

1

Thesis Proposal

2

Christophe Rouleau-Desrochers

3

December 2, 2025

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). Understanding the consequences of these shifts on ecosystems requires understanding how much the
24 growing season has changed (Duputié *et al.*, 2015).

25

26 *1.1.1.2. Drivers of spring phenology:* Spring phenological events (e.g. budburst and leafout) have been
27 advancing from 0.5 (Wolfe *et al.*, 2005) to 4.2 days/decade (Chmielewski & Rötzer, 2001; Fu *et al.*, 2014)
28 and are mainly driven by temperature (Chuine, 2010; Cleland *et al.*, 2007; Peñuelas & Filella, 2001). In the
29 winter, when trees are still in dormancy, they accumulate cold temperatures (chilling) for which a certain
30 amount is required to be ready to accumulate heat (forcing) (Vitasse *et al.*, 2014). Then, in the spring, a
31 certain amount of forcing is required to initiate budburst (Fu *et al.*, 2015). Heat requirement is met sooner
32 in warm springs, thus explaining the advancement of spring events over the last decades (Fu *et al.*, 2015,
33 2013; Laube *et al.*, 2014).

34

35 *1.1.1.3. Drivers of autumn phenology:* In contrast, autumn phenology (e.g. budset and leaf senescence)
36 is delayed, though to a much lesser extent than spring (Gallinat *et al.*, 2015; Jeong & Medvigh, 2014). The
37 drivers regulating autumn phenology are far less understood than those of spring for many reasons. First,
38 autumn phenology has attracted much less attention compared to spring (Piao *et al.*, 2019). Second, the
39 data is often much noisier, since meteorological conditions in the fall can drastically influence phenological
40 phenomena. To illustrate this, trees going through leaf senescence are subjected to a gradual leaf abscission
41 that follows nutrient reabsorption, and the leaves within the same individual might be at different senescence
42 stages, but a strong wind spell may trigger leaf drop for all leaves, thus affecting the temporal resolution of
43 these data (Wu *et al.*, 2024). However, there is a general belief that autumn phenophases are driven by short-
44 ening photoperiod and colder temperatures (Cooke *et al.*, 2012; Flynn & Wolkovich, 2018; Körner & Basler,

45 2010; Delpierre *et al.*, 2016). Different hypotheses are proposed to explain delayed autumn phenophases.
46 First, warmer autumn temperatures may extend the activity of photosynthetic enzymes, which could be
47 maintained at a higher level. Thus, the degradation rate of chlorophyll would decrease and the timing of
48 senescence would be delayed (Yan *et al.*, 2021). Second, summer droughts could make trees pause their
49 activity schedule and delay senescence to increase carbon assimilation (Dox *et al.*, 2022). Third, there could
50 be an antagonistic effect of warming and brightening—caused by reductions in atmospheric pollution and
51 cloud cover (Sanchez-Lorenzo *et al.*, 2015)—on leaf senescence (Wu *et al.*, 2021). Brightening accelerates
52 the leaf senescence processes and reduces the temperature sensitivity during that period, counteracting the
53 expected warming-induced delays in leaf senescence (Wu *et al.*, 2021). The photo-protection and sink limi-
54 tation hypotheses provide plausible explanations for the negative effect of radiation on leaf senescence and
55 the declining effect of temperature sensitivity of leaf senescence in response to brightening (Wu *et al.*, 2021;
56 Zani *et al.*, 2020).

57

58 **1.1.2. How these shifts translate into effects on trees/forests is not clear - Pros and cons of** 59 **early/late start/end of season**

60 Shifts in spring and autumn phenology support a long-lasting and intuitive assumption that earlier spring
61 and delayed autumn events lead to longer seasons—and thus increased growth (Keenan *et al.*, 2014; Stridbeck
62 *et al.*, 2022). However, research from the past three years has cast doubt on this hypothesis (Dow *et al.*,
63 2022; Green & Keenan, 2022; Silvestro *et al.*, 2023b). For instance, (Dow *et al.*, 2022) showed that despite an
64 earlier growth onset, neither growth rate nor overall annual increment was increased by longer seasons. This
65 could substantially affect carbon-cycle model projections and thus feedbacks to future climate (Richardson
66 *et al.*, 2013; Swidrak *et al.*, 2013). Starting to grow earlier and stopping later both have pros and cons
67 (Figure 1).

68 Understanding these findings requires answering why trees do not grow more despite longer growing sea-
69 sons. While carbon allocation to above-ground biomass is one of the largest carbon sinks, how this carbon is
70 allocated into wood is poorly understood. Indeed, the linear relationship assumption between wood growth
71 and carbon assimilation is not well supported mechanistically and represents an important limitation of
72 vegetation models (Cabon *et al.*, 2022). Net primary production represents the difference between photosyn-
73 thesis and plant respiration, but this commonly used metric completely omits the representation of growth
74 processes. This is perhaps because of a long-lasting paradigm of source-limited photosynthesis. This has
75 now been debunked with carbon fertilization experiments, supporting evidence that direct environmental
76 constraints on growth may be stronger than those on photosynthesis (Friend *et al.*, 2019; Parent *et al.*,
77 2010). This opens up a new—poorly tested—temperature sensitivity relationship between cambial activity
78 and photosynthesis. Growing evidence suggests that cambial activity may be more sensitive than photo-
79 synthesis to a range of environmental conditions, such as water and nutrient availability, and temperature
80 (Cabon *et al.*, 2022, 2020; Muller *et al.*, 2011; Peters *et al.*, 2021). This demonstrates that carbon projection
81 models that heavily rely on vegetation alone may mislead the amount of carbon sequestered in our forests.

82

83 **1.1.3. Growing season shifts and consequences on forest ecosystems and services**

84 Spring and fall phenological events are shifting with debatable consequences on tree growth. The sensitivity
85 of cambial activity to water, temperature and nutrients has the potential to have far-reaching consequences
86 given the hard-to-predict nature of future climate change, where any of these variables could vary from low to
87 high amplitude (Almagro *et al.*, 2025; Cabon *et al.*, 2022). This expected asymmetry of future environmental
88 changes makes understanding the internal and external limits to growth critical. Especially, the capacity
89 to tease apart different biomes—as for example boreal vs tropical forests are expected to react differently
90 (REF)—is critical and empirical data coming from experiments, but also from observations are paramount
91 to predict the changes of forest carbon offset from human GHG emissions (Wolkovich *et al.*, 2025).

