season in climate change research. *Trends in Ecology & Evolution*, 30, 169–176.

Gazol, A., Camarero, J.J., Vicente-Serrano, S.M., Sánchez-Salguero, R., Gutiérrez, E., De Luis, M., Sangüesa-Barreda, G., Novak, K., Rozas, V., Tíscar, P.A., Linares, J.C., Martín-Hernández, N., Martínez Del Castillo, E., Ribas, M., García-González, I., Silla, F., Camisón, A., Génova, M., Olano, J.M., Longares, L.A., Hevia, A., Tomás-Burguera, M. & Galván, J.D. (2018). Forest resilience to drought varies across biomes. *Global Change Biology*, 24, 2143–2158.

Gessler, A. & Zweifel, R. (2024). Beyond source and sink control – toward an integrated approach to understand the carbon balance in plants. *New Phytologist*, 242, 858–869.

Green, J.K. & Keenan, T.F. (2022). The limits of forest carbon sequestration. *Science*, 376, 692–693.

Hauck, M., Schneider, T., Bahlinger, S., Fischbach, J., Oswald, G., Csapek, G. & Dulamsuren, C. (2025). Heat tolerance of temperate tree species from Central Europe. *Forest Ecology and Management*, 580, 122541.

Hidalgo, H.G., Das, T., Dettinger, M.D., Cayan, D.R., Pierce, D.W., Barnett, T.P., Bala, G., Mirin, A., Wood, A.W., Bonfils, C., Santer, B.D. & Nozawa, T. (2009). Detection and Attribution of Streamflow Timing Changes to Climate Change in the Western United States. *Journal of Climate*, 22, 3838–3855.

Huey, R.B., Kearney, M.R., Krockenberger, A., Holtum, J.A.M., Jess, M. & Williams, S.E. (2012). Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367, 1665–1679.

Hufkens, K., Melaas, E.K., Mann, M.L., Foster, T., Ceballos, F., Robles, M. & Kramer, B. (2019). Monitoring crop phenology using a smartphone based near-surface remote sensing approach. *Agricultural and Forest Meteorology*, 265, 327–337.

Intergouvernemental panel on climate change (ed.) (2007). *Climate change 2007: the physical science basis.* Cambridge university press, Cambridge.

Intergovernmental Panel On Climate Change (Ipcc) (2023). *Climate Change 2022 – Impacts, Adaptation and Vulnerability: Working Group II Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change.* 1st edn. Cambridge University Press.

Jeong, S. & Medvigy, D. (2014). Macroscale prediction of autumn leaf coloration throughout the continental United States. *Global Ecology and Biogeography*, 23, 1245–1254.

Keenan, T.F., Gray, J., Friedl, M.A., Toomey, M., Bohrer, G., Hollinger, D.Y., Munger, J.W., O'Keefe, J., Schmid, H.P., Wing, I.S., Yang, B. & Richardson, A.D. (2014). Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Nature Climate Change*, 4, 598–604.

Kurnik, B., Barbosa, P. & Vogt, J. (2011). Testing two different precipitation datasets to compute the standardized precipitation index over the Horn of Africa. *International Journal of Remote Sensing*, 32, 5947–5964.

Körner, C. & Basler, D. (2010). Phenology Under Global Warming. *Science*, 327, 1461–1462. Publisher: American Association for the Advancement of Science.

Körner, C., Möhl, P. & Hiltbrunner, E. (2023). Four ways to define the growing season. *Ecology Letters*, 26, 1277–1292.

Laube, J., Sparks, T.H., Estrella, N., Höfler, J., Ankerst, D.P. & Menzel, A. (2014). Chilling outweighs photoperiod in preventing precocious spring development. *Global Change Biology*, 20, 170–182.

Laurance, W.F. (2007). Have we overstated the tropical biodiversity crisis? *Trends in Ecology & Evolution*, 22, 65–70.

Li, Y., Zhang, W., Schwalm, C.R., Gentine, P., Smith, W.K., Ciais, P., Kimball, J.S., Gazol, A., Kannenberg, S.A., Chen, A., Piao, S., Liu, H., Chen, D. & Wu, X. (2023). Widespread spring phenology effects on drought recovery of Northern Hemisphere ecosystems. *Nature Climate Change*, 13, 182–188.

