



HAL
open science

Interaction of drought and frost in tree ecophysiology: rethinking the timing of risks.

Guillaume Charrier, Nicolas Martin-StPaul, Claire Damesin, Nicolas N. Delpierre, Heikki Hänninen, Jose Manuel Torres Ruiz, Hendrik Davi

► To cite this version:

Guillaume Charrier, Nicolas Martin-StPaul, Claire Damesin, Nicolas N. Delpierre, Heikki Hänninen, et al.. Interaction of drought and frost in tree ecophysiology: rethinking the timing of risks.. 2020. hal-02475505v3

HAL Id: hal-02475505

<https://hal.science/hal-02475505v3>

Preprint submitted on 14 Sep 2020 (v3), last revised 28 Sep 2020 (v4)

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Interaction of drought and frost in tree ecophysiology:**
2 **rethinking the timing of risks.**

3 Guillaume Charrier¹, Nicolas Martin-StPaul², Claire Damesin³, Nicolas Delpierre³, Heikki
4 Hänninen⁴, Jose M. Torres-Ruiz¹, Hendrik Davi²

5 ¹ Université Clermont Auvergne, INRAE, PIAF, F-63000 Clermont–Ferrand, France.

6 ² INRAE, URFM, Domaine Saint Paul, INRAE Centre de recherche PACA, 228 route de
7 l'Aérodrome, CS 40509, Domaine Saint-Paul, Site Agroparc, France

8 ³ Ecologie Systématique Evolution, Univ. Paris-Sud, CNRS, AgroParisTech, Université Paris-
9 Saclay, Orsay, France

10 ⁴ State Key Laboratory of Subtropical Silviculture, Zhejiang Agriculture & Forestry University,
11 Hangzhou 311300, China

12

13 **Author contributions**

14 GC, NMSP and HD developed the ideas presented in this viewpoint piece and wrote the
15 manuscript, with contributions from CD, ND, HH and JMTR.

16

17 **Conflict of interest disclosure**

18 The authors of this preprint declare that they have no financial conflict of interest with the
19 content of this article. GC and NMSP are PCI FWS recommenders.

20

21 **Keywords:** Abiotic stress, Acclimation, Carbon availability, Drought, Frost, Phenology, Risk
22 assessment, Tree ecophysiology, Water balance

23 **Abstract**

24 In temperate, boreal and alpine areas, the edges of plant distribution are strongly affected by
25 abiotic constraints. For example, heat waves and drought are major constraints at low latitude
26 and elevation while cold and frost are key factors at high latitude and elevation. Over the next
27 few decades, climate variability is expected to increase, enhancing the probability of extreme
28 events and thus the potential stress imposed by abiotic constraints. Moreover, the likelihood of
29 co-occurring and successive constraints, such as drought and frost, could increase in parallel. It
30 is likely that initial exposure to a first constraint would affect the vulnerability to a subsequent
31 one. Three integrative physiological processes, namely water status, carbon status and the
32 timing of phenological stages, are crucial to understanding how trees will respond to these stress
33 factors. Although these processes have largely been studied alone, in response to a single
34 constraint, their interaction has rarely been investigated. In this paper, we have examined how
35 water and carbon status interact with the growth cycle and affect both the vulnerability and the
36 exposure to climatic constraints via two different focuses: (i) How would the interaction of frost
37 and drought constraints modulate the vulnerability to a subsequent constraint? (ii) How
38 vulnerability to a given constraint and phenology interact? In the light of numerous papers, we
39 suggest that the interaction between frost and drought constraints should in the short-term
40 influence water status and, in the longer term, the carbon status, both consequently affecting
41 further vulnerability, potentially leading to a decline. This vulnerability can also be modulated
42 by a shift in the annual phenological cycle induced by a previous constraint. Furthermore, we
43 have identified significant gaps of knowledge in the ecophysiological tree response to
44 interacting stresses based on three major points: (i) the spatio-temporal variation in
45 carbohydrate composition, fluxes and allocation in relation to environmental drivers, (ii) the
46 spatio-temporal variation in water content, water and osmotic potentials, (iii) the modulation of
47 phenological processes in response to stress. This framework can help to improve the current
48 process based models and to identify interactions that needs to be better described in order to

49 obtain a more quantitative and dynamic view of drought and frost vulnerabilities integrating the

50 life history of the individual plant.

51

52 **Introduction**

53 Abiotic (*e.g.* temperature, water, light, nutrients) and biotic factors (*e.g.* intra and
54 interspecific competition, predation, parasitism) are the major drivers of plant distribution and,
55 therefore, evolutionary change (Erwin 2009; Klanderud *et al.*, 2015). Although biotic factors
56 drive the population dynamics in the entire range, abiotic factors can be highly relevant at the
57 rear and leading edges of the distribution (Hampe & Petit, 2005). Within the boreal, alpine,
58 temperate and Mediterranean areas, plants are likely to be exposed to both drought and frost
59 stress, although it may not happen every year. At the rear edge, drought stress is one of the
60 critical abiotic factors (*e.g.* at low latitude and elevation in Europe; Loehle, 1998; Lines *et al.*,
61 2010; Ruiz-Benito *et al.*, 2013). At the leading edge (high latitude and elevation), cold and
62 freezing temperatures usually limit the plant distribution (Gusta *et al.*, 1983; Körner, 1998;
63 Larcher, 2005; Charrier *et al.*, 2013a). Along a latitudinal gradient within the niche of a species,
64 drought and frost constraints are clearly separated, *i.e.* episodes of mild or severe drought are
65 observed on the rear edge during the summer, and frost stress on the leading edge during the
66 winter. This has led to define the autoecological approach to predict the distribution of plant
67 species within frost-exposed areas (boreal, alpine, temperate and Mediterranean areas),
68 considering individual limitations, such as minimum temperature at the leading edge or water
69 deficit at the rear edge (Guisan & Thuillier, 2005; Cheaib *et al.*, 2012). However, drought and
70 frost can co-occur at high elevation when, late in the winter, air temperature increases while
71 soil is still frozen, inducing the so-called winter drought (Tranquillini, 1979; Mayr & Charra-
72 Vaskou, 2007; Charrier *et al.*, 2017). An alternative approach is thus required for taking the
73 different involved processes into account, and, more importantly, for addressing their
74 interaction to improve the actual species distribution models.

75 This is even more crucial since dramatic changes in climate are likely to increase exposure
76 to abiotic constraints over all biomes (IPCC, 2012). Mean surface temperature increased at a
77 rate of 0.2°C per decade over the last decades, leading to species migration at higher latitudes

78 and elevation (Parmesan & Yohe, 2003; Lenoir *et al.*, 2008). Ecosystem functioning is likely
79 to be affected by these changes, however, through contradictory effects. On the one hand,
80 increased productivity is expected in relation to longer growing season (early flushing dates and
81 delayed senescence; Schaber & Badeck, 2005; Menzel *et al.*, 2006; Fu *et al.*, 2014; Keenan &
82 Richardson, 2015). However, on the other hand, a substantial deterioration in various
83 physiological processes is expected to be induced by *e.g.* an insufficient winter chilling that
84 would alter plant development (Chuine *et al.*, 2016; Delpierre *et al.*, 2016), or increased climatic
85 hazards such as drought (Porporato *et al.*, 2004; Allen *et al.*, 2010; Carnicer *et al.*, 2012) or late
86 frosts events (Leinonen & Hänninen, 2002; Augspurger, 2013).

87 The extreme climatic events (*e.g.* drought, frost, heat spell and storm) play a major role in
88 the distribution, survival and, therefore, in the adaptation of plants (Chapin *et al.*, 1993; van
89 Peer *et al.*, 2004), as well as in the productivity and the composition of communities (Knapp *et*
90 *al.*, 2002). The expected increase in climate variability will inevitably lead to an increase in the
91 frequency, intensity and duration of extreme events (IPCC, 2012; Rummukainen, 2012;
92 Seneviratne *et al.*, 2012). If the return period of two extreme events is divided by two (*e.g.* a
93 100-year episode occurring twice more often), the return period of the interaction between these
94 two constraints should happen four times more often. How these extreme events will affect
95 ecosystem functions is a key issue for climatologists, ecologists and modelers from IPCC
96 (IPCC, 2014). In this regard, perennial plants, and especially trees, which are keystones
97 structuring many ecosystems, sheltering biodiversity and being an important carbon stock, are
98 the most likely to be affected by an increased exposure to abiotic constraints, even though they
99 may not reach the lethal threshold at once (Chuste *et al.*, 2019). An accurate assessment of the
100 emerging risks and their impacts on the physiology of trees is therefore urgently needed to
101 predict dynamics of forest ecosystems and ultimately their influence on the water and carbon
102 cycles at the global scale.

103 The risk of developing significant damages is only achieved at the crossing between climatic
104 hazards (*e.g.* drought or frost constraint), stress exposure (*e.g.* low water potential or organ
105 temperature) and tree vulnerability (*e.g.* low resistance to embolism or insufficient frost
106 hardiness; Bréda & Peiffer, 2014). The prediction of emerging risks therefore needs accurate
107 assessments of (i) the exposure to a given abiotic constraint (type, intensity, duration and
108 frequency) and (ii) the spatio-temporal patterns of vulnerability and subsequent damages. The
109 timing of critical phenological stages (*e.g.* bud burst date and leaf full expansion date with
110 respect to frost and drought, respectively) would thus modulate risk and subsequent damages.
111 How the exposure to a given abiotic constraint at a given time instant would influence the
112 vulnerability to the same or a different constraint in the future is a critical issue that has been
113 only rarely investigated (Miao *et al.*, 2009, Anderegg *et al.*, 2013; Batlori *et al.*, 2017; Hossain
114 *et al.*, 2019).

115 The vulnerability to abiotic constraints (which is the susceptibility to develop damages
116 facing a given stress intensity) has been studied for decades via three different focuses, namely
117 phenology (Fig. 1 Frame C; Hänninen & Tanino, 2011), water use (Fig. 1 Frame D, Choat *et*
118 *al.*, 2012; Anderegg *et al.*, 2015) and carbon availability (Fig.1 Frame B, Sala *et al.*, 2012;
119 Hartmann & Trumbore, 2016). The individual responses of each tree eco-physiological process
120 has been integrated into process-based models such as PHENOFIT (Morin & Chuine, 2005),
121 SUREAU (Martin-StPaul *et al.*, 2017) or CASTANEA (Dufrene *et al.*, 2005), for phenology,
122 water use and carbon availability, respectively. Facing constraints, the response of each process
123 may not be linear. Therefore, the response to simultaneous or successive constraints may
124 generate complex behavior. Integrating the physiological response to abiotic constraints is
125 therefore needed to predict various forms of emergent behavior under new conditions imposed
126 by climate change (Bartholomeus *et al.*, 2011).

127 This paper summarizes the state-of-the-art of tree responses to drought and frost constraints

128 from the cellular to the individual scale and subsequent damages with the aim of emphasizing
129 the undervalued role of their interactions at the short term scale (i.e. from the day to the year).
130 Furthermore, different communities are interested in single process or sets of processes (e.g.
131 hydraulic in response to drought, frost hardiness and damages, phenological cycles,...). The
132 influence of previous stress factors on plant vulnerability, is mainly relevant on woody plants
133 and will be mainly explored at the annual level through two main questions (i) How would the
134 interaction of drought and frost constraints modulate the vulnerability to a subsequent
135 constraint? (ii) How do vulnerability to a given constraint and phenology interact? Addressing
136 these questions will provide novel information about the interaction between climate and trees
137 from a wider, multifactorial and temporal perspective. This framework would be crucial to
138 understand and predict local mortality dynamics and ultimately to improve actual species
139 distribution models.