92

1.2 Nature of the problem, and how to address it

93

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

94 Observed phenological trends in the last decades cannot be used directly to extrapolate future phenological
95 changes because: (1) the mechanisms guiding them aren't clear, and (2) phenological responses of trees
96 to warming are very likely to be non-linear (Ettinger *et al.*, 2020; Fu *et al.*, 2013). Indeed, accurate pre-

97 ditions require an in-depth, accurate mechanistic understanding of phenophases and their sensitivities to
98 environmental drivers, especially to temperature and photoperiod (Fu *et al.*, 2013). Therefore, the very
99 foundation of the assumption that longer seasons increase growth may shift with future climate change. The
100 well-observed advance in spring phenology may decelerate, and delayed fall phenology may shift towards
101 earlier leaf senescence (through summer drought-induced growth cessation).

102 **1.2.2. The assumption that longer seasons lead to increased growth is called into question**

103 **1.2.2.1. Absence of growth despite better conditions and strategies that can be used** Recent work shows
104 an absence of increased growth despite apparent better environmental conditions, thus casting doubt on a
105 simple and intuitive positive relationship between growing season length and growth. This paradox further
106 emphasizes the need to better understand the drivers regulating growth across biomes, but also how these
107 drivers vary across the species within these biomes. Phenology varies greatly across species (e.g. closely
108 related species tend to budburst at similar times under similar conditions) (Wolkovich *et al.*, 2014), but
109 so does the relationship between growth and season length, which may explain the wide variation of this
110 relationship within communities (Buckley & Kingsolver, 2012). This highlights another weakness of current
111 carbon sequestration models that pool species together, which likely overpasses important nuances in the
112 growth responses that could be explained by species differences. This may mislead the future of forest carbon
113 source-sink ratios (Green & Keenan, 2022; Cabon *et al.*, 2022). To better understand how different species
114 respond to warming, different strategies can be used.

115
116 **1.2.2.2. Experiments:** First, experiments are paramount to robustly tease apart the external vs internal
117 drivers (e.g. warmer springs from severe drought later in the season—a common co-occurring reality in natu-
118 ral environments) (Morin *et al.*, 2010; Primack *et al.*, 2015). However, experiments are most often performed
119 on juvenile trees, which are critical for their role in forest regeneration projections, but their responses can
120 hardly be translated to mature trees, which hold the overwhelming carbon biomass proportion of forests
121 (Augspurger & Bartlett, 2003; Silvestro *et al.*, 2023b; Vitasse, 2013).

122
123 **1.2.2.3. Ground based observations:** Second, leaf phenology through ground-based observations can pro-
124 vide valuable insights into the growth temporality trees that are not suitable for experimental trials. Since
125 cambial and leaf phenology are closely linked to the other, having the more accessible leaf phenology data
126 can act as a reliable proxy for the onset and end of tree growth. It is to say that knowing when leaves
127 elongate and colour can guide when trees start and stop growing—fundamental metrics to determine the
128 growing season length. Ground observations have the advantage of providing accurate data on phenological
129 events for specific sites and species. Recently, the widespread use of smartphones has opened a whole new
130 world of possible phenological monitoring through citizen scientists' records of data over much larger areas
131 and for a wider range of species (Dickinson *et al.*, 2012; Hufkens *et al.*, 2019; Piao *et al.*, 2019). While there
132 are drawbacks to these observations (e.g. non-standard protocols, highly uneven spatiotemporal distribution
133 of these observations), these methods have a huge potential to diversify the phenology data.

134
135 **1.2.3. Goals of my thesis**
136 Using citizen science data, a common garden study and a large-scale experiment, I aim to better understand
137 how different tree species, at different lifespan stages, vary in their growth responses to different season
138 length. Answering these patterns requires defining growth and the growing season.

140 **1.3 Complexity of measuring growth and defining growing season length**

141 **1.3.1.1. What is a growing season?**
142 To understand how trees respond to growing season conditions, it is important to clarify what a growing
143 season and growth are.
144 First, a problem that arises when one tries to quantify how shifting growing seasons affect growth comes from
145 the definition of the growing season itself. Recently, Körner *et al.* (2023) proposed four definitions addressing
146 this issue: (1) true growing season, based on measurable growth; (2) phenological season, based on visible
147 phenological markers; (3) the productive season, based on primary production and (4) meteorological season,
148 based on 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" during which
151 meteorological conditions will be used to calculate growing degree days (GDD). I am using the meteorological
152 season within a constrained window, instead of simply using it irrespective of phenology because of the illusion
153 that an absolute increase in GDD over the last decades—irrespective of the timing of phenophases—also
154 increases growth. Springs are warmer, falls are also sometimes warmer, and summers are warmer, which
155 together increase the number of GDD, which may appear to be a reliable proxy for better environmental
156 conditions. However, models that accumulate GDD before and/or after trees grow could mislead about how
157 this variable drives growth.

158 *1.3.1.2. What is growth?*

159 Wood formation (xylogenesis) is the major biological process by which carbon is allocated and long-term
160 stored in woody plants. Radial growth is determined by the production of xylem and phloem cells that
161 begins with cambial activation and cell production (Etzold *et al.*, 2022; Silvestro *et al.*, 2025). The rate and
162 duration of these phases lead to irreversible radial growth increments usually represented through tree rings.
163 In these, secondary xylem cells account disproportionately to the number of cells produced because they
164 divide more than phloem cells (Plomion *et al.*, 2001; Rathgeber *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 to infer allometries that could give them a
168 good estimate of how much wood they could harvest in a forest (e.g. (Meyer, 1940; Saunders & Wagner,
169 2008)). The widely used method in forestry is to measure diameter at breast height at punctual time
170 intervals (Yuancai & Parresol, 2001). However, these measurements don't provide short-term indicators of
171 growth—especially if taken at multiple-year intervals. Therefore, extreme events affecting growth are likely
172 to be missed. In addition, many forest inventories only report diameter measurements and exclude height,
173 because of logistical constraints ((Saunders & Wagner, 2008)), which reduces biomass estimation quality.
174 This growth data lacks the temporal resolution necessary to properly infer a relationship between growth
175 and environmental conditions.