Lieth, H., Jacobs, J., Lange, O.L., Olson, J.S. & Wieser, W. (eds.) (1974). *Phenology and Seasonality Modeling.* vol. 8 of *Ecological Studies.* Springer Berlin Heidelberg, Berlin, Heidelberg.

Lynas, M., Houlton, B.Z. & Perry, S. (2021). Greater than 99% consensus on human caused climate change in the peer-reviewed scientific literature. *Environmental Research Letters*, 16, 114005.

Manzanedo, R.D. & Pederson, N. (2019). Towards a More Ecological Dendroecology. *Tree-Ring Research*, 75, 152.

Marvel, K., Cook, B.I., Bonfils, C.J.W., Durack, P.J., Smerdon, J.E. & Williams, A.P. (2019). Twentieth-century hydroclimate changes consistent with human influence. *Nature*, 569, 59–65.

Marx, W., Haunschild, R. & Bornmann, L. (2021). Heat waves: a hot topic in climate change research. *Theoretical and Applied Climatology*, 146, 781–800.

Meehl, G.A. & Tebaldi, C. (2004). More Intense, More Frequent, and Longer Lasting Heat Waves in the 21st Century. *Science*, 305, 994–997.

Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Mestre, A., Peñuelas, J., Pirinen, P., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wielgolaski, F., Zach, S. & Zust, A. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology*, 12, 1969–1976.

Meyer, B.F., Buras, A., Gregor, K., Layritz, L.S., Principe, A., Kreyling, J., Rammig, A. & Zang, C.S. (2024). Frost matters: incorporating late-spring frost into a dynamic vegetation model regulates regional productivity dynamics in European beech forests. *Biogeosciences*, 21, 1355–1370.

Meyer, H.A. (1940). A Mathematical Expression for Height Curves. *Journal of Forestry*, 38, 415–420.

Morin, X., Roy, J., Sonié, L. & Chuine, I. (2010). Changes in leaf phenology of three European oak species in response to experimental climate change. *New Phytologist*, 186, 900–910.

Muller, B., Pantin, F., Génard, M., Turc, O., Freixes, S., Piques, M. & Gibon, Y. (2011). Water deficits uncouple growth from photosynthesis, increase C content, and modify the relationships between C and growth in sink organs. *Journal of Experimental Botany*, 62, 1715–1729.

Oreskes, N. (2004). The Scientific Consensus on Climate Change. *Science*, 306, 1686–1686.

Parent, B., Turc, O., Gibon, Y., Stitt, M. & Tardieu, F. (2010). Modelling temperature-compensated physiological rates, based on the co-ordination of responses to temperature of developmental processes. *Journal of Experimental Botany*, 61, 2057–2069.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A. & Warren, M. (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, 399, 579–583.

Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42.

Peters, R.L., Steppe, K., Cuny, H.E., De Pauw, D.J., Frank, D.C., Schaub, M., Rathgeber, C.B., Cabon, A. & Fonti, P. (2021). Turgor – a limiting factor for radial growth in mature conifers along an elevational gradient. *New Phytologist*, 229, 213–229.

Peñuelas, J. & Filella, I. (2001). Responses to a Warming World. *Science*, 294, 793–795. Publisher: American Association for the Advancement of Science.

Piao, S., Liu, Q., Chen, A., Janssens, I.A., Fu, Y., Dai, J., Liu, L., Lian, X., Shen, M. & Zhu, X. (2019). Plant phenology and global climate change: Current progresses and challenges. *Global Change Biology*, 25, 1922–1940.

Plomion, C., Leprovost, G. & Stokes, A. (2001). Wood Formation in Trees. *Plant Physiology*, 127, 1513–1523.

Polgar, C.A. & Primack, R.B. (2011). Leaf-out phenology of temperate woody plants: from trees to ecosystems. *New Phytologist*, 191, 926–941.

Primack, R.B., Laube, J., Gallinat, A.S. & Menzel, A. (2015). From observations to experiments in phenology research: investigating climate change impacts on trees and shrubs using dormant twigs. *Annals of Botany*, 116, 889–897.