140 **How would the interaction of drought and frost constraints modulate the**
141 **vulnerability to a subsequent constraint?**

142 Over the last decades, ecophysiological studies have led to a comprehensive understanding
143 on the direct relation between abiotic constraints and physiological processes (Frame #1 and
144 #2; Fig. 1). From a physical perspective, both drought and frost constraints are related to a
145 limited liquid water availability. Similar damages are generated at both the cellular (i.e.
146 plasmolysis and cell lysis; Levitt, 1980; Siminovitch & Cloutier, 1983) and vascular levels (i.e.
147 cavitation and embolism when a critical level of water potential is reached; Sperry & Sullivan,
148 1992; Charrier *et al.*, 2014). A critical factor in the response to both stresses is the accumulation
149 of solutes to maintain a solvation layer around macromolecules. Plants have thus developed
150 similar molecular responses to drought and frost constraints (Beck *et al.*, 2007), under the
151 control of abscisic acid (ABA; Chandler & Robertson, 1994), inducing, for instance, the
152 synthesis of dehydrins (Welling *et al.*, 2002). Interestingly, the molecular response to both

153 constraint involves the same regulatory mechanisms (*e.g.* Dehydration Responsive Elements
154 containing Cold Binding Factors; Stockinger *et al.*, 1997; Baker *et al.*, 1994). The same
155 pathways are thus activated in both cold and drought responses (Yamaguchi-Shinozaki &
156 Shinozaki, 1994).

157 The onset of drought-induced damages is triggered by hydraulic failure and involves the
158 interaction between water and carbon status (Frame 1 and reviews from Choat *et al.*, 2018;
159 Martinez-Vilalta *et al.*, 2019, for extensive description of drought stress syndromes), as frost-
160 induced damages relies on (Charrier *et al.*, 2013b). At the vascular level, species more
161 vulnerable to winter embolism seem to be also more vulnerable to summer embolism (Charrier
162 *et al.*, 2014). This may be related to the ability of air to propagate within xylem under high
163 frost- or drought-related tension through pit membrane (Cochard *et al.*, 1992). However, many
164 tree species are able to restore their hydraulic conductivity, for instance to supply growth in
165 spring. One refilling mechanism involves an osmoregulation via solutes compounds generating
166 osmotic pressure in the lumen of the vessels during winter (Ewers *et al.*, 2001; Améglio *et al.*,
167 2002), and eventually summer (Nardini *et al.*, 2011). In conifers, the involved mechanism
168 remains to be clarified, but many species seem able to do so (Sperry & Sullivan 1992; Sperry
169 *et al.*, 1994; Mayr *et al.*, 2003; 2014). Positive sap pressure has also been measured at the whole
170 plant scale from the pressurization of the root system, notably in woody lianas (Priestley 1920;
171 Sperry *et al.*, 1987; Charrier *et al.*, 2016).

172 Even if xylem conduits were completely refilled, residual bubbles within the xylem would
173 expand at lower tension if the tree is exposed again to drought after winter or at higher freezing
174 temperature occurring late in the winter (*i.e.* after the winter refilling process). Such a higher
175 vulnerability after the initial stress exposure and release would occur through physical or
176 chemical deformation of the pit ultrastructure (*i.e.* fatigue; Christensen-Dalsgaard & Tyree,
177 2014).

178 However, despite high xylem embolism has been suggested to cause trees death (Brodribb
179 & Cochard, 2009), higher embolism than 50% and, even 90%, is frequently observed and
180 recovered in over-wintering trees without impairing their survival suggesting that it does not
181 constitute a lethal threshold by itself (Sperry *et al.*, 1994; Mayr *et al.*, 2003; 2006; 2019;
182 Charrier *et al.*, 2013a). High xylem embolism rather seem to constitute an empirically
183 correlated trait than a clear physiological lethal threshold (Mayr *et al.*, 2019).

184 Although, drought and frost stresses affect many physiological processes in the same way,
185 it is not clear how the response to a repeated exposure could affect vulnerability to a given
186 stress. As a first approximation, one would expect that a stress affecting the carbon balance
187 would make the tree more vulnerable to subsequent stresses, *e.g.* defoliated oaks would decline
188 within two years (Wargo, 1981), or carbon-deprived spruces would die more rapidly from
189 drought (Hartmann *et al.*, 2013). This hypothesis fed into the so-called ‘boxer theory’,
190 suggesting the successive stresses would cause trees to decline (Wargo, 1996; Bréda & Peiffer,
191 2014). Wood growth has been used as an integrative marker following frost and drought stress
192 (Vanoni *et al.*, 2017; d’Andrea *et al.*, 2020). However, due to the difficulty of conducting long-
193 term studies, few studies have been able to accurately characterize the affected
194 ecophysiological processes.

195 Two alternative hypothesis, although not mutually exclusive, should be taken into account
196 to predict the interaction between stress factors. Legacy is considered as a passive change of
197 physiological status in response to previous stress exposure. We suggest that the modulation of
198 either carbon or water pools would result in the modulation of vulnerability (McDowell *et al.*,
199 2008). Altered water and carbon status would generate potential feedback physiological loops
200 and trade-offs during successive abiotic stress exposures (legacy effect). Memory, which is also
201 called priming in plant defense facing biotic and also abiotic stress (Savvides *et al.*, 2016), is
202 considered as an active process shifting biological processes enhancing a basal level of
203 resistance at the cost of reducing primary metabolism such as growth (Bruce *et al.*, 2007; Walter

204 *et al.*, 2013; Martinez-Medina *et al.*, 2016). It requires pre exposure to the stress factor in
205 contrast with acclimation that occurs in anticipation. In long living organisms such as trees, the
206 concept of memory is uncommon because most of the studies dealing with memory have
207 focused on short-term memory in annual plants. Some studies have evaluated how the
208 vulnerability to a given constrain, *i.e.* frost or drought, is affected by a repeated exposure of the
209 trees to it (Mayr *et al.*, 2003; Tomasella *et al.*, 2019). However, studies evaluating the feedback
210 between constraints and vulnerability (*i.e.* the effect of drought on vulnerability to frost and
211 vice versa) are very few (*e.g.* Kreyling, *et al.*, 2014; Sierra-Almeida *et al.*, 2016). We attempted
212 to draw a generic picture as both constraints affect the same physiological processes (Fig. 1).

213 **Effect of drought on vulnerability to frost**

214 This interaction is likely to occur under montane/boreal climate. Such increase in solute
215 concentration (*i.e.* lower osmotic potential) would decrease the freezing point ($-1.86^{\circ}\text{C}\cdot\text{mol}^{-1}\cdot\text{kg}^{-1}$;
216 Hansen & Beck, 1988) in both living cells (Charrier *et al.*, 2013b) and the apoplasm
217 (Lintunen *et al.*, 2018). Soil water deficits can indeed initiate the early stages of frost hardiness
218 in Douglas-fir (Timmis & Tanaka, 1976). This effect is likely to be canceled during the
219 transition from drought- to frost-exposed period, in case of a wet autumn period. However,
220 changes in the water regime, as predicted by future climate predictions, could cause this dry
221 summer and autumn conjunction to occur more regularly.

222 Lower frost vulnerability of trees pre-exposed to drought is thus expected through two
223 potential side-effects (i) lower probability of ice formation under similar sub-zero temperatures
224 and (ii) higher probability of ice nucleation within the apoplasm, pulling symplasmic water
225 towards extracellular ice lattice. However, this effect may be balanced by a decrease in non-
226 structural carbohydrates, due to photosynthesis limitation by stomatal closure, leading to
227 similar, or even lower solute concentration in drought-exposed trees. In fact, both effects have
228 been observed in winter frost damages following summer drought. Increasing frost hardiness is

229 thus expected for relatively moderate dehydration (Fig. 3 as observed in Benzioni *et al.*, 1992;
230 Kreyling *et al.*, 2012; Sierra-Almeida *et al.*, 2016). It should also be noted that growth-related
231 processes being more sensitive to water stress than photosynthesis (Fig. 2A), mild water stress
232 would also promote transient increase in non-structural carbohydrates (McDowell, 2011;
233 Granda & Camarero, 2017). However, would this transient increase result in higher reserves
234 (potentially enhancing frost acclimation) or be allocated to other processes such as belowground
235 growth? Finally, lower frost hardiness would be observed for higher drought stress level in
236 relation to carbon depletion (Fig. 3 right Wong *et al.*, 2009; Galvez *et al.*, 2013; Fig. 3).

237 From the xylem/hydraulic point of view, the resulting vulnerability is frost-induced
238 embolism is only generated when sap is under moderate tension (Mayr *et al.*, 2007). Freeze-
239 thaw cycles will thus exacerbate the pre-existing tension promoting air seeding from vessels to
240 vessels in dehydrated trees (Fig. 2B; Tyree & Sperry, 1989; Mayr *et al.*, 2007; Kasuga *et al.*,
241 2015). Drought episodes during the growing season lead to the reduction in vessel diameter
242 (Lovisololo & Schubert, 1998; Beikircher & Mayr, 2009) that would result in higher resistance
243 to freeze-thaw induced embolism. However, a reduced level of non-structural carbohydrates
244 would limit the ability of the tree to refill embolized vessels during winter via active mechanism
245 (*e.g.* stem pressure; Améglio *et al.*, 2001). The main positive effect (*i.e.* decreasing the
246 vulnerability to frost-induced embolism) therefore would lie in the higher ability of sap to
247 supercool and therefore avoid the phase shift from liquid to ice and the resulting formation of
248 air bubbles (Lintunen *et al.*, 2018).

249 **Effect of frost on vulnerability to drought**

250 This interaction is likely to occur under temperate climate. Major gaps of knowledge remain
251 with respect to frost exposure onto drought vulnerability, although assumptions can be made.
252 Overall, frost damages before drought exposure would mainly have negative effects for the

253 trees, through limited hydraulic conductivity and/or biomass destruction although the affected
254 organs as well as the consequences for the tree can be various. However, in our literature review,
255 we did not find a single study that specifically explored the physiological consequences of frost
256 damages during the following growing season and after, although Charrier *et al.* (2018a)
257 highlighted a significant negative correlation between autumnal frost damages and fruit yield
258 the following summer in walnut.

259 Low, but not necessarily frozen, soil temperature limits root water uptake (Améglio *et al.*,
260 2002). Thanks to thermal inertia, the combination of cold soil and warm and dry air can promote
261 the aboveground dehydration and hydraulic failure. This phenomenon, called winter drought,
262 is typical of late winter conditions at high altitudes (Mayr *et al.*, 2006; Charrier *et al.*, 2017;
263 Earles *et al.*, 2018). Winter drought- and freeze/thaw-induced embolism increase the volume of
264 gas within the xylem conduits, therefore facilitating the spreading of air through conduits (Lens
265 *et al.*, 2011). Furthermore, higher porosity of the pit membrane following freeze-thaw events
266 has been observed for different species when evaluating defrosted wood samples (Li *et al.*,
267 2016). Such changes in the pit membrane thickness is likely to increase drought-vulnerability
268 through air seeding (Charrier *et al.*, 2014; Li *et al.*, 2016). Such an increased vulnerability would
269 only remain if the embolism is not refilled.