176
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
179 well 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.

183
184 **1.3.3. Asynchrony between primary and secondary growth (internal growth control?)**
185 I argue that internal growth control in trees may shape their growth responses to growing season length, and
186 these can be split into two categories: primary and secondary growth synchronicity and growth determinancy.

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

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

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

207 Thus, primary versus secondary growth allocation, coupled with growth determinacy, 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 by
213 artificially manipulating growing season length and analyze how this translates (or not) into growth, during
214 the current year (2024) and in the following year (2025). I will also conduct a secondary experiment to
215 examine whether trees can absorb nutrients late in the season and if that translates into growth during the
216 following season. For the CookieSpotters 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 *necessary after the objectives? It feels redundant...*

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

225

226 2 Methodology

227 2.1 Coringtreespotters

228 1.

229 3 Supplemental material

230 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	

232

3.2. Drought

	<p>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).</p>
	<p>Mechanisms</p> <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)
233	<p>Global trend of occurrence</p> <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)
234	<p>Consequences (Individual and Ecosystem level consequences)</p> <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))
235	<p>Differences across species/provenance</p>

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>
236 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)

237 References

- 238 Aitken, S.N. & Bemmels, J.B. (2016). Time to get moving: assisted gene flow of forest trees. *Evolutionary Applications*, 9, 271–290.
- 239
- 240 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.
- 241
- 242
- 243 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.
- 244
- 245 Babst, F., Wright, W.E., Szejner, P., Wells, L., Belmecheri, S. & Monson, R.K. (2016). Blue intensity parameters derived from Ponderosa pine tree rings characterize intra-annual density fluctuations and reveal seasonally divergent water limitations. *Trees*, 30, 1403–1415.
- 246
- 247
- 248 Baumgarten, F., Aitken, S., Vitasse, Y., Guy, R.D. & Wolkovich, E. (2025). Invest now, get paid later? Limits and opportunities of woody plants to time growth in a future climate. *In review*.
- 249
- 250 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.
- 251
- 252 Bonhomme, R. (2000). Bases and limits to using ‘degree.day’ units. *European Journal of Agronomy*, 13, 1–10.
- 253

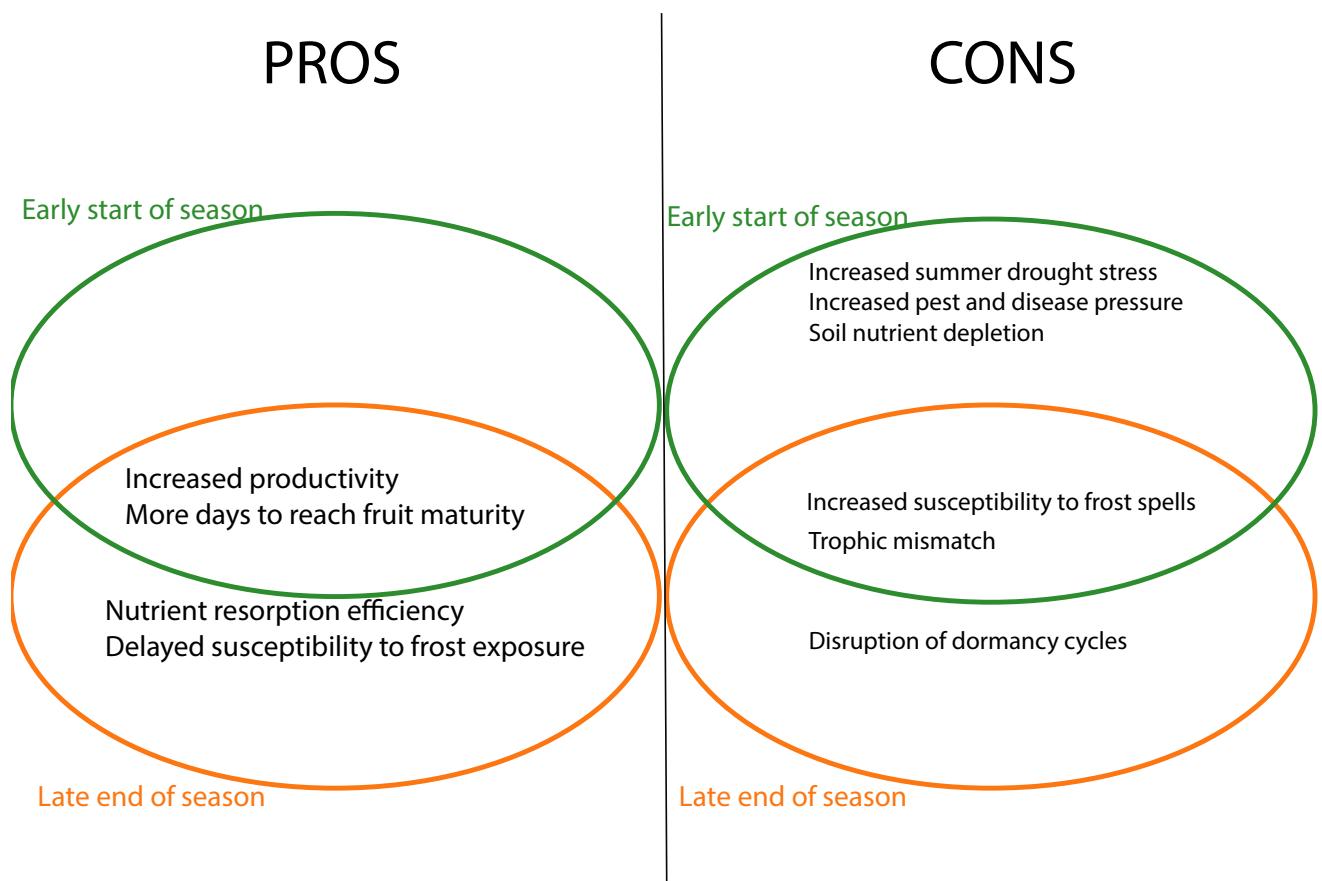


Figure 1: Pros and cons of early start and late end of growing season.

