



**HAL**  
open science

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

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

► **To cite this version:**

Guillaume Charrier, Nicolas Martin-StPaul, Claire Damesin, Nicolas Delpierre, Heikki Hänninen, et al.. Interaction of drought and frost in tree ecophysiology: rethinking the timing risk.. 2020. hal-02475505v1

**HAL Id: hal-02475505**

**<https://hal.science/hal-02475505v1>**

Preprint submitted on 12 Feb 2020 (v1), 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 risk.**

3 Guillaume Charrier<sup>1</sup>, Nicolas Martin-StPaul<sup>2</sup>, Claire Damesin<sup>3</sup>, Nicolas Delpierre<sup>3</sup>, Heikki  
4 Hänninen<sup>4</sup>, Jose M. Torres-Ruiz<sup>1</sup>, Hendrik Davi<sup>2</sup>

5 <sup>1</sup> Université Clermont Auvergne, INRAE, PIAF, F-63000 Clermont–Ferrand, France.

6 <sup>2</sup> 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 <sup>3</sup> Ecologie Systématique Evolution, Univ. Paris-Sud, CNRS, AgroParisTech, Université Paris-  
9 Saclay, Orsay, France

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

12

13 Keywords: Abiotic stress, Acclimation, Carbon availability, Drought, Frost, Phenology, Risk  
14 assessment, Tree ecophysiology, Water balance

15 **Abstract (332 words)**

16 The edges of plant distribution are mainly defined by abiotic constraints. For example, in  
17 temperate, boreal and alpine area, heatwaves and drought are major constraints at low latitude  
18 and elevation whereas cold and frost are key factors at high latitude and elevation. Over next  
19 decades, climate variability is expected to increase, enhancing the probability of extreme events  
20 and therefore, the stress imposed by abiotic constraints. Moreover, the probability of co-  
21 occurring and successive constraints, such as drought and frost, could increase in parallel. It is  
22 still unclear how an initial exposure to a first constraint would affect the vulnerability to a  
23 subsequent one. Three physiological processes, namely water regulation, carbon balance and  
24 the timing of phenological stages, are crucial to maintain tree survival when facing these abiotic  
25 constraints. Although these processes have been extensively studied alone, in response to a  
26 single constraint, their interaction is largely unknown. In this paper, we explored how plant  
27 water and carbon cycles interact with growth cycle and affect both the vulnerability and the  
28 exposure to climatic constraints. How would the physiological processes driving the responses  
29 of trees to drought and frost interact and would the potential effect on tree distribution be  
30 detailed via two different focus: (i) How would the interaction of drought and frost constraints  
31 modulate the vulnerability to a subsequent constraint? (ii) How vulnerability to a given  
32 constraint and phenology interact? In the light of numerous papers, we suggest that the  
33 interaction between constraints should in the short-term influence water status and, in the longer  
34 term, the carbon status, both consequently affecting further vulnerability, potentially leading to  
35 a decline. However, annual cycle could also be affected by a constraint exposure and therefore  
36 modulate this direct mechanistic response. Furthermore, we identified significant gaps and  
37 therefore propose a framework for building a new generation of process-based models as well  
38 as for experimentally testing these hypotheses.

## 39 **Introduction**

40 Abiotic (*e.g.* temperature, water, light, nutrients) and biotic factors (*e.g.* intra and  
41 interspecific competition, predation, parasitism) are the major drivers of plant distribution and,  
42 therefore, evolutionary change (Erwin 2009; Klanderud *et al.*, 2015). Although biotic factors  
43 drive the population dynamics in the core of their distribution, abiotic factors are more relevant  
44 at the rear and leading edges (Hampe & Petit, 2005). At the rear edge, drought stress is one of  
45 the critical abiotic factors (*e.g.* at low elevation and latitude in Europe; Loehle, 1998; Lines *et*  
46 *al.*, 2010; Ruiz-Benito *et al.*, 2013). At the leading edge (high latitude and elevation), cold and  
47 freezing temperatures limit the plant distribution (Gusta *et al.*, 1983; Koerner, 1998; Larcher,  
48 2005; Charrier *et al.*, 2013a). Along a latitudinal gradient within a species' niche, drought and  
49 frost constraints are clearly divided *i.e.* mild or severe drought events at the rear edge during  
50 summer, and frost stress at the leading edge during winter. This has led to define the  
51 autoecological approach to predict the distribution of plant species, considering individual  
52 limitations, such as minimal temperature at the leading edge or water deficit at the rear edge  
53 (Guisan & Thuillier, 2005; Cheaib *et al.*, 2012). However, drought and frost can co-occur at  
54 high elevation when, late in the winter, air temperature increases while soil is still frozen,  
55 inducing the so-called winter drought (Tranquillini, 1979; Mayr & Charra-Vaskou, 2007;  
56 Charrier *et al.*, 2017). Alternative approach is thus required for taking the different involved  
57 process into account, and, more importantly, for addressing their interaction to improve the  
58 actual species distribution models.