270 When the winter precipitation regimes change from solid to liquid, the shorter snow cover
271 duration is likely to expose soil to lower temperature, damaging the root system more
272 frequently (Francon *et al.*, 2020). This would alter the whole tree hydraulic architecture by
273 decreasing water supply and decreasing the ability to recover, ultimately increasing xylem
274 embolism (Cox & Malcom, 1997; Zhu *et al.*, 2000). This syndrome has been identified as pre-
275 disposing dieback for Yellow birch (Cox & Zhu, 2003).

276 Lower hydraulic conductivity, from winter embolism and limited spring refilling would limit

277 plant transpiration, which should result in lower leaf water potential and stomatal conductance.
278 As partially open stomata allow sufficient CO₂ diffusion while limiting the amount of transpired
279 water, it is likely that water use efficiency would be increased. Soil water content would be
280 depleted more slowly which should thus delay drought onset and intensity. The same dynamic
281 is expected after late frost damages, as leaves would expand later in the season. However, at
282 the stand scale, the competition for water resources from other tree individuals or other plant
283 species (less vulnerable to winter embolism or frost damages) may delete this potential benefit.

284 One important aspect to consider regarding frost damages is the temporality, higher damages
285 being observed during the elongation period of new growth units in spring (Chaar & Colin,
286 1999). By destroying the developing organs late frost damage (leaf, flowers and new shoots)
287 would immediately reduce the transpiration (water output) and the photosynthesis (carbon
288 input), but, on a longer term, the remobilization of carbon reserves to reconstruct annual organs
289 may result in a significant carbon depletion (Wargo 1996). Although under non-stressing
290 circumstances carbon reserves are quickly restored, under drought stress we could expect a
291 significant limitation in the ability of the tree to maintain the stomata open and related carbon
292 input in depleted trees (O'Brien *et al.*, 2014). Furthermore, assuming an increase in resistance
293 to drought-induced embolism along the growing season, the newly formed xylem will be more
294 vulnerable whereas drought exposure will be higher (Charrier *et al.*, 2018b).

295 **Potential interaction between vulnerability to constraints and phenology**

296 The annual phenological cycle consists of developmental events related to the alternation of
297 growth and dormancy of the trees. Longer growing seasons, such as predicted by vegetation
298 models due to climate change, are expected to increase the carbon uptake and the ecosystem
299 net primary production (Angert *et al.*, 2005, Delpierre *et al.*, 2009; Wolf *et al.*, 2016). However,
300 this would be at the cost of longer periods of effective transpiration that would, ultimately,
301 deplete soil water content and thus increase the exposure to drought stress. Although timing is

302 a crucial parameter in the exposure to a seasonal abiotic constraint, the models predicting tree
303 seasonality developed so far mostly consider non-stressing conditions (see Lang *et al.*, 1987;
304 Delpierre *et al.*, 2016).

305 Photoperiod and temperature are key signals regulating plant phenology (Maurya &
306 Bhalearao, 2017). In spring, ecodormancy release and growth (both primary and secondary) are
307 accelerated by warm temperature, in some species in interaction with photoperiod (Laube *et al.*,
308 2014). At the end of the growing season, growth cessation, bud set and endodormancy are
309 controlled by photoperiod and temperature through two separate, but temporally connected
310 processes: one photosensitive (short day) and one thermosensitive (low temperature) process
311 (Tanino *et al.*, 2010). Endodormancy is subsequently released by chilling temperature. Among
312 these different stages, we can distinguish two different processes: temperature promoted
313 processes (*i.e.* occurring at a rate proportional to temperature such as ecodormancy release,
314 primary and secondary growth, and budset) and signal-limited processes (*i.e.* occurring after a
315 specific threshold has been reached such as growth cessation, endodormancy induction, leaf
316 fall), which are indirectly affected by photoperiod and temperature. However, the effect of
317 abiotic stress on the different phenological processes and, furthermore, how carry-over effects
318 can modulate pluri-annual dynamics, have not been explored yet (Fu *et al.*, 2014). Thus,
319 depending on the timing of the previous stage, the onset of the following ones will be affected,
320 leading to unpredictable behavior (Hänninen & Tanino, 2011). For instance, an increase in
321 temperature would hasten or delay growth cessation depending on the diurnal dynamics of
322 temperature (see Rohde *et al.*, 2011 and Kalcsits *et al.*, 2009, respectively), affecting the
323 subsequent stages (budset, endodormancy and budburst; Fig. 4). Leaf senescence timing is
324 positively correlated with budburst timing once removing the influence of autumn temperature
325 (Fu *et al.*, 2014). This carry-over effect is, however, of second order (Liu *et al.*, 2019) and
326 potentially hidden by the prominent role of environmental variables such as temperature and
327 photoperiod (Vitasse *et al.*, 2009). Such an interacting process has been incorporated in a leaf

328 senescence model (Delpierre *et al.*, 2009) by modulating the cold temperature sum leading to
329 leaf senescence by the budburst date (Keenan & Richardson, 2015).

330 Drought stress affects radial (*i.e.* secondary) growth but its effects on primary growth is
331 relatively unexplored. Drought exposure can significantly hasten the primary growth onset in
332 *Erica multiflora*, although not in *Globularia alipum* (Bernal *et al.*, 2011). However, also no
333 effect on growth cessation has been reported (Bernal *et al.*, 2011). One would expect that earlier
334 growth onset would favor drought avoidance during springtime, but it could hasten soil water
335 depletion and this may be at the cost of the alteration of the development of shoot, leaves and
336 buds (Misson *et al.*, 2011). Autumnal drought is expected to induce earlier endodormancy,
337 probably through the induction of ABA (Maurya & Bhalerao, 2017; Tylewicz *et al.*, 2018).
338 Furthermore, higher temperatures associated to drought events would induce deeper dormancy
339 (Heide, 2003; Tanino *et al.*, 2010; Rohde *et al.*, 2011). As this would result in later budburst
340 the following year, these trees are likely to be more drought-exposed since they would expand
341 their leaves during a period of more pronounced water deficit. Delayed dormancy and budburst
342 are thus expected through synergistic combination between drought exposure and carry-over
343 effect (Xie *et al.*, 2015).

344 The impact of frost events on phenology has essentially been reported in spring when it
345 affects developing organs such as flushing buds, flowers and new leaves. After a single
346 damaging event, the resulting leaf area (*i.e.* post growth) can be reduced (up to more than 50%)
347 and leaf full expansion delayed (16 to 34 days; Augspurger, 2013), exposing the tree to summer
348 constraints, although leaf area and carbon reserves are reduced (Menzel *et al.*, 2015; d'Andrea
349 *et al.*, 2019; 2020). During late summer, after growth cessation and dormancy induction, frost
350 exposure may promote the dormancy release and, as cold temperature, induces leaf fall (Rinne
351 *et al.*, 1997). So depending on the timing, frost damages could delay or hasten the annual cycle
352 (later leaf full expansion or earlier endodormancy release, after spring and autumn frost
353 damages, respectively). However, frost events may induce both cellular and vascular damages

354 in the distal organs, resulting in re-growth from more basal buds. After several years, the whole
355 tree architecture may be affected resulting in smaller and denser canopy, which would be less
356 frost exposed, but at the cost of canopy light transmittance and subsequent photosynthesis.

357 **A holistic modelling framework for tree stress physiology: a tentative outline**

358 A living tree is a functionally holistic system including constantly interacting growth units.
359 Accordingly, the various physiological processes are linked to each other. Two different
360 physiological variables such as water potential and frost hardiness, represent, at least partially,
361 different manifestations of the same physiological phenomena (as described by the correlations
362 between frost hardiness, water content and water potential).

363 Ecophysiological models have been developed separately for frost stress (Fuchigami *et al.*,
364 1982; Leinonen 1996; Charrier *et al.*, 2018a) and drought stress (Sperry *et al.*, 1998; Zweifel *et*
365 *al.*, 2005; Martin-StPaul *et al.*, 2017). By addressing the seasonal alternation of growth and
366 dormancy, the annual phenological cycle also reflects major changes in the physiology of trees
367 that could enhance or mitigate the vulnerability to stress factors. Accordingly, the integrated
368 models of frost hardiness simulates the environmental responses of changes in frost hardiness
369 according to the phenological stage (Kellomäki *et al.*, 1992; 1995; Leinonen 1996; Charrier *et*
370 *al.*, 2018a). Seasonality is indeed located at the core of any modelling framework related to
371 seasonal frost or drought stress factors. We first propose that existing ecophysiological models
372 explicitly integrate seasonality weighing relevant parameters by the variables describing
373 phenological processes (*e.g.* sum of growth degree days, sum of chilling units,...). Although
374 not being mechanistic, these variables would unify the framework of the models, allowing
375 further research into the deterministic relations between three highlighted processes
376 (phenological, carbon and hydraulics). Such an integrated modeling approach should be used
377 to the interaction between stresses factors through the following steps:

- 378 (i) Quantitative description of the variable(s) of interest *e.g.* loss of hydraulic conductivity,
379 cellular lysis.
- 380 (ii) Identification of the relevant physiological drivers with special attention dedicated to the
381 ones that interact with several variables of interest *e.g.* water or carbohydrate content.
- 382 (iii) Description of the relation between the drivers and the variable of interest *e.g.* relation
383 between frost hardiness, tissue water content, carbohydrate and temperature (Poirier *et*
384 *al.*, 2010).
- 385 (iv) Experimentally-based description of the relation between physiological drivers and
386 external climatic drivers to ensure realistic behavior.
- 387 (v) Mathematical description of the relationship between physiological driver and external
388 climatic drivers *e.g.* carbohydrate content depending on air temperature (Charrier *et al.*,
389 2018c).
- 390 (vi) Coupling the models obtained at Steps (ii) and (iv) and development of a model predicting
391 the variable of interest with input data being climatic, state variables (such as specific
392 parameters or initial values) and intermediate physiological drivers.
- 393 (vii) Simulate the tree response and compare with stress-related variable such as frost
394 hardiness *vs* daily minimum temperature (Charrier *et al.*, 2018a).

395 Finally, such approach would easily simulate both legacy and memory effects (as a function of
396 previous level of damages, water and carbon contents).

397 **Conclusion and perspectives**

398 Exposures to drought and frost constraints exert potential feedbacks on the sensitivity to
399 future constraints by affecting physiological components such as non-structural carbohydrates

400 and water balance (*i.e.* legacy Fig. 2). Phenological processes has been for long only studied in
401 non-stressed plants, although physiological seasonality is altered by stress (Fig. 4). Major
402 advances are needed in characterizing environmental control of phenological processes in trees
403 during or after stress. Notably do critical sums of temperature (*e.g.* chilling or forcing
404 temperature) vary with stress intensity, potentially explaining the residual variance in
405 phenological predictions?

406 Phenological processes are likely to exhibit legacy through carbon balance *e.g.* trophic
407 limitation of meristem growth (Bonhomme *et al.*, 2009), disturbed glycan deposition onto
408 plasmodesmata (Rinne *et al.*, 2001). However, previous exposure to stress factors may also
409 alter the rate of the future ecophysiological response through memory effect via accumulation
410 of regulatory proteins, transcription factors or histone methylation (Bruce *et al.*, 2007; Walter
411 *et al.*, 2013). As already performed in annual plants, there is a clear need for multi-constrained
412 and longer term studies in woody plants.