- 254 Brienen, R.J.W., Caldwell, L., Duchesne, L., Voelker, S., Barichivich, J., Baliva, M., Ceccantini, G., Di Fil-
255 ippo, A., Helama, S., Locosselli, G.M., Lopez, L., Piovesan, G., Schöngart, J., Villalba, R. & Gloor, E.
256 (2020). Forest carbon sink neutralized by pervasive growth-lifespan trade-offs. *Nature Communications*,
257 11, 4241.
- 258 Buckley, L.B. & Kingsolver, J.G. (2012). Functional and Phylogenetic Approaches to Forecasting Species'
259 Responses to Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, 43, 205–226.
- 260 Büntgen, U., Wacker, L., Galván, J.D., Arnold, S., Arseneault, D., Baillie, M., Beer, J., Bernabei, M.,
261 Bleicher, N., Boswijk, G., Bräuning, A., Carrer, M., Ljungqvist, F.C., Cherubini, P., Christl, M., Christie,
262 D.A., Clark, P.W., Cook, E.R., Esper, J., Fowler, A.M., Gennaretti, F., Grießinger, J., Grissino-Mayer,
263 H., Grudd, H., Gunnarson, B.E., Hantemirov, R., Herzig, F., Hessl, A., Heussner, K.U., Jull, A.J.T.,
264 Kukarskikh, V., Kirdyanov, A., Krusic, P.J., Kyncl, T., Lara, A., LeQuesne, C., Linderholm, H.W., Loader,
265 N.J., Luckman, B., Miyake, F., Myglan, V.S., Nicolussi, K., Oppenheimer, C., Palmer, J., Panyushkina, I.,
266 Pederson, N., Rybníček, M., Schweingruber, F.H., Seim, A., Sigl, M., Churakova, O., Speer, J.H., Synal,
267 H.A., Tegel, W., Treydte, K., Villalba, R., Wiles, G., Wilson, R., Winship, L.J., Wunder, J., Yang, B. &
268 Young, G.H.F. (2018). Tree rings reveal globally coherent signature of cosmogenic radiocarbon events in
269 774 and 993 CE. *Nature Communications*, 9, 3605.
- 270 Cabon, A., Fernández-de-Uña, L., Gea-Izquierdo, G., Meinzer, F.C., Woodruff, D.R., Martínez-Vilalta, J. &
271 De Cáceres, M. (2020). Water potential control of turgor-driven tracheid enlargement in Scots pine at its
272 xeric distribution edge. *New Phytologist*, 225, 209–221.
- 273 Cabon, A., Kannenberg, S.A., Arain, A., Babst, F., Baldocchi, D., Belmecheri, S., Delpierre, N., Guerrieri,
274 R., Maxwell, J.T., McKenzie, S., Meinzer, F.C., Moore, D.J.P., Pappas, C., Rocha, A.V., Szejner, P.,
275 Ueyama, M., Ulrich, D., Vincke, C., Voelker, S.L., Wei, J., Woodruff, D. & Anderegg, W.R.L. (2022).
276 Cross-biome synthesis of source versus sink limits to tree growth. *Science*, 376, 758–761.
- 277 Camarero, J.J., Olano, J.M. & Parras, A. (2010). Plastic bimodal xylogenesis in conifers from continental
278 Mediterranean climates. *New Phytologist*, 185, 471–480.
- 279 Campbell, L.M., Hagerman, S. & Gray, N.J. (2014). Producing Targets for Conservation: Science and Politics
280 at the Tenth Conference of the Parties to the Convention on Biological Diversity. *Global Environmental
281 Politics*, 14, 41–63.
- 282 Campbell, R., McCarroll, D., Loader, N.J., Grudd, H., Robertson, I. & Jalkanen, R. (2007). Blue intensity
283 in *Pinus sylvestris* tree-rings: developing a new palaeoclimate proxy. *The Holocene*, 17, 821–828.
- 284 Ceballos, G., Ehrlich, P.R. & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction
285 signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*,
286 114.
- 287 Change, I.P.O.C. (2014). Detection and Attribution of Climate Change: from Global to Regional. In:
288 *Climate Change 2013 – The Physical Science Basis*. Cambridge University Press, pp. 867–952. 1st edn.
- 289 Chiang, F., Mazdiyasni, O. & AghaKouchak, A. (2021). Evidence of anthropogenic impacts on global drought
290 frequency, duration, and intensity. *Nature Communications*, 12, 2754.
- 291 Chmielewski, F.M. & Rötzer, T. (2001). Response of tree phenology to climate change across Europe.
292 *Agricultural and Forest Meteorology*, 108, 101–112.
- 293 Choat, B., Brodribb, T.J., Brodersen, C.R., Duursma, R.A., López, R. & Medlyn, B.E. (2018). Triggers of
294 tree mortality under drought. *Nature*, 558, 531–539.
- 295 Chuine, I. (2010). Why does phenology drive species distribution? *Philosophical Transactions of the Royal
296 Society B: Biological Sciences*, 365, 3149–3160.
- 297 Chuine, I. & Régnière, J. (2017). Process-Based Models of Phenology for Plants and Animals. *Annual
298 Review of Ecology, Evolution, and Systematics*, 48, 159–182.