59 This is even more crucial since dramatic changes in climate are likely to increase exposure  
60 to abiotic constraints over all biomes (IPCC, 2014). Mean surface temperature increased at a  
61 rate of 0.2°C per decade over the last decades, leading to species migration at higher latitudes  
62 and altitudes (Parmesan & Yohe, 2003; Lenoir *et al.*, 2008). Ecosystem functioning is likely to  
63 be affected by these changes, however, through contradictory effects. On the one hand,

64 increased productivity is expected in relation with longer growing season (early flushing dates  
65 and delayed senescence; Schaber & Badeck, 2005; Menzel *et al.*, 2006; Fu *et al.*, 2014; Keenan  
66 & Richardson, 2015). However, on the other hand, a substantial deterioration in various  
67 physiological processes is expected to be induced by *e.g.* an insufficient winter chilling that  
68 would compromise the development of the leaves (Chuine *et al.*, 2016), or increased climatic  
69 hazards such as drought (Porporato *et al.*, 2004; Allen *et al.*, 2010; Carnicer *et al.*, 2012) or late  
70 frosts events (Leinonen & Hanninen, 2002; Augspurger, 2013).

71 The extreme climatic events (*e.g.* drought, frost, heat spell and storm) play a major role in  
72 the distribution, survival and, therefore, in the adaptation of plants (Chapin *et al.*, 1993; van  
73 Peer *et al.*, 2004), as well as in the productivity and the biodiversity of communities (Knapp *et*  
74 *al.*, 2002). The expected increase in climate variability will inevitably lead to an increase in the  
75 frequency, intensity and duration of extreme events (IPCC, 2012; Rummukainen, 2012;  
76 Seneviratne *et al.*, 2012). Drought and frost constraints may induce abrupt decreases in growth  
77 and, as a last resort, tree mortality (Vanoni *et al.*, 2016). How these extreme events will affect  
78 ecosystem functions is a key issue for climatologists, and modelers from IPCC (IPCC, 2014).  
79 In this regard, perennial plants, and especially trees, which are keystones structuring many  
80 ecosystems, sheltering biodiversity and being an important carbon stock, are the most likely to  
81 be affected by an increased exposure to abiotic constraints, even though they may not reach the  
82 lethal threshold at once (Chuste *et al.*, 2019). An accurate assessment of the emerging risks and  
83 their impacts on the physiology of trees is therefore urgently needed to predict dynamics of  
84 forest ecosystems and *in fine* their influence on the water and carbon cycles at the global scale.

85 The risk of developing significant damages is only achieved at the crossing between climatic  
86 hazards (*e.g.* drought or frost constraint), stress exposure (*e.g.* low water potential or organ  
87 temperature) and tree vulnerability (*e.g.* low resistance to embolism or insufficient frost  
88 hardiness; Breda & Peiffer, 2014). The prediction of emerging risks therefore needs accurate

89 assessments of (i) the exposure to a given abiotic constraint (type, intensity, duration and  
90 frequency) and (ii) the spatio-temporal patterns of vulnerability and subsequent damages. The  
91 timing of critical phenological stages (*e.g.* bud burst date and leaf full expansion date with  
92 respect to frost and drought, respectively) would thus modulate risk and subsequent damages.  
93 However, despite its relevance, how the exposure to a given abiotic constraints at a given time  
94 instant would influence the vulnerability to the same or a different constraint in the future has  
95 not yet been characterized.

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

108 This paper summarizes the state-of-the-art of tree responses to drought and frost constraints  
109 from the cellular to the individual scale and subsequent damages with the aim of emphasizing  
110 the gap of knowledge with respect to their interactions. The influence of previous damages on  
111 plant vulnerability will be mainly explored at the annual level through two main questions (i)  
112 How would the interaction of drought and frost constraints modulate the vulnerability to a  
113 subsequent constraint? (ii) How vulnerability to a given constraint and phenology interact?

114 Addressing these questions will provide novel information about the interaction between  
115 climate and trees from a wider, multifactorial and temporal perspective. This framework would  
116 be crucial to understand local mortality dynamics and ultimately to improve actual species  
117 distribution models.

118

## **Frame #1 Mechanisms leading to drought-induced damages**

Extensive research effort has been conducted to determine the main drivers of drought-induced tree mortality (*ca.* 13,500 studies since the 1990's, source Web of Knowledge), revolving around two physiological processes and their interaction: carbon starvation and hydraulic failure (see *e.g.* McDowell *et al.*, 2008; McDowell, 2011; Hartmann, 2015). Despite both mechanisms interact during drought, recent studies have shown that tree survival under extreme drought depends to a large extent on the tree capacity to retain xylem hydraulic functioning, therefore avoiding desiccation of living tissues (Brodrigg & Cochard, 2009; Adams *