413 To specifically deal with the interaction between constraints, we need to i) develop a systemic
414 approach at the plant scale integrating ontogenic and histological differences as well as carbon
415 and water use coupled with the phenological dynamic; and ii) develop a multi-colinearity
416 approach aimed to evaluate the interactions between different constraints in the tree survival
417 capacity both at short and a long time scale. Interesting insights have been brought by
418 integrative studies, for instance, focusing on carbon availability and hydraulic failure facing
419 drought (*e.g.* McDowell *et al.*, 2008). It is especially relevant to develop this type of approaches
420 on different species exhibiting contrasted combinations of drought and frost tolerance,
421 including provenances originating from the entire species' distribution range (core and edges)
422 to unravel local adaptations (Kreyling *et al.*, 2014). The effect of different successive and
423 concomitant constraints at different periods of the year should help to develop deterministic
424 relationships between different physiological variables and processes in response to each of

425 them. It would simulate the life history of the tree and modulated response through legacy and
426 memory effects as a function of previous level of damages, water and carbon contents.
427 Improving the descriptive range of these interrelations at the individual and population scales
428 would subsequently allow quantitative and dynamic description of drought and frost resistance
429 in interaction. This would improve existing mechanistic models simulating these interacting
430 processes in order to predict accurately the effect of cumulative stress on tree physiology and
431 survival.

432

433 **Frame 1: Mechanisms leading to drought-induced damages**

434 Water stress results from an imbalance between inwards (root water absorption) and outwards
435 water fluxes (transpiration and evaporation). Trees have developed resistance mechanisms to
436 avoid water stress (maintaining high water potential; Fig. 1) by a tight control of both inwards
437 (*e.g.* deep rooting) and outward water fluxes (*e.g.* stomatal closure, leaf shedding, low cuticular
438 transpiration; Choat *et al.*, 2018; Martin-StPaul *et al.*, 2017). Maintaining xylem hydraulic
439 function under high tension is also a critical trait avoiding dehydration, and ultimately
440 desiccation, of living tissues (Fig. 1 #14; Sperry *et al.*, 1998, Brodribb & Cochard, 2009).
441 However, ontogenic changes in xylem vulnerability to embolism may modulate thus the tree's
442 resistance across seasons (Charrier *et al.*, 2018b).

443 In some species, leaves are more drought-sensitive than perennial organs (*i.e.* hydraulic
444 vulnerability segmentation) and usually fall after the exposure to drought (Fig. 1 #6 Tyree *et*
445 *al.*, 1993). Such a deciduous behavior can be too sudden to allow recycling nutrients (Fig. 1 #5
446 Bréda *et al.*, 2006) but not in all cases (Marchin *et al.*, 2010). Following leaf fall, the
447 reestablishment of a new cohort of leaves would mobilize non-structural carbohydrate reserves,
448 which may not be restored before winter. Long-term drought induces stomatal closure to
449 maintain the functionality of the hydraulic system. As respiration is maintained and even
450 increased during warm spells, while carbon assimilation is reduced, carbon reserves steadily
451 depletes (Fig. 2; McDowell *et al.*, 2008). Finally, two pools, namely solutes, including
452 carbohydrates, and water, interact to maintain a solvation layer around biomolecules avoiding
453 critical denaturation and related cellular death (Martinez Vilalta *et al.*, 2019).

455 **Frame 2: Mechanisms leading to frost-induced damages**

456 Low temperature drives tree species distribution through different processes: including
457 resistance to freezing temperature and to frost-induced embolism (Charrier *et al.*, 2013a), and
458 the time to complete the annual cycle and seedling survival (Koerner *et al.*, 2016). In fully
459 hydrated organs, ice formation can induce mechanical strains and frost cracks (Kubler, 1983;
460 Cinotti, 1991). In moderately dehydrated organs, ice nucleation and propagation redistributes
461 water towards nucleation sites (Ball *et al.*, 2006; Mayr & Charra-Vaskou, 2007) and likely
462 provoke air-seeding within pits (Charrier *et al.*, 2014). However, frost-induced embolism in the
463 distal parts would insulate the trunk from further dehydration (Fig. 1 #15; Lemoine *et al.*, 1999;
464 Charrier *et al.*, 2017). Critical thresholds can be reached when the root water absorption could
465 not compensate the evaporative demand during periods of sunny days alternating with freezing
466 nights (*i.e.* winter drought; Tranquillini, 1979; Charrier *et al.*, 2017). At the cellular level, the
467 low chemical potential of ice pulls water molecules from the cells towards extracellular ice
468 lattice, causing pronounced cell dehydration and shrinkage (Dowgert and Steponkus, 1984;
469 Charra-Vaskou *et al.*, 2016). To cope with seasonal frost stress, trees transiently increase their
470 frost resistance in frost-exposed organs through the synthesis of cryoprotective solutes (Charrier
471 *et al.*, 2013b). Cryoprotective solutes (*e.g.* carbohydrates, amino-acids or organic acids) can
472 protect macromolecules by maintaining a solvation layer around it. Being the main substrate
473 and energetic source, non-structural carbohydrates content in autumn is thus tightly related to
474 maximum frost resistance reached during winter (Fig. 1 # 1; Palonen & Buszard, 1997; Morin
475 *et al.*, 2007; Charrier *et al.*, 2013a; 2018c). As non-structural carbohydrates content usually
476 increases with elevation through temperature limited-growth rather than by carbon availability
477 (Hoch *et al.*, 2002; Shi *et al.*, 2008; Koerner, 2015), the increase in NSC at higher elevation
478 would help plants to reach sufficient level of frost resistance in winter.

479 **References**

- 480 Allen, C. D., Macalady, A. K., Chenchouni, H. *et al.*, (2010). A global overview of drought and
481 heat-induced tree mortality reveals emerging climate change risks for forests. *Forest*
482 *Ecology and Management*, 259: 660-684.
- 483 Améglio, T., Ewers, F. W., Cochard, H., Martignac, M., Vandame, M., Bodet, C., & Cruiziat,
484 P. (2001). Winter stem xylem pressure in walnut trees: effects of carbohydrates, cooling
485 and freezing. *Tree Physiology*, 21: 387-394.
- 486 Améglio, T., Bodet, C., Lacoite, A., & Cochard, H. (2002). Winter embolism, mechanisms of
487 xylem hydraulic conductivity recovery and springtime growth patterns in walnut and peach
488 trees. *Tree Physiology*, 22: 1211-1220.
- 489 Améglio, T., Decourteix, M., Alves, G. *et al.*, (2004). Temperature effects on xylem sap
490 osmolarity in walnut trees: evidence for a vitalistic model of winter embolism repair. *Tree*
491 *Physiology*, 24: 785-793.
- 492 Anderegg, W. R., Plavcová, L., Anderegg, L. D., Hacke, U. G., Berry, J. A., & Field, C. B.
493 (2013). Drought's legacy: multiyear hydraulic deterioration underlies widespread aspen
494 forest die-off and portends increased future risk. *Global change biology*, 19(4), 1188-1196.
- 495 Anderegg, W. R., Flint, A., Huang, C. Y. *et al.*, (2015). Tree mortality predicted from drought-
496 induced vascular damage. *Nature Geoscience*, 8: 367-371.
- 497 Angert, A., Biraud, S., Bonfils, C. *et al.*, (2005). Drier summers cancel out the CO₂ uptake
498 enhancement induced by warmer springs. *Proceedings of the National Academy of*
499 *Sciences of the United States of America*, 102: 10823-10827.
- 500 Augspurger, C. K. (2013). Reconstructing patterns of temperature, phenology, and frost damage
501 over 124 years: spring damage risk is increasing. *Ecology*, 94: 41-50.
- 502 Baker S. S., Wilhelm K. S., & Thomashow M.F. (1994). The 50- region of *Arabidopsis thaliana*
503 *cor15a* has cis-acting elements that confer cold, drought, and ABA-regulated gene
504 expression. *Plant Molecular Biology* 24: 701-713.
- 505 Ball, M. C., Canny, M. J., Huang, C. X., Egerton, J. J. G., & Wolfe, J. (2006). Freeze/thaw-
506 induced embolism depends on nadir temperature: the heterogeneous hydration hypothesis.
507 *Plant, Cell & Environment*, 29: 729-745.
- 508 Bartholomeus, R. P., Witte, J. P. M., van Bodegom, P. M., van Dam, J. C., & Aerts, R. (2011).
509 Climate change threatens endangered plant species by stronger and interacting water-
510 related stresses. *Journal of Geophysical Research: Biogeosciences*, 116(G4).
- 511 Batllori, E., De Cáceres, M., Brotons, L., Ackerly, D. D., Moritz, M. A., & Lloret, F. (2017).
512 Cumulative effects of fire and drought in Mediterranean ecosystems. *Ecosphere*, 8: e01906.
- 513 Beck, E. H., Fettig, S., Knake, C., Hartig, K., & Bhattarai, T. (2007). Specific and unspecific
514 responses of plants to cold and drought stress. *Journal of Biosciences*, 32: 501-510.
- 515 Beikircher B, & Mayr S (2009). Intraspecific differences in drought tolerance and acclimation
516 in hydraulics of *Ligustrum vulgare* and *Viburnum lantana*. *Tree Physiol* 29:765-775
- 517 Benzioni, A., Palzkill, D. A., & Nelson, J. M. (1992). Flower bud dormancy, ABA
518 concentration, and survival during frost of jojoba genotypes under water stress. *Journal of*
519 *the American Society for Horticultural Science*, 117: 976-980.
- 520 Bernal, M., Estiarte, M., & Peñuelas, J. (2011). Drought advances spring growth phenology of
521 the Mediterranean shrub *Erica multiflora*. *Plant Biology*, 13: 252-257.
- 522 Bréda, N., Huc, R., Granier, A., & Dreyer, E. (2006). Temperate forest trees and stands under
523 severe drought: a review of ecophysiological responses, adaptation processes and longterm
524 consequences. *Annals of Forest Science*, 63: 625-644.
- 525 Bréda, N., & Peiffer, M. (2014). Vulnerability to forest decline in a context of climate changes:
526 new prospects about an old question in forest ecology. *Annals of Forest Science*, 71: 627-
527 631.
- 528 Brodribb, T. J., & Cochard, H. (2009). Hydraulic failure defines the recovery and point of death

529 in water-stressed conifers. *Plant physiology*, 149: 575-584.

530 Bruce, T. J., Matthes, M. C., Napier, J. A., & Pickett, J. A. (2007). Stressful “memories” of
531 plants: evidence and possible mechanisms. *Plant Science*, 173: 603-608.

532 Carnicer, J., Brotons, L., Stefanescu, C., & Penuelas, J. (2012). Biogeography of species
533 richness gradients: linking adaptive traits, demography and diversification. *Biological*
534 *Reviews*, 87: 457-479.

535 Char, H., & Colin, F. (1999). Impact of late frost on height growth in young sessile oak
536 regenerations. *Annals of forest science*, 56: 417-429.

537 Chandler, P. M., & Robertson, M. (1994). Gene expression regulated by abscisic acid and its
538 relation to stress tolerance. *Annual Review of Plant Biology*, 45: 113-141.

539 Chapin III, F. S., Autumn, K., & Pugnaire, F. (1993). Evolution of suites of traits in response
540 to environmental stress. *American Naturalist*, S78-S92.

541 Charra-Vaskou, K., Badel, E., Charrier, G. *et al.*, (2016). Cavitation and water fluxes driven by
542 ice water potential in *Juglans regia* during freeze–thaw cycles. *Journal of Experimental*
543 *Botany*, 67: 739-750.

544 Charrier, G., Bonhomme, M., Lacoïnte, A., & Améglio, T. (2011). Are budburst dates,
545 dormancy and cold acclimation in walnut trees (*Juglans regia* L.) under mainly genotypic
546 or environmental control?. *International Journal of Biometeorology*, 55: 763-774.