- 299 Cleland, E., Chuine, I., Menzel, A., Mooney, H. & Schwartz, M. (2007). Shifting plant phenology in response
300 to global change. *Trends in Ecology & Evolution*, 22, 357–365.
- 301 Cooke, J.E.K., Eriksson, M.E. & Junntila, O. (2012). The dynamic nature of bud dormancy in trees:
302 environmental control and molecular mechanisms. *Plant, Cell & Environment*, 35, 1707–1728.
- 303 Delpierre, N., Vitasse, Y., Chuine, I., Guillemot, J., Bazot, S., Rutishauser, T. & Rathgeber, C.B.K. (2016).
304 Temperate and boreal forest tree phenology: from organ-scale processes to terrestrial ecosystem models.
305 *Annals of Forest Science*, 73, 5–25.
- 306 Dickinson, J.L., Shirk, J., Bonter, D., Bonney, R., Crain, R.L., Martin, J., Phillips, T. & Purcell, K. (2012).
307 The current state of citizen science as a tool for ecological research and public engagement. *Frontiers in
308 Ecology and the Environment*, 10, 291–297.
- 309 Dosio, A., Mentaschi, L., Fischer, E.M. & Wyser, K. (2018). Extreme heat waves under 1.5 °C and 2 °C
310 global warming. *Environmental Research Letters*, 13, 054006.
- 311 Douglass, A. (1928). Climate and trees. *Nature Magazine*, 12, 51–53.
- 312 Dow, C., Kim, A.Y., D'Orangeville, L., Gonzalez-Akre, E.B., Helcoski, R., Herrmann, V., Harley, G.L.,
313 Maxwell, J.T., McGregor, I.R., McShea, W.J., McMahon, S.M., Pederson, N., Tepley, A.J. & Anderson-
314 Teixeira, K.J. (2022). Warm springs alter timing but not total growth of temperate deciduous trees.
315 *Nature*, 608, 552–557.
- 316 Dox, I., Skrøppa, T., Decoster, M., Prislan, P., Gascó, A., Gričar, J., Lange, H. & Campioli, M. (2022).
317 Severe drought can delay autumn senescence of silver birch in the current year but advance it in the next
318 year. *Agricultural and Forest Meteorology*, 316, 108879.
- 319 Driscoll, D.A., Bland, L.M., Bryan, B.A., Newsome, T.M., Nicholson, E., Ritchie, E.G. & Doherty, T.S.
320 (2018). A biodiversity-crisis hierarchy to evaluate and refine conservation indicators. *Nature Ecology &
321 Evolution*, 2, 775–781.
- 322 Duputié, A., Rutschmann, A., Ronce, O. & Chuine, I. (2015). Phenological plasticity will not help all species
323 adapt to climate change. *Global Change Biology*, 21, 3062–3073.
- 324 Ettinger, A.K., Chamberlain, C.J., Morales-Castilla, I., Buonaiuto, D.M., Flynn, D.F.B., Savas, T., Samaha,
325 J.A. & Wolkovich, E.M. (2020). Winter temperatures predominate in spring phenological responses to
326 warming. *Nature Climate Change*, 10, 1137–1142.
- 327 Etzold, S., Sterck, F., Bose, A.K., Braun, S., Buchmann, N., Eugster, W., Gessler, A., Kahmen, A., Peters,
328 R.L., Vitasse, Y., Walthert, L., Ziemińska, K. & Zweifel, R. (2022). Number of growth days and not length
329 of the growth period determines radial stem growth of temperate trees. *Ecology Letters*, 25, 427–439.
- 330 Flynn, D.F.B. & Wolkovich, E.M. (2018). Temperature and photoperiod drive spring phenology across all
331 species in a temperate forest community. *New Phytologist*, 219, 1353–1362.
- 332 Friend, A.D., Eckes-Shephard, A.H., Fonti, P., Rademacher, T.T., Rathgeber, C.B.K., Richardson, A.D. &
333 Turton, R.H. (2019). On the need to consider wood formation processes in global vegetation models and
334 a suggested approach. *Annals of Forest Science*, 76, 49.
- 335 Fritts, H. & Swetnam, T. (1989). Dendroecology: A Tool for Evaluating Variations in Past and Present
336 Forest Environments. In: *Advances in Ecological Research*. Elsevier, vol. 19, pp. 111–188.
- 337 Fu, Y.H., Campioli, M., Deckmyn, G. & Janssens, I.A. (2013). Sensitivity of leaf unfolding to experimental
338 warming in three temperate tree species. *Agricultural and Forest Meteorology*, 181, 125–132.
- 339 Fu, Y.H., Piao, S., Op De Beeck, M., Cong, N., Zhao, H., Zhang, Y., Menzel, A. & Janssens, I.A. (2014).
340 Recent spring phenology shifts in western Central Europe based on multiscale observations. *Global Ecology
341 and Biogeography*, 23, 1255–1263.

- 342 Fu, Y.H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., Ciais, P., Huang, M., Menzel, A., Peñuelas,
343 J., Song, Y., Vitassee, Y., Zeng, Z. & Janssens, I.A. (2015). Declining global warming effects on the
344 phenology of spring leaf unfolding. *Nature*, 526, 104–107. Publisher: Nature Publishing Group.
- 345 Gagne, M.A., Smith, D.D. & McCulloh, K.A. (2020). Limited physiological acclimation to recurrent heat-
346 waves in two boreal tree species. *Tree Physiology*, 40, 1680–1696.
- 347 Gallinat, A.S., Primack, R.B. & Wagner, D.L. (2015). Autumn, the neglected season in climate change
348 research. *Trends in Ecology & Evolution*, 30, 169–176.
- 349 Gazol, A., Camarero, J.J., Vicente-Serrano, S.M., Sánchez-Salguero, R., Gutiérrez, E., De Luis, M.,
350 Sangüesa-Barreda, G., Novak, K., Rozas, V., Tíscar, P.A., Linares, J.C., Martín-Hernández, N., Martínez
351 Del Castillo, E., Ribas, M., García-González, I., Silla, F., Camisón, A., Génova, M., Olano, J.M., Longares,
352 L.A., Hevia, A., Tomás-Burguera, M. & Galván, J.D. (2018). Forest resilience to drought varies across
353 biomes. *Global Change Biology*, 24, 2143–2158.
- 354 Gilmore, E.C. & Rogers, J.S. (1958). Heat Units as a Method of Measuring Maturity in Corn. *Agronomy
355 Journal*, 50, 611–615.
- 356 Green, J.K. & Keenan, T.F. (2022). The limits of forest carbon sequestration. *Science*, 376, 692–693.
- 357 Griffin, D., Porter, S.T., Trumper, M.L., Carlson, K.E., Crawford, D.J., Schwalen, D. & McFadden, C.H.
358 (2021). Gigapixel Macro Photography of Tree Rings. *Tree-Ring Research*, 77.
- 359 Hauck, M., Schneider, T., Bahlinger, S., Fischbach, J., Oswald, G., Csapek, G. & Dulamsuren, C. (2025).
360 Heat tolerance of temperate tree species from Central Europe. *Forest Ecology and Management*, 580,
361 122541.
- 362 Helama, S. (2023). Distinguishing Type I and II errors in statistical tree-ring dating. *Quaternary Geochronol-
363 ogy*, 78, 101470.
- 364 Hidalgo, H.G., Das, T., Dettinger, M.D., Cayan, D.R., Pierce, D.W., Barnett, T.P., Bala, G., Mirin, A.,
365 Wood, A.W., Bonfils, C., Santer, B.D. & Nozawa, T. (2009). Detection and Attribution of Streamflow
366 Timing Changes to Climate Change in the Western United States. *Journal of Climate*, 22, 3838–3855.
- 367 Huey, R.B., Kearney, M.R., Krockenberger, A., Holtum, J.A.M., Jess, M. & Williams, S.E. (2012). Predicting
368 organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philosophical
369 Transactions of the Royal Society B: Biological Sciences*, 367, 1665–1679.
- 370 Hufkens, K., Melaas, E.K., Mann, M.L., Foster, T., Ceballos, F., Robles, M. & Kramer, B. (2019). Monitoring
371 crop phenology using a smartphone based near-surface remote sensing approach. *Agricultural and Forest
372 Meteorology*, 265, 327–337.
- 373 Intergovernmental panel on climate change (ed.) (2007). *Climate change 2007: the physical science basis*.
374 Cambridge university press, Cambridge.
- 375 Intergovernmental Panel On Climate Change (Ipcc) (2023). *Climate Change 2022 – Impacts, Adaptation and
376 Vulnerability: Working Group II Contribution to the Sixth Assessment Report of the Intergovernmental
377 Panel on Climate Change*. 1st edn. Cambridge University Press.
- 378 Jeong, S. & Medvigy, D. (2014). Macroscale prediction of autumn leaf coloration throughout the continental
379 United States. *Global Ecology and Biogeography*, 23, 1245–1254.
- 380 Keenan, T.F., Gray, J., Friedl, M.A., Toomey, M., Bohrer, G., Hollinger, D.Y., Munger, J.W., O'Keefe, J.,
381 Schmid, H.P., Wing, I.S., Yang, B. & Richardson, A.D. (2014). Net carbon uptake has increased through
382 warming-induced changes in temperate forest phenology. *Nature Climate Change*, 4, 598–604.
- 383 Kolář, T., Giagli, K., Trnka, M., Bednářová, E., Vavrčík, H. & Rybníček, M. (2016). Response of the leaf
384 phenology and tree-ring width of European beech to climate variability. *Silva Fennica*, 50.