Rathgeber, C.B.K., Cuny, H.E. & Fonti, P. (2016). Biological Basis of Tree-Ring Formation: A Crash Course. *Frontiers in Plant Science*, 7.

Reinmann, A.B., Bowers, J.T., Kaur, P. & Kohler, C. (2023). Compensatory responses of leaf physiology reduce effects of spring frost defoliation on temperate forest tree carbon uptake. *Frontiers in Forests and Global Change*, 6, 988233.

Richardson, A.D., Keenan, T.F., Migliavacca, M., Ryu, Y., Sonnentag, O. & Toomey, M. (2013). Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology*, 169, 156–173.

Sanchez-Lorenzo, A., Wild, M., Brunetti, M., Guijarro, J.A., Hakuba, M.Z., Calbó, J., Mystakidis, S. & Bartok, B. (2015). Reassessment and update of long-term trends in downward surface shortwave radiation over Europe (1939–2012). *Journal of Geophysical Research: Atmospheres*, 120, 9555–9569.

Saunders, M.R. & Wagner, R.G. (2008). Height-diameter models with random coefficients and site variables for tree species of Central Maine. *Annals of Forest Science*, 65, 203–203.

Sgubin, G., Swingedouw, D., Dayon, G., García De Cortázar-Atauri, I., Ollat, N., Pagé, C. & Van Leeuwen, C. (2018). The risk of tardive frost damage in French vineyards in a changing climate. *Agricultural and Forest Meteorology*, 250-251, 226–242.

Silvestro, R., Deslauriers, A., Prislan, P., Rademacher, T., Rezaie, N., Richardson, A.D., Vitasse, Y. & Rossi, S. (2025). From Roots to Leaves: Tree Growth Phenology in Forest Ecosystems. *Current Forestry Reports*, 11, 12.

Silvestro, R., Zeng, Q., Buttò, V., Sylvain, J.D., Drolet, G., Mencuccini, M., Thiffault, N., Yuan, S. & Rossi, S. (2023). A longer wood growing season does not lead to higher carbon sequestration. *Scientific Reports*, 13, 4059.

Spinoni, J., Naumann, G., Carrao, H., Barbosa, P. & Vogt, J. (2014). World drought frequency, duration, and severity for 1951-2010. *International Journal of Climatology*, 34, 2792–2804.

Spinoni, J., Vogt, J.V., Naumann, G., Barbosa, P. & Dosio, A. (2018). Will drought events become more frequent and severe in Europe? *International Journal of Climatology*, 38, 1718–1736.

Stridbeck, P., Björklund, J., Fuentes, M., Gunnarson, B.E., Jönsson, A.M., Linderholm, H.W., Ljungqvist, F.C., Olsson, C., Rayner, D., Rocha, E., Zhang, P. & Seftigen, K. (2022). Partly decoupled tree-ring width and leaf phenology response to 20th century temperature change in Sweden. *Dendrochronologia*, 75, 125993.

Swidrak, I., Schuster, R. & Oberhuber, W. (2013). Comparing growth phenology of co-occurring deciduous and evergreen conifers exposed to drought. *Flora: Morphology, Distribution, Functional Ecology of Plants*, 208, 609–617.

Teskey, R., Wertin, T., Bauweraerts, I., Ameye, M., Mcguire, M.A. & Steppe, K. (2015). Responses of tree species to heat waves and extreme heat events. *Plant, Cell & Environment*, 38, 1699–1712.

Trenberth, K.E., Dai, A., Van Der Schrier, G., Jones, P.D., Barichivich, J., Briffa, K.R. & Sheffield, J. (2014). Global warming and changes in drought. *Nature Climate Change*, 4, 17–22.

Tyree, M.T. & Zimmermann, M.H. (2002). *Xylem Structure and the Ascent of Sap*. Springer Series in Wood Science. Springer Berlin Heidelberg, Berlin, Heidelberg.

Vitasse, Y. (2013). Ontogenic changes rather than difference in temperature cause understory trees to leaf out earlier. *New Phytologist*, 198, 149–155.