547 Charrier, G., Cochard, H., & Améglio, T. (2013a). Evaluation of the impact of frost resistances
548 on potential altitudinal limit of trees. *Tree Physiology*, 33: 891–902.

549 Charrier G., Poirier M., Bonhomme M., Lacoïnte A., Améglio T. (2013b). Frost acclimation in
550 different organs of walnut trees *Juglans regia* L.: How to link physiology and modelling?
551 *Tree Physiology* 33: 1229-1241.

552 Charrier, G., Charra-Vaskou, K., Kasuga, J., Cochard, H., Mayr, S., & Améglio, T. (2014).
553 Freeze-thaw stress: effects of temperature on hydraulic conductivity and ultrasonic activity
554 in ten woody angiosperms. *Plant Physiology*, 164: 992–998.

555 Charrier, G., Ngao, J., Saudreau M., & Améglio, T. (2015) Effects of environmental factors and
556 management practices on microclimate, winter physiology, and frost resistance in trees.
557 *Frontiers in Plant Science*. 6: 259.

558 Charrier, G., Torres-Ruiz, J. M., Badel, E. *et al.*, (2016). Evidence for hydraulic vulnerability
559 segmentation and lack of xylem refilling under tension. *Plant Physiology*, 172: 16571668.

560 Charrier, G., Nolf, M., Leitinger, G. *et al.*, (2017). Monitoring of freezing dynamics in trees: a
561 simple phase shift causes complexity. *Plant Physiology*, 173: 2196-2207.

562 Charrier, G., Chuine, I., Bonhomme, M., & Améglio, T. (2018a). Assessing frost damages using
563 dynamic models in walnut trees: exposure rather than vulnerability controls frost risks.
564 *Plant, Cell & Environment*, 41: 1008-1021.

565 Charrier, G., Delzon, S., Domec, J. C. *et al.*, (2018b). Drought will not leave your glass empty:
566 Low risk of hydraulic failure revealed by long-term drought observations in world’s top
567 wine regions. *Science Advances*, 4: eaao6969.

568 Charrier, G., Lacoïnte, A., & Améglio, T. (2018c). Dynamic modeling of carbon metabolism
569 during the dormant period accurately predicts the changes in frost hardiness in walnut trees
570 *Juglans regia* L.. *Frontiers in Plant Science*, 9: 1746.

571 Chaves, M. M., Pereira, J. S., Maroco, J., Rodrigues, M. L., Ricardo, C. P. P., Osório, M. L.,
572 ... & Pinheiro, C. (2002). How plants cope with water stress in the field? Photosynthesis
573 and growth. *Annals of botany*, 89: 907-916.

574 Cheaib, A., Badeau, V., Boe, J. *et al.*, (2012). Climate change impacts on tree ranges: model
575 intercomparison facilitates understanding and quantification of uncertainty. *Ecology*
576 *letters*, 15: 533-544.

577 Choat B, Jansen S, Brodribb TJ *et al.*, (2012). Global convergence in the vulnerability of forests
578 to drought. *Nature*, 491: 752–5

579 Choat, B., Brodribb, T. J., Brodersen, C. R., Duursma, R. A., López, R., & Medlyn, B. E.
580 (2018). Triggers of tree mortality under drought. *Nature*, 558: 531.

581 Christensen-Dalsgaard, K. K., & Tyree, M. T. (2014). Frost fatigue and spring recovery of
582 xylem vessels in three diffuse-porous trees in situ. *Plant, Cell & Environment*, 37:
583 10741085.

584 Chuine, I., Bonhomme, M., Legave, J. M., García de Cortázar-Atauri, I., Charrier, G., Lacoite,
585 A., & Améglio, T. (2016). Can phenological models predict tree phenology accurately in
586 the future? The unrevealed hurdle of endodormancy break. *Global Change Biology*. 22:
587 3444-3460.

588 Chuste, P. A., Maillard, P., Bréda, N., Levillain, J., Thirion, E., Wortemann, R., & Massonnet,
589 C. (2019). Sacrificing growth and maintaining a dynamic carbohydrate storage are key
590 processes for promoting beech survival under prolonged drought conditions. *Trees*, 1-14.

591 Cinotti, B. (1991). Investigation of the intrinsic properties of wood for explaining the
592 occurrence of frost-crack in *Quercus petraea* Liebl. and *Quercus robur* L. *Annales des*
593 *Sciences Forestières*, 48: 453-68.

594 Cochard, H., Cruiziat, P., & Tyree, M. T. (1992). Use of positive pressures to establish
595 vulnerability curves: further support for the air-seeding hypothesis and implications for
596 pressure-volume analysis. *Plant physiology*, 100: 205-209.

597 Cox, R. M., & Malcolm, J. W. (1997). Effects of duration of a simulated winter thaw on dieback
598 and xylem conductivity of *Betula papyrifera*. *Tree Physiology*, 17: 389-396.

599 Cox, R. M., & Zhu, X. B. (2003). Effects of simulated thaw on xylem cavitation, residual
600 embolism, spring dieback and shoot growth in yellow birch. *Tree Physiology*, 23: 615624.

601 D'Andrea, E., Rezaie, N., Battistelli, A. *et al.*, (2019). Winter's bite: Beech trees survive
602 complete defoliation due to spring late-frost damage by mobilizing old C reserves. *New*
603 *Phytologist*. D'Andrea, E., Rezaie, N., Prislán, P., Muhr, J., Collalti, A., Matteucci, G., &
604 Gričar, J. (2020). The cold and the drought: effects of extreme weather events on Stem
605 Carbon dynamic in a Mediterranean beech forest. *Plant Cell & Environment*.

606 Delpierre, N., Soudani, K., Francois, C. *et al.*, (2009). Exceptional carbon uptake in European
607 forests during the warm spring of 2007: a data-model analysis. *Global Change Biology*,
608 15: 1455-1474.

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

612 Dowgert, M. F., & Steponkus, P. L. (1984). Behavior of the plasma membrane of isolated
613 protoplasts during a freeze-thaw cycle. *Plant Physiology*, 75: 1139-1151.

614 Dufrêne, E., Davi, H., François, C., Le Maire, G., Le Dantec, V., & Granier, A. (2005).
615 Modelling carbon and water cycles in a beech forest: Part I: Model description and
616 uncertainty analysis on modelled NEE. *Ecological Modelling*, 185: 407-436.

617 Earles, J. M., Stevens, J. T., Sperling, O., Orozco, J., North, M. P., & Zwieniecki, M. A. (2018).
618 Extreme mid-winter drought weakens tree hydraulic-carbohydrate systems and slows
619 growth. *New Phytologist*, 219: 89-97.

620 Erwin, D. H. (2009). Climate as a driver of evolutionary change. *Current Biology*, 19: R575-
621 R583.

622 Ewers, F. W., Améglio, T., Cochard, H. *et al.*, (2001). Seasonal variation in xylem pressure of
623 walnut trees: root and stem pressures. *Tree Physiology*, 21: 1123-1132.

624 Francon, L., Corona, C., Till-Bottraud, I., Choler, P., Carlson, B. Z., Charrier, G., ... & Lopez-
625 Saez, J. (2020). Assessing the effects of earlier snow melt-out on alpine shrub growth: The
626 sooner the better?. *Ecological Indicators*, 115: 106455.

627 Fu, Y. S., Campioli, M., Vitasse, Y. *et al.*, (2014). Variation in leaf flushing date influences
628 autumnal senescence and next year's flushing date in two temperate tree species.

629 Proceedings of the National Academy of Sciences, 111: 7355-7360.

630 Fuchigami, L. H., Weiser, C. J., Kobayashi, K., Timmis, R., & Gusta, L. V. (1982). A degree
631 growth stage (GS) model and cold acclimation in temperate woody plants. Plant cold
632 hardiness and freezing stress. Mechanisms and crop implications, 2: 93-116.

633 Galvez, D. A., Landhäusser, S. M., & Tyree, M. T. (2013). Low root reserve accumulation
634 during drought may lead to winter mortality in poplar seedlings. New Phytologist, 198:
635 139-148.

636 Ghesquière, M., Barre, P., Durand, J. L., Litrico, I., Sampoux, J. P., Mournet, P., & Volaire, F.
637 (2014). Genetic Response to Climate Scenarios in Dactylis and Festuca of Temperate
638 Versus Mediterranean Origin. In *Quantitative Traits Breeding for Multifunctional*
639 *Grasslands and Turf* (pp. 41-48). Springer, Dordrecht

640 Granda, E., & Camarero, J. J. (2017). Drought reduces growth and stimulates sugar
641 accumulation: new evidence of environmentally driven non-structural carbohydrate use.
642 Tree Physiology, 37: 997-1000.

643 Guisan, A., & Thuiller, W. (2005). Predicting species distribution: offering more than simple
644 habitat models. Ecology Letters, 8: 993-1009.

645 Gusta, L. V., Tyler, N. J., and Chen, T. H. H. (1983). Deep undercooling in woody taxa growing
646 north of the 40°C isotherm. Plant Physiology, 72: 122-128.

647 Hampe, A., & Petit, R. J. (2005). Conserving biodiversity under climate change: the rear edge
648 matters. Ecology Letters, 8: 461-467.

649 Hänninen, H., & Tanino, K. (2011). Tree seasonality in a warming climate. Trends in Plant
650 Science, 16: 412-416.

651 Hänninen, H. (1991). Does climatic warming increase the risk of frost damage in northern
652 trees?. Plant, Cell & Environment, 14: 449-454.

653 Hansen, J., & Beck, E. (1988). Evidence for ideal and non-ideal equilibrium freezing of leaf
654 water in frosthady ivy (*Hedera helix*) and winter barley (*Hordeum vulgare*). Botanica
655 Acta, 101: 76-82.

656 Hartmann, H., & Trumbore, S. (2016). Understanding the roles of nonstructural carbohydrates
657 in forest trees—from what we can measure to what we want to know. New Phytologist, 211:
658 386-403. Hartmann, H., Ziegler, W., Kollé, O., & Trumbore, S. (2013). Thirst beats
659 hunger—declining hydration during drought prevents carbon starvation in Norway spruce
660 saplings. *New Phytologist*, 200(2), 340-349.

661 Heide, O. M. (2003). High autumn temperature delays spring bud burst in boreal trees,
662 counterbalancing the effect of climatic warming. Tree Physiology, 23: 931-936.

663 Hoch, G., Popp, M., & Körner, C. (2002). Altitudinal increase of mobile carbon pools in *Pinus*
664 *cembra* suggests sink limitation of growth at the Swiss treeline. Oikos, 98: 361374.

665 Hossain, M., Veneklaas, E. J., Hardy, G. E. S. J., & Poot, P. (2019). Tree host–pathogen
666 interactions as influenced by drought timing: linking physiological performance,
667 biochemical defence and disease severity. *Tree Physiology*, 39(1), 6-18.

668 Intergovernmental Panel on Climate Change. (2012). Managing the Risks of Extreme Events
669 and Disasters to Advance Climate Change Adaptation. A Special Report of Working
670 Groups I and II of the Intergovernmental Panel on Climate Change [Field, C.B., V. Barros,
671 T.F. Stocker, D. Qin, D.J. Dokken, K.L. Ebi, M.D. Mastrandrea, K.J. Mach, G.K. Plattner,
672 S.K. Allen, M. Tignor, and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge,
673 UK, and New York, NY, USA, 582 pp.

674 Intergovernmental Panel on Climate Change. (2014). Climate Change 2014—Impacts,
675 Adaptation and Vulnerability: Regional Aspects. Cambridge University Press.