- 385 Kurnik, B., Barbosa, P. & Vogt, J. (2011). Testing two different precipitation datasets to compute the
386 standardized precipitation index over the Horn of Africa. *International Journal of Remote Sensing*, 32,
387 5947–5964.
- 388 Körner, C. & Basler, D. (2010). Phenology Under Global Warming. *Science*, 327, 1461–1462. Publisher:
389 American Association for the Advancement of Science.
- 390 Körner, C., Möhl, P. & Hiltbrunner, E. (2023). Four ways to define the growing season. *Ecology Letters*, 26,
391 1277–1292.
- 392 Laube, J., Sparks, T.H., Estrella, N., Höfler, J., Ankerst, D.P. & Menzel, A. (2014). Chilling outweighs
393 photoperiod in preventing precocious spring development. *Global Change Biology*, 20, 170–182.
- 394 Laurance, W.F. (2007). Have we overstated the tropical biodiversity crisis? *Trends in Ecology & Evolution*,
395 22, 65–70.
- 396 Levanič, T. (2007). Atrics – A New System for Image Acquisition in Dendrochronology. *Tree-Ring Research*,
397 63, 117–122.
- 398 Li, Y., Zhang, W., Schwalm, C.R., Gentine, P., Smith, W.K., Ciais, P., Kimball, J.S., Gazol, A., Kannenberg,
399 S.A., Chen, A., Piao, S., Liu, H., Chen, D. & Wu, X. (2023). Widespread spring phenology effects on
400 drought recovery of Northern Hemisphere ecosystems. *Nature Climate Change*, 13, 182–188.
- 401 Lieth, H., Jacobs, J., Lange, O.L., Olson, J.S. & Wieser, W. (eds.) (1974). *Phenology and Seasonality
402 Modeling*. vol. 8 of *Ecological Studies*. Springer Berlin Heidelberg, Berlin, Heidelberg.
- 403 Lynas, M., Houlton, B.Z. & Perry, S. (2021). Greater than 99% consensus on human caused climate change
404 in the peer-reviewed scientific literature. *Environmental Research Letters*, 16, 114005.
- 405 Manzanedo, R.D. & Pederson, N. (2019). Towards a More Ecological Dendroecology. *Tree-Ring Research*,
406 75, 152.
- 407 Marvel, K., Cook, B.I., Bonfils, C.J.W., Durack, P.J., Smerdon, J.E. & Williams, A.P. (2019). Twentieth-
408 century hydroclimate changes consistent with human influence. *Nature*, 569, 59–65.
- 409 Marx, W., Haunschild, R. & Bornmann, L. (2021). Heat waves: a hot topic in climate change research.
410 *Theoretical and Applied Climatology*, 146, 781–800.
- 411 McMaster, G. (1997). Growing degree-days: one equation, two interpretations. *Agricultural and Forest
412 Meteorology*, 87, 291–300.
- 413 Meehl, G.A. & Tebaldi, C. (2004). More Intense, More Frequent, and Longer Lasting Heat Waves in the
414 21st Century. *Science*, 305, 994–997.
- 415 Meng, L., Mao, J., Zhou, Y., Richardson, A.D., Lee, X., Thornton, P.E., Ricciuto, D.M., Li, X., Dai, Y., Shi,
416 X. & Jia, G. (2020). Urban warming advances spring phenology but reduces the response of phenology
417 to temperature in the conterminous United States. *Proceedings of the National Academy of Sciences*, 117,
418 4228–4233.
- 419 Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská,
420 O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Defila, C., Donnelly, A., Filella, Y., Jatczak,
421 K., Mestre, A., Peñuelas, J., Pirinen, P., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wiel-
422 golaski, F., Zach, S. & Zust, A. (2006). European phenological response to climate change matches the
423 warming pattern. *Global Change Biology*, 12, 1969–1976.
- 424 Meyer, B.F., Buras, A., Gregor, K., Layritz, L.S., Principe, A., Kreyling, J., Rammig, A. & Zang, C.S.
425 (2024). Frost matters: incorporating late-spring frost into a dynamic vegetation model regulates regional
426 productivity dynamics in European beech forests. *Biogeosciences*, 21, 1355–1370.
- 427 Meyer, H.A. (1940). A Mathematical Expression for Height Curves. *Journal of Forestry*, 38, 415–420.