Vitasse, Y., eLenz, A. & eKoerner, C. (2014). The interaction between freezing tolerance and phenology in temperate deciduous trees. *Frontiers in Plant Science*, 5. Publisher: Frontiers Media S.A.

Wolfe, D.W., Schwartz, M.D., Lakso, A.N., Otsuki, Y., Pool, R.M. & Shaulis, N.J. (2005). Climate change and shifts in spring phenology of three horticultural woody perennials in northeastern USA. *International Journal of Biometeorology*, 49, 303–309.

Wolkovich, E.M., Cook, B.I. & Davies, T.J. (2014). Progress towards an interdisciplinary science of plant phenology: building predictions across space, time and species diversity. *New Phytologist*, 201, 1156–1162. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1111/nph.12599.

15

Wolkovich, E.M., Ettinger, A.K., Chin, A.R., Chamberlain, C.J., Baumgarten, F., Pradhan, K., Manzanedo, R.D. & Hille Ris Lambers, J. (2025). Why longer seasons with climate change may not increase tree growth. *Nature Climate Change*, 15, 1283–1292.

Woolway, R.I., Sharma, S., Weyhenmeyer, G.A., Debolskiy, A., Golub, M., Mercado-Bettín, D., Perroud, M., Stepanenko, V., Tan, Z., Grant, L., Ladwig, R., Mesman, J., Moore, T.N., Shatwell, T., Vanderkelen, I., Austin, J.A., DeGasperi, C.L., Dokulil, M., La Fuente, S., Mackay, E.B., Schladow, S.G., Watanabe, S., Marcé, R., Pierson, D.C., Thiery, W. & Jennings, E. (2021). Phenological shifts in lake stratification under climate change. *Nature Communications*, 12, 2318.

Wu, J. (2013). Key concepts and research topics in landscape ecology revisited: 30 years after the Allerton Park workshop. *Landscape Ecology*, 28, 1–11.

Wu, X., Niu, C., Liu, X., Hu, T., Feng, Y., Zhao, Y., Liu, S., Liu, Z., Dai, G., Zhang, Y., Van Meerbeek, K., Wu, J., Liu, L., Guo, Q. & Su, Y. (2024). Canopy structure regulates autumn phenology by mediating the microclimate in temperate forests. *Nature Climate Change*, 14, 1299–1305.

Wu, Z., Chen, S., De Boeck, H.J., Stenseth, N.C., Tang, J., Vitasse, Y., Wang, S., Zohner, C. & Fu, Y.H. (2021). Atmospheric brightening counteracts warming-induced delays in autumn phenology of temperate trees in Europe. *Global Ecology and Biogeography*, 30, 2477–2487.

Yan, T., Fu, Y.H., Campioli, M., Peñuelas, J. & Wang, X. (2021). Divergent responses of phenology and growth to summer and autumnal warming. *Global Change Biology*, 27, null.

Yuancai, L. & Parresol, B.R. (2001). Remarks on Height-Diameter Modeling. Tech. Rep. SRS-RN-10, U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.

Zohner, C.M., Mo, L., Renner, S.S., Svenning, J.C., Vitasse, Y., Benito, B.M., Ordonez, A., Baumgarten, F., Bastin, J.F., Sebald, V., Reich, P.B., Liang, J., Nabuurs, G.J., de Miguel, S., Alberti, G., Antón-Fernández, C., Balazy, R., Brändli, U.B., Chen, H.Y.H., Chisholm, C., Cienciala, E., Dayanandan, S., Fayle, T.M., Frizzera, L., Gianelle, D., Jagodzinski, A.M., Jaroszewicz, B., Jucker, T., Kepfer-Rojas, S., Khan, M.L., Kim, H.S., Korjus, H., Johannsen, V.K., Laarmann, D., Lang, M., Zawila-Niedzwiecki, T., Niklaus, P.A., Paquette, A., Pretzsch, H., Saikia, P., Schall, P., Šebeň, V., Svoboda, M., Tikhonova, E., Viana, H., Zhang, C., Zhao, X. & Crowther, T.W. (2020). Late-spring frost risk between 1959 and 2017 decreased in North America but increased in Europe and Asia. *Proceedings of the National Academy of Sciences*, 117, 12192–12200.