676 Kalcsits, L. A., Silim, S., & Tanino, K. (2009). Warm temperature accelerates short
677 photoperiod-induced growth cessation and dormancy induction in hybrid poplar (*Populus*×
678 spp.). Trees, 23: 971-979.

679 Kasuga, J., Charrier, G., Uemura, M., & Améglio, T. (2015). Characteristics of ultrasonic
680 acoustic emissions from walnut branches during freeze–thaw-induced embolism
681 formation. *Journal of Experimental Botany*, 66: 1965-1975.

682 Keenan, T. F., & Richardson, A. D. (2015). The timing of autumn senescence is affected by the
683 timing of spring phenology: implications for predictive models. *Global Change Biology*,
684 21: 2634-2641.

685 Kellomäki, S., Väisänen, H., Hänninen, H., Kolström, T., Lauhanen, R., Mattila, U., & Pajari,
686 B. (1992). A simulation model for the succession of the boreal forest ecosystem.

687 Kellomäki, S., Hanninen, H., & Kolstrom, M. (1995). Computations on frost damage to Scots
688 pine under climatic warming in boreal conditions. *Ecological Applications*, 5: 42-52.

689 Klanderud, K., Vandvik, V., & Goldberg, D. (2015). The importance of biotic vs. abiotic drivers
690 of local plant community composition along regional bioclimatic gradients. *PloS one*, 10:
691 e0130205.

692 Knapp, A. K., Fay, P. A., Blair, J. M. *et al.*, (2002). Rainfall variability, carbon cycling, and
693 plant species diversity in a mesic grassland. *Science*, 298: 2202-2205.

694 Koerner, C. (2015). Paradigm shift in plant growth control. *Current Opinion in Plant Biology*,
695 25, 107-114.

696 Koerner, C., Basler, D., Hoch, G. *et al.*, (2016). Where, why and how? Explaining the low-
697 temperature range limits of temperate tree species. *Journal of Ecology*, 104: 10761088.

698 Koerner, C. (1998). A re-assessment of high elevation treeline positions and their explanation.
699 *Oecologia* 115: 445–459.

700 Kreyling, J., Buhk, C., Backhaus, S. *et al.*, (2014). Local adaptations to frost in marginal and
701 central populations of the dominant forest tree *Fagus sylvatica* L. as affected by
702 temperature and extreme drought in common garden experiments. *Ecology and Evolution*,
703 4: 594-605.

704 Kreyling, J., Wiesenberg, G. L., Thiel, D. *et al.*, (2012). Cold hardiness of *Pinus nigra* Arnold
705 as influenced by geographic origin, warming, and extreme summer drought. *Environmental*
706 *and Experimental Botany*, 78: 99-108.

707 Kubler, H. (1983). Mechanism of frost crack formation in trees—a review and synthesis. *Forest*
708 *Science*, 29: 559-568. Lang, G.A., Early, J.D., Martin, G.C., Darnell, R.L. (1987). Endo-,
709 para- and ecodormancy: physiological terminology and classification for dormancy
710 research. *Hortscience* 22: 371–377

711 Larcher, W. (2005). Climatic constraints drive the evolution of low temperature resistance in
712 woody plants. *Journal of Agricultural Meteorology*, 61: 189–202.

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

716 Leinonen, I. (1996). A simulation model for the annual frost hardiness and freeze damage of
717 Scots pine. *Annals of Botany*, 78: 687-693.

718 Leinonen, I., & Hänninen, H. (2002). Adaptation of the timing of bud burst of Norway spruce
719 to temperate and boreal climates. *Silva Fennica*, 36: 695–701.

720 Lemoine, D., Granier, A., & Cochard, H. (1999). Mechanism of freeze-induced embolism in
721 *Fagus sylvatica* L. *Trees*, 13: 206-210.

722 Lenoir, J., Gégout, J. C., Marquet, P. A., De Ruffray, P., & Brisse, H. (2008). A significant
723 upward shift in plant species optimum elevation during the 20th century. *Science*, 320:
724 1768-1771.

725 Lens, F., Sperry, J. S., Christman, M. A., Choat, B., Rabaey, D., & Jansen, S. (2011). Testing
726 hypotheses that link wood anatomy to cavitation resistance and hydraulic conductivity in
727 the genus *Acer*. *New Phytologist*, 190: 709-723.

728 Levitt, J. (1980). *Responses of Plants to Environmental Stress, Volume 1: Chilling, Freezing,*

729 and High Temperature Stresses. Academic Press.

730 Li, S., Lens, F., Espino, S. *et al.*, (2016). Intervessel pit membrane thickness as a key
731 determinant of embolism resistance in angiosperm xylem. *IAWA Journal*, 37: 152-171.

732 Lines, E.R., Coomes, D.A., Purves, D.W. (2010) Influences of forest structure, climate and
733 species composition on tree mortality across the eastern US. (ed Hector A). *PloS One*, 5,
734 e13212

735 Lintunen, A., Mayr, S., Salmon, Y., Cochard, H., & Hölttä, T. (2018). Drivers of apoplastic
736 freezing in gymnosperm and angiosperm branches. *Ecology and evolution*, 8: 333-343.

737 Liu, G., Chen, X., Fu, Y., & Delpierre, N. (2019). Modelling leaf coloration dates over
738 temperate China by considering effects of leafy season climate. *Ecological modelling*, 394:
739 34-43.

740 Loehle, C. (1998). Height growth rate tradeoffs determine northern and southern range limits
741 for trees. *Journal of Biogeography*, 25: 735-742.

742 Lovisolo C, Schubert A (1998) Effects of water stress on vessel size and xylem hydraulic
743 conductivity in *Vitis vinifera* L. *Journal of Experimental Botany* 49: 693–700

744 Marchin, R., Zeng, H., & Hoffmann, W. (2010). Drought-deciduous behavior reduces nutrient
745 losses from temperate deciduous trees under severe drought. *Oecologia*, 163: 845-854.

746 Martinez-Medina, A., Flors, V., Heil, M., Mauch-Mani, B., Pieterse, C. M., Pozo, M. J., ... &
747 Conrath, U. (2016). Recognizing plant defense priming. *Trends in Plant Science*, 21: 818-
748 822.

749 Martinez-Vilalta, J., Anderegg, W. R., Sapes, G., & Sala, A. (2019). Greater focus on water
750 pools may improve our ability to understand and anticipate drought-induced mortality in
751 plants. *New Phytologist*, 223: 22-32.

752 Martin_ StPaul, N., Delzon, S., & Cochard, H. (2017). Plant resistance to drought depends on
753 timely stomatal closure. *Ecology Letters*, 20: 1437-1447.

754 Maurya, J.P., & Bhalerao, R.P. (2017). Photoperiod-and temperature-mediated control of
755 growth cessation and dormancy in trees: a molecular perspective. *Annals of Botany*, 120:
756 351-360.

757 Mayr, S., & Charra_ Vaskou, K. (2007). Winter at the alpine timberline causes complex within
758 _ tree patterns of water potential and embolism in *Picea abies*. *Physiologia plantarum*, 131:
759 131-139.

760 Mayr, S., Gruber, A., & Bauer, H. (2003). Repeated freeze–thaw cycles induce embolism in
761 drought stressed conifers (Norway spruce, stone pine). *Planta*, 217: 436-441.

762 Mayr, S., Hacke, U., Schmid, P., Schwienbacher, F., & Gruber, A. (2006). Frost drought in
763 conifers at the alpine timberline: xylem dysfunction and adaptations. *Ecology*, 87:
764 31753185.

765 Mayr, S., Cochard, H., Améglio, T., & Kikuta, S. B. (2007). Embolism formation during
766 freezing in the wood of *Picea abies*. *Plant Physiology*, 143: 60-67.

767 Mayr, S., Schmid, P., Laur, J., Rosner, S., Charra-Vaskou, K., Dämon, B., & Hacke, U. G.
768 (2014). Uptake of water via branches helps timberline conifers refill embolized xylem in
769 late winter. *Plant Physiology*, 164: 1731-1740.

770 Mayr, S., Schmid, P., Beikircher, B., Feng, F., & Badel, E. (2019). Die hard: timberline conifers
771 survive annual winter embolism. *New Phytologist*

772 McDowell, N., Pockman, W. T., Allen, C. D. *et al.*, (2008). Mechanisms of plant survival and
773 mortality during drought: why do some plants survive while others succumb to drought?.
774 *New Phytologist*, 178: 719-739.

775 McDowell, N. G. (2011). Mechanisms linking drought, hydraulics, carbon metabolism, and
776 vegetation mortality. *Plant Physiology*, 155: 1051-1059.

777 Menzel, A., Helm, R., & Zang, C. (2015). Patterns of late spring frost leaf damage and recovery
778 in a European beech (*Fagus sylvatica* L.) stand in south-eastern Germany based on repeated

779 digital photographs. *Frontiers in Plant Science* 6.

780 Menzel, A., Sparks, T. H., Estrella, N. *et al.*, (2006). European phenological response to climate
781 change matches the warming pattern. *Global Change Biology*, 12: 1969-1976. Miao, S.,
782 Zou, C. B., & Breshears, D. D. (2009). Vegetation responses to extreme hydrological
783 events: sequence matters. *The American Naturalist*, 173: 113-118.

784 Misson, L., Degueldre, D., Collin, C., Rodriguez, R., Rocheteau, A., Ourcival, J. M., &
785 Rambal, S. (2011). Phenological responses to extreme droughts in a Mediterranean forest.
786 *Global Change Biology*, 17: 1036-1048.

787 Morin, X., Améglio, T., Ahas, R. *et al.*, (2007). Variation in cold hardiness and carbohydrate
788 concentration from dormancy induction to bud burst among provenances of three European
789 oak species. *Tree Physiology*, 27: 817-825.

790 Morin, X., & Chuine, I. (2005). Sensitivity analysis of the tree distribution model PHENOFIT
791 to climatic input characteristics: implications for climate impact assessment. *Global*
792 *Change Biology*, 11: 1493-1503.

793 Nardini, A., Gullo, M. A. L., & Salleo, S. (2011). Refilling embolized xylem conduits: is it a
794 matter of phloem unloading?. *Plant Science*, 180: 604-611.

795 O'Brien, M. J., Leuzinger, S., Philipson, C. D., Tay, J., & Hector, A. (2014). Drought survival
796 of tropical tree seedlings enhanced by non-structural carbohydrate levels. *Nature Climate*
797 *Change*, 4: 710-714.

798 Palonen, P., & Buszard, D. (1997). Current state of cold hardiness research on fruit crops.
799 *Canadian Journal of Plant Science*, 77: 399-420.

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

802 Poirier, M., Lacoïnte, A., & Améglio, T. (2010). A semi-physiological model of cold hardening
803 and dehardening in walnut stem. *Tree Physiology*, 30: 1555-1569.

804 Porporato, A., Daly, E., & Rodriguez-Iturbe, I. (2004). Soil water balance and ecosystem
805 response to climate change. *The American Naturalist*, 164: 625-632.

806 Priestley, J. H. (1920). The mechanism of root pressure. *New Phytologist*, 19: 189-200.

807 Rinne, P., Hänninen, H., Kaikuranta, P., Jalonen, J. E., & Repo, T. (1997). Freezing exposure
808 releases bud dormancy in *Betula pubescens* and *B. pendula*. *Plant, Cell & Environment*,
809 20: 1199-1204.

810 Rinne, P. L., Kaikuranta, P. M., & Van Der Schoot, C. (2001). The shoot apical meristem
811 restores its symplasmic organization during chilling-induced release from dormancy. *The*
812 *Plant Journal*, 26: 249-264.