- 428 Moore, J.L. & Remais, J.V. (2014). Developmental Models for Estimating Ecological Responses to Environmental Variability: Structural, Parametric, and Experimental Issues. *Acta Biotheoretica*, 62, 69–90.
- 430 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.
- 432 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.
- 435 Oreskes, N. (2004). The Scientific Consensus on Climate Change. *Science*, 306, 1686–1686.
- 436 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.
- 439 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.
- 442 Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42.
- 444 Pearl, J.K., Keck, J.R., Tintor, W., Siekacz, L., Herrick, H.M., Meko, M.D. & Pearson, C.L. (2020). New frontiers in tree-ring research. *The Holocene*, 30, 923–941.
- 446 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.
- 449 Peñuelas, J. & Filella, I. (2001). Responses to a Warming World. *Science*, 294, 793–795. Publisher: American Association for the Advancement of Science.
- 451 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.
- 454 Plomion, C., Leprovost, G. & Stokes, A. (2001). Wood Formation in Trees. *Plant Physiology*, 127, 1513–1523.
- 455 Polgar, C.A. & Primack, R.B. (2011). Leaf-out phenology of temperate woody plants: from trees to ecosystems. *New Phytologist*, 191, 926–941.
- 457 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.
- 460 Rathgeber, C.B.K., Cuny, H.E. & Fonti, P. (2016). Biological Basis of Tree-Ring Formation: A Crash Course. *Frontiers in Plant Science*, 7.
- 462 Reimer, P.J., Austin, W.E.N., Bard, E., Bayliss, A., Blackwell, P.G., Bronk Ramsey, C., Butzin, M., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Hajdas, I., Heaton, T.J., Hogg, A.G., Hughen, K.A., Kromer, B., Manning, S.W., Muscheler, R., Palmer, J.G., Pearson, C., Van Der Plicht, J., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Turney, C.S.M., Wacker, L., Adolphi, F., Büntgen, U., Capano, M., Fahrni, S.M., Fogtmann-Schulz, A., Friedrich, R., Köhler, P., Kudsk, S., Miyake, F., Olsen, J., Reinig, F., Sakamoto, M., Sookdeo, A. & Talamo, S. (2020). The IntCal20 Northern Hemisphere Radiocarbon Age Calibration Curve (0–55 cal kBP). *Radiocarbon*, 62, 725–757.
- 469 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.

- 472 Richardson, A.D., Keenan, T.F., Migliavacca, M., Ryu, Y., Sonnentag, O. & Toomey, M. (2013). Climate
 473 change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural*
 474 and *Forest Meteorology*, 169, 156–173.
- 475 Rossi, S., Anfodillo, T. & Menardi, R. (2006). Trehpor: A New Tool for Sampling Microcores from tree
 476 stems. *IAWA Journal*, 27, 89–97.
- 477 Sanchez-Lorenzo, A., Wild, M., Brunetti, M., Guijarro, J.A., Hakuba, M.Z., Calbó, J., Mystakidis, S. &
 478 Bartok, B. (2015). Reassessment and update of long-term trends in downward surface shortwave radiation
 479 over Europe (1939–2012). *Journal of Geophysical Research: Atmospheres*, 120, 9555–9569.
- 480 Saunders, M.R. & Wagner, R.G. (2008). Height-diameter models with random coefficients and site variables
 481 for tree species of Central Maine. *Annals of Forest Science*, 65, 203–203.
- 482 Sgubin, G., Swingedouw, D., Dayon, G., García De Cortázar-Atauri, I., Ollat, N., Pagé, C. & Van Leeuwen,
 483 C. (2018). The risk of tardive frost damage in French vineyards in a changing climate. *Agricultural and*
 484 *Forest Meteorology*, 250–251, 226–242.
- 485 Silvestro, R., Deslauriers, A., Prislan, P., Rademacher, T., Rezaie, N., Richardson, A.D., Vitassee, Y. &
 486 Rossi, S. (2025). From Roots to Leaves: Tree Growth Phenology in Forest Ecosystems. *Current Forestry*
 487 *Reports*, 11, 12.
- 488 Silvestro, R., Mura, C., Alano Bonacini, D., De Lafontaine, G., Faubert, P., Mencuccini, M. & Rossi, S.
 489 (2023a). Local adaptation shapes functional traits and resource allocation in black spruce. *Scientific*
 490 *Reports*, 13, 21257.
- 491 Silvestro, R., Zeng, Q., Buttò, V., Sylvain, J.D., Drolet, G., Mencuccini, M., Thiffault, N., Yuan, S. & Rossi,
 492 S. (2023b). A longer wood growing season does not lead to higher carbon sequestration. *Scientific Reports*,
 493 13, 4059.
- 494 Soolanayakanahally, R.Y., Guy, R.D., Silim, S.N. & Song, M. (2013). Timing of photoperiodic competency
 495 causes phenological mismatch in balsam poplar (*Populus balsamifera* L.). *Plant, Cell & Environment*, 36,
 496 116–127.
- 497 Spinoni, J., Naumann, G., Carrao, H., Barbosa, P. & Vogt, J. (2014). World drought frequency, duration,
 498 and severity for 1951–2010. *International Journal of Climatology*, 34, 2792–2804.
- 499 Spinoni, J., Vogt, J.V., Naumann, G., Barbosa, P. & Dosio, A. (2018). Will drought events become more
 500 frequent and severe in Europe? *International Journal of Climatology*, 38, 1718–1736.
- 501 Stridbeck, P., Björklund, J., Fuentes, M., Gunnarson, B.E., Jönsson, A.M., Linderholm, H.W., Ljungqvist,
 502 F.C., Olsson, C., Rayner, D., Rocha, E., Zhang, P. & Seftigen, K. (2022). Partly decoupled tree-ring
 503 width and leaf phenology response to 20th century temperature change in Sweden. *Dendrochronologia*,
 504 75, 125993.
- 505 Swidrak, I., Schuster, R. & Oberhuber, W. (2013). Comparing growth phenology of co-occurring deciduous
 506 and evergreen conifers exposed to drought. *Flora: Morphology, Distribution, Functional Ecology of Plants*,
 507 208, 609–617.
- 508 Teskey, R., Werten, T., Bauweraerts, I., Ameye, M., McGuire, M.A. & Steppe, K. (2015). Responses of tree
 509 species to heat waves and extreme heat events. *Plant, Cell & Environment*, 38, 1699–1712.
- 510 Trenberth, K.E., Dai, A., Van Der Schrier, G., Jones, P.D., Barichivich, J., Briffa, K.R. & Sheffield, J.
 511 (2014). Global warming and changes in drought. *Nature Climate Change*, 4, 17–22.
- 512 Tyree, M.T. & Zimmermann, M.H. (2002). *Xylem Structure and the Ascent of Sap*. Springer Series in Wood
 513 Science. Springer Berlin Heidelberg, Berlin, Heidelberg.
- 514 Vitasse, Y. (2013). Ontogenetic changes rather than difference in temperature cause understory trees to leaf
 515 out earlier. *New Phytologist*, 198, 149–155.