813 Rohde, A., Bastien, C., & Boerjan, W. (2011). Temperature signals contribute to the timing of
814 photoperiodic growth cessation and bud set in poplar. *Tree Physiology*, 31: 472-482.

815 Ruiz-Benito, P., Lines, E.R., Gómez-Aparicio, L., Zavala, M.A., Coomes, D.A. (2013). Patterns
816 and drivers of tree mortality in Iberian forests: climatic effects are modified by competition.
817 *PloS One*.

818 Rummukainen, M. (2012). Changes in climate and weather extremes in the 21st century. *Wiley*
819 *Interdisciplinary Reviews: Climate Change*, 3: 115-129.

820 Sala, A., Woodruff, D. R., & Meinzer, F. C. (2012). Carbon dynamics in trees: feast or famine?.
821 *Tree Physiology*, 32: 764-775.

822 Savvides, A., Ali, S., Tester, M., & Fotopoulos, V. (2016). Chemical priming of plants against
823 multiple abiotic stresses: mission possible?. *Trends in plant science*, 21: 329-340.

824 Schaber, J., & Badeck, F. W. (2005). Plant phenology in Germany over the 20th century.
825 *Regional Environmental Change*, 5: 37-46.

826 Schuster, C., Kirchner, M., Jakobi, G., & Menzel, A. (2014). Frequency of inversions affects
827 senescence phenology of *Acer pseudoplatanus* and *Fagus sylvatica*. *International Journal*
828 *of Biometeorology*, 58: 485-498.

829 Seneviratne, S. I., Nicholls, N., Easterling, D. *et al.*, (2012). Changes in climate extremes and
830 their impacts on the natural physical environment. Managing the risks of extreme events
831 and disasters to advance climate change adaptation, 109-230.

832 Shi, P., Koerner, C., & Hoch, G. (2008). A test of the growth limitation theory for alpine tree
833 line formation in evergreen and deciduous taxa of the eastern Himalayas. *Functional*
834 *Ecology*, 22: 213-220.

835 Sierra-Almeida, A., Reyes-Bahamonde, C., & Cavieres, L. A. (2016). Drought increases the
836 freezing resistance of high-elevation plants of the Central Chilean Andes. *Oecologia*, 113.

837 Siminovitch, D., & Cloutier, Y. (1983). Drought and freezing tolerance and adaptation in plants:
838 some evidence of near equivalences. *Cryobiology*, 20: 487-503.

839 Sperry, J. S., & Sullivan, J. E. (1992). Xylem embolism in response to freeze-thaw cycles and
840 water stress in ring-porous, diffuse-porous, and conifer species. *Plant Physiology*, 100:
841 605-613.

842 Sperry, J. S., Holbrook, N.M., Zimmermann, M. H., & Tyree, M. T. (1987). Spring filling of
843 xylem vessels in wild grapevine. *Plant Physiology*, 83: 414-417.

844 Sperry, J. S., Nichols, K. L., Sullivan, J. E., & Eastlack, S.E. (1994). Xylem embolism in ring-
845 porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska. *Ecology*,
846 75: 1736-1752.

847 Sperry, J. S., Adler, F. R., Campbell, G. S., & Comstock, J. P. (1998). Limitation of plant water
848 use by rhizosphere and xylem conductance: results from a model. *Plant, Cell &*
849 *Environment*, 21: 347-359.

850 Stockinger, E. J., Gilmour, S. J., & Thomashow, M. F. (1997). *Arabidopsis thaliana* CBF1
851 encodes an AP2 domain-containing transcriptional activator that binds to the Crepeat/DRE,
852 a cis-acting DNA regulatory element that stimulates transcription in response to low
853 temperature and water deficit. *Proceedings of the National Academy of Sciences*, 94: 1035-
854 1040.

855 Svystun, T., Bhalerao, R. P., & Jönsson, A. M. (2019). Modelling *Populus* autumn phenology:
856 The importance of temperature and photoperiod. *Agricultural and Forest Meteorology*,
857 271: 346-354.

858 Tanino, K. K., Kalcsits, L., Silim, S., Kendall, E., & Gray, G. R. (2010). Temperature-driven
859 plasticity in growth cessation and dormancy development in deciduous woody plants: a
860 working hypothesis suggesting how molecular and cellular function is affected by
861 temperature during dormancy induction. *Plant Molecular Biology*, 73: 49-65.

862 Timmis, R., & Tanaka Y. 1976. Effects of container density and plant water stress on growth
863 and cold hardiness of Douglas-fir seedlings. *For. Sci.* 22:167-172.

864 Tomasella, M., Nardini, A., Hesse, B. D., Machlet, A., Matyssek, R., Häberle, K. H. (2019).
865 Close to the edge: effects of repeated severe drought on stem hydraulics and nonstructural
866 carbohydrates in European beech saplings. *Tree Physiology*, 39: 717-728.

867 Tranquillini W. 1979. *Physiological ecology of the alpine timberline*. - Ecological Studies 31,
868 Springer Verlag Berlin, Heidelberg, New York.

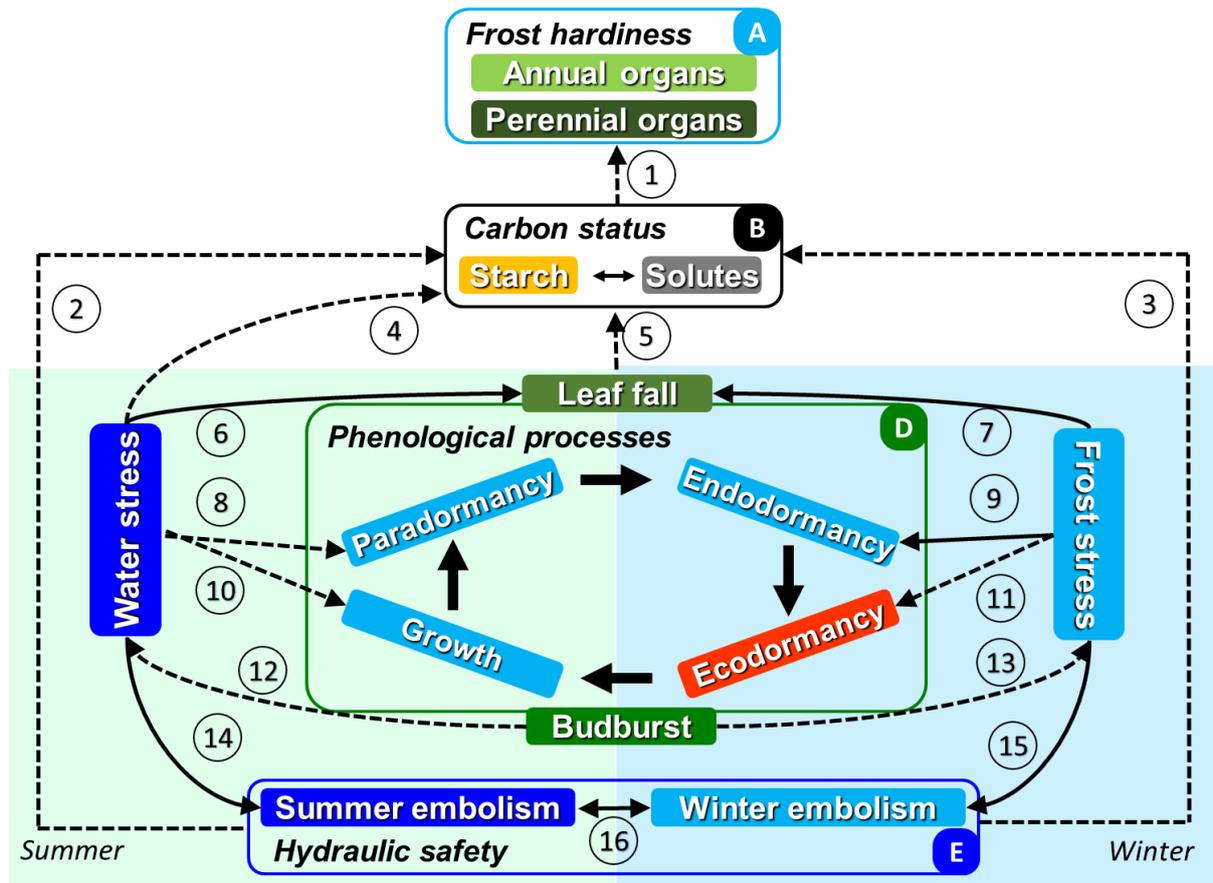
869 Tylewicz, S., Petterle, A., Marttila, S. *et al.*, (2018). Photoperiodic control of seasonal growth
870 is mediated by ABA acting on cell-cell communication. *Science*, eaan8576.

871 Tyree, M. T., Cochard, H., Cruziat, P., Sinclair, B., & Ameglio, T. (1993). Drought-induced
872 leaf shedding in walnut: evidence for vulnerability segmentation. *Plant, Cell &*
873 *Environment*, 16: 879-882.

874 Tyree, M. T., & Sperry, J. S. (1989). Vulnerability of xylem to cavitation and embolism. *Annual*
875 *Review of Plant Biology*, 40: 19-36.

876 Van Peer, L., Nijs, I., Reheul, D., & De Cauwer, B. (2004). Species richness and susceptibility
877 to heat and drought extremes in synthesized grassland ecosystems: compositional vs
878 physiological effects. *Functional Ecology*, 18: 769-778.

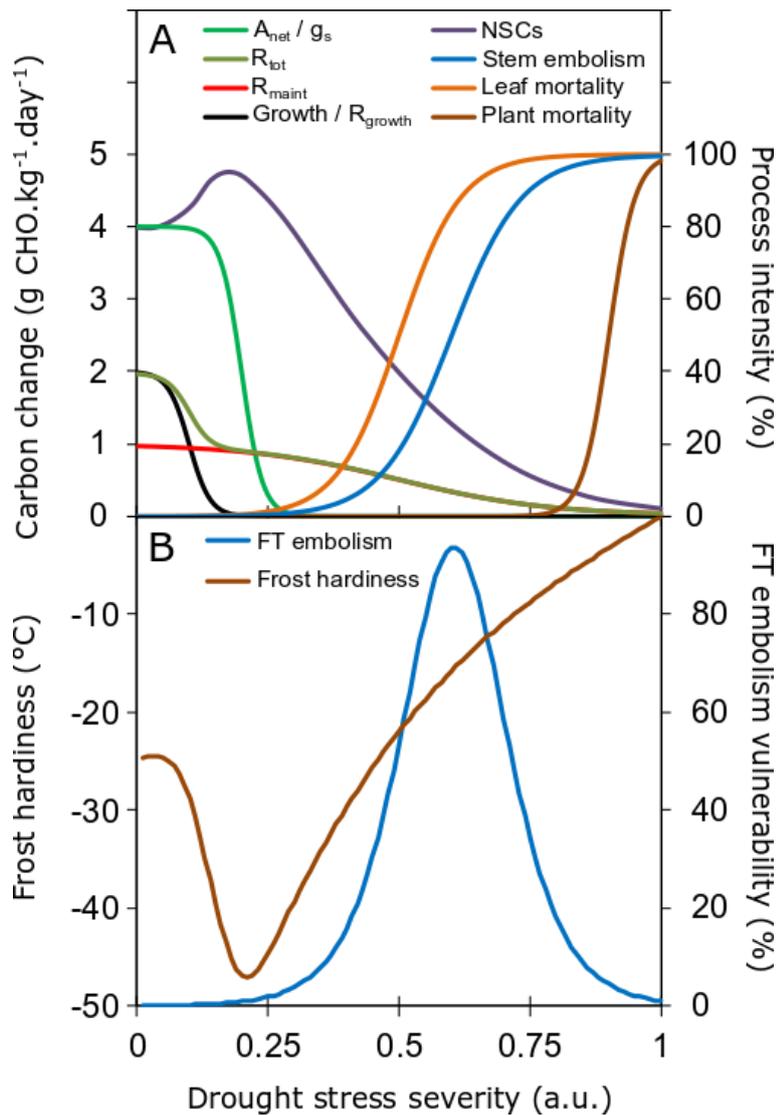
- 879 Vanoni, M., Bugmann, H., Nötzli, M., & Bigler, C. (2016). Drought and frost contribute to
880 abrupt growth decreases before tree mortality in nine temperate tree species. *Forest*
881 *Ecology and Management*, 382: 51-63.
- 882 Vitasse, Y., Porté, A. J., Kremer, A., Michalet, R., & Delzon, S. (2009). Responses of canopy
883 duration to temperature changes in four temperate tree species: relative contributions of
884 spring and autumn leaf phenology. *Oecologia*, 161: 187-198.
- 885 Walter, J., Jentsch, A., Beierkuhnlein, C., & Kreyling, J. (2013). Ecological stress memory and
886 cross stress tolerance in plants in the face of climate extremes. *Environmental and*
887 *Experimental Botany*, 94, 3-8.
- 888 Wargo, P. M. (1981). Defoliation, dieback and mortality. The gypsy moth: research toward
889 integrated pest management. Edited by CC Doane and ML McManus. US Dep. Agric.
890 Tech. Bull, 1584, 240-248.
- 891 Wargo, P. M. (1996). Consequences of environmental stress on oak: predisposition to
892 pathogens. *Annales des Sciences Forestières*, 53: 359-368.
- 893 Welling, A., Moritz, T., Palva, E. T., & Junntila, O. (2002). Independent activation of cold
894 acclimation by low temperature and short photoperiod in hybrid aspen. *Plant Physiology*,
895 129: 1633-1641.
- 896 Wolf, S., Keenan, T. F., Fisher, J. B., Baldocchi, D. D., Desai, A. R., Richardson, A. D., ... &
897 Peters, W. (2016). Warm spring reduced carbon cycle impact of the 2012 US summer
898 drought. *Proceedings of the National Academy of Sciences*, 201519620.
- 899 Wong, B. L., Baggett, K. L., & Rye, A. H. (2009). Cold-season patterns of reserve and soluble
900 carbohydrates in sugar maple and ice-damaged trees of two age classes following drought.
901 *Botany*, 87: 293-305.
- 902 Xie, Y., Wang, X., & Silander, J. A. (2015). Deciduous forest responses to temperature,
903 precipitation, and drought imply complex climate change impacts. *Proceedings of the*
904 *National Academy of Sciences*, 112: 13585-13590.
- 905 Yamaguchi-Shinozaki, K., & Shinozaki, K. (1994). A novel cis-acting element in an
906 *Arabidopsis* gene is involved in responsiveness to drought, low-temperature, or high-salt
907 stress. *The Plant Cell*, 6: 251-264.
- 908 Zhu, X. B., Cox, R. M., & Arp, P. A. (2000). Effects of xylem cavitation and freezing injury on
909 dieback of yellow birch (*Betula alleghaniensis*) in relation to a simulated winter thaw. *Tree*
910 *Physiology*, 20: 541-547.
- 911 Zweifel, R., Zimmermann, L., & Newbery, D. M. (2005). Modeling tree water deficit from
912 microclimate: an approach to quantifying drought stress. *Tree Physiology*, 25: 147-156.



913

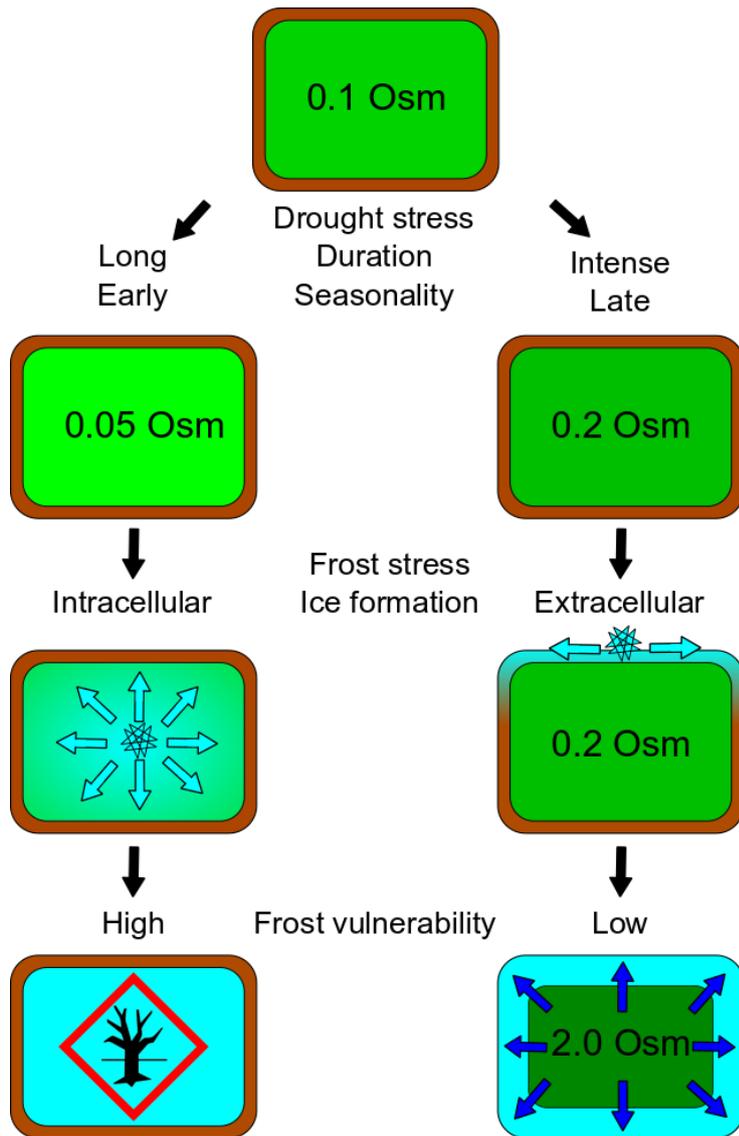
914 **Figure 1.** Involved processes affected by water (mainly during summer period) and frost stress
 915 (mainly during winter period). Positive (solid) and negative (dashed) effects of stresses are
 916 expected on three functional components, namely carbon status, phenological processes and
 917 hydraulic safety. Positive relations between timing events (phenological stages such as leaf fall
 918 and budburst) and other processes indicate that earlier event induce higher level, and vis-versa).
 919 All represented processes are interrelated either directly and indirectly. Both winter and summer
 920 stresses affect the same processes either synergistically or antagonistically. Main effects are
 921 reported, although non-linear and thresholds could make the response more complex. The
 922 numbers refer to studies that document these effects (1. Morin *et al.*, 2007; 2. O'Brien *et al.*,
 923 2014; 3. Améglio *et al.*, 2004; 4. McDowell *et al.*, 2008; 5. Bréda *et al.*, 2006; 6. Tyree *et al.*,
 924 1993; 7. Schuster *et al.*, 2014; 8. Xie *et al.*, 2015; 9. Rinne *et al.*, 1997; 10. Chaves *et al.*, 2002;
 925 11. Charrier *et al.*, 2011; 12. Ghesquière *et al.*, 2014; 13. Hänninen, 1991; 14. Sperry *et al.*,
 926 1998; 15. Charra-Vaskou *et al.*, 2016; 16. Charrier *et al.*, 2014).

927



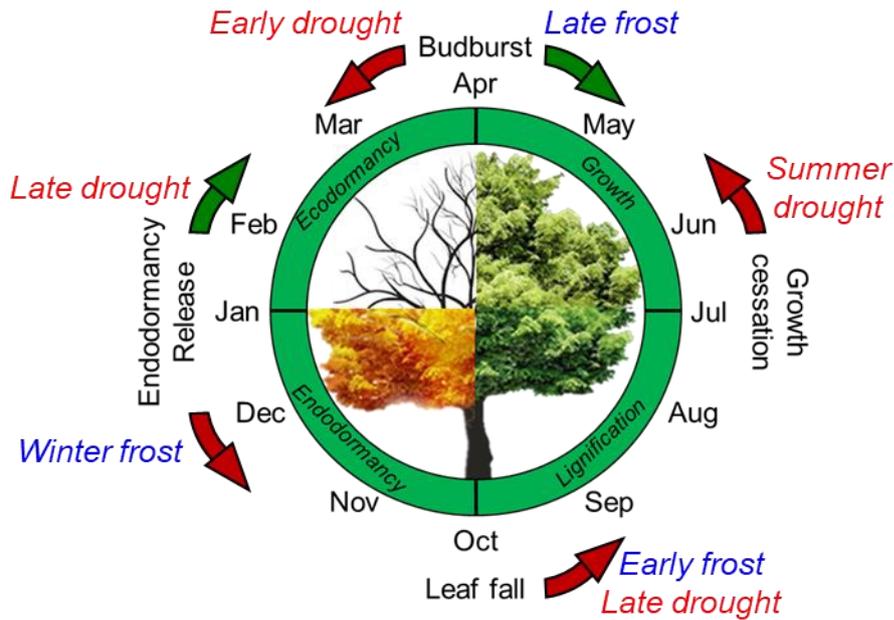
928

929 **Figure 2. A.** Processes and pools affected by drought stress intensity (Photosynthesis A_{net} ,
 930 stomatal conductance g_s , respiration (growth R_{growth} , maintenance R_{maint} and total R_{tot}), non
 931 structural carbohydrates (NSCs), stem embolism, leaf and plant mortality. Growth being more
 932 sensitive to water stress than photosynthesis, and respiration, the NSCs pool initially increases
 933 (McDowell, 2011). After photosynthesis declines, NSCs decline whereas leaf mortality,
 934 embolism and plant mortality increase (Charrier *et al.*, 2018b). **B.** Potential effect generated by
 935 drought stress on frost hardiness of living cell (through the non-linear relation between NSC
 936 and water content) and vulnerability to freeze-thaw induced embolism.



937
 938
 939
 940
 941
 942
 943
 944
 945
 946
 947

Figure 3. Alternative pathways that would explain why contrasted frost vulnerabilities are observed after previous drought exposure. Osmolarity of intracellular sap, controlled notably by the ratio between soluble carbohydrates and water content, could be considered as the main driver. On the right path, intense and/or late drought is expected to concentrate cell sap, increasing the probability of extra cellular ice nucleation. The low chemical potential of ice would pull water, further increasing cell osmolarity. On the left path, long and/or early drought prevents timely increase in solutes, through reduction in carbon reserves. Intracellular freezing through is expected to happen more often and at higher freezing temperature, inducing cellular damages.



948
 949 **Figure 4.** Hastening (brown arrow) or delaying (green arrow) phenological stages in response
 950 to drought and frost events. At the center is presented the typical seasonal phenological stages
 951 in a deciduous tree in Northern hemisphere and, outside the potential effects of drought and
 952 frost stress depending on their timing. It should be noted that stress factors can have a lagged
 953 effect onto phenology (*e.g.* late drought in late summer delaying winter dormancy release).
 954 Early and late drought typically happen in May-June and September, respectively. Early and
 955 late frost typically happen in September-October and April-May, respectively.