- 516 Vitasse, Y., eLenz, A. & eKoerner, C. (2014). The interaction between freezing tolerance and phenology in
517 temperate deciduous trees. *Frontiers in Plant Science*, 5. Publisher: Frontiers Media S.A.
- 518 Von Arx, G. & Carrer, M. (2014). ROXAS – A new tool to build centuries-long tracheid-lumen chronologies
519 in conifers. *Dendrochronologia*, 32, 290–293.
- 520 Way, D.A. & Montgomery, R.A. (2015). Photoperiod constraints on tree phenology, performance
521 and migration in a warming world. *Plant, Cell & Environment*, 38, 1725–1736. _eprint:
522 <https://onlinelibrary.wiley.com/doi/pdf/10.1111/pce.12431>.
- 523 Wolfe, D.W., Schwartz, M.D., Lakso, A.N., Otsuki, Y., Pool, R.M. & Shaulis, N.J. (2005). Climate change
524 and shifts in spring phenology of three horticultural woody perennials in northeastern USA. *International
525 Journal of Biometeorology*, 49, 303–309.
- 526 Wolkovich, E.M., Auerbach, J., Chamberlain, C.J., Buonaiuto, D.M., Ettinger, A.K., Morales-Castilla, I.
527 & Gelman, A. (2021). A simple explanation for declining temperature sensitivity with warming. *Global
528 Change Biology*, 27, 4947–4949.
- 529 Wolkovich, E.M., Cook, B.I. & Davies, T.J. (2014). Progress towards an interdisciplinary science of plant
530 phenology: building predictions across space, time and species diversity. *New Phytologist*, 201, 1156–1162.
531 _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/nph.12599>.
- 532 Wolkovich, E.M., Ettinger, A.K., Chin, A., Chamberlain, C.J., Baumgarten, F., Pradhan, K., Manzanedo,
533 R.D. & Lambers, J.H.R. (2025). Why longer seasons with climate change may not increase tree growth.
534 *In review*.
- 535 Woolway, R.I., Sharma, S., Weyhenmeyer, G.A., Debolskiy, A., Golub, M., Mercado-Bettín, D., Perroud,
536 M., Stepanenko, V., Tan, Z., Grant, L., Ladwig, R., Mesman, J., Moore, T.N., Shatwell, T., Vanderkelen,
537 I., Austin, J.A., DeGasperi, C.L., Dokulil, M., La Fuente, S., Mackay, E.B., Schladow, S.G., Watanabe,
538 S., Marcé, R., Pierson, D.C., Thiery, W. & Jennings, E. (2021). Phenological shifts in lake stratification
539 under climate change. *Nature Communications*, 12, 2318.
- 540 Wu, J. (2013). Key concepts and research topics in landscape ecology revisited: 30 years after the Allerton
541 Park workshop. *Landscape Ecology*, 28, 1–11.
- 542 Wu, X., Niu, C., Liu, X., Hu, T., Feng, Y., Zhao, Y., Liu, S., Liu, Z., Dai, G., Zhang, Y., Van Meerbeek, K.,
543 Wu, J., Liu, L., Guo, Q. & Su, Y. (2024). Canopy structure regulates autumn phenology by mediating
544 the microclimate in temperate forests. *Nature Climate Change*, 14, 1299–1305.
- 545 Wu, Z., Chen, S., De Boeck, H.J., Stenseth, N.C., Tang, J., Vitasse, Y., Wang, S., Zohner, C. & Fu, Y.H.
546 (2021). Atmospheric brightening counteracts warming-induced delays in autumn phenology of temperate
547 trees in Europe. *Global Ecology and Biogeography*, 30, 2477–2487.
- 548 Yan, T., Fu, Y.H., Campioli, M., Peñuelas, J. & Wang, X. (2021). Divergent responses of phenology and
549 growth to summer and autumnal warming. *Global Change Biology*, 27, null.
- 550 Yuancai, L. & Parresol, B.R. (2001). Remarks on Height-Diameter Modeling. Tech. Rep. SRS-RN-10, U.S.
551 Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.
- 552 Zani, D., Crowther, T.W., Mo, L., Renner, S.S. & Zohner, C.M. (2020). Increased growing-season productiv-
553 ity drives earlier autumn leaf senescence in temperate trees. *Science*, 370, 1066–1071. Publisher: American
554 Association for the Advancement of Science.
- 555 Zohner, C.M., Mirzagholi, L., Renner, S.S., Mo, L., Rebindaine, D., Bucher, R., Palouš, D., Vitasse, Y., Fu,
556 Y.H., Stocker, B.D. & Crowther, T.W. (2023). Effect of climate warming on the timing of autumn leaf
557 senescence reverses after the summer solstice. *Science*, 381.

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

567 Čufar, K., Prislan, P., De Luis, M. & Gričar, J. (2008). Tree-ring variation, wood formation and phenology
568 of beech (*Fagus sylvatica*) from a representative site in Slovenia, SE Central Europe. *Trees*, 22, 749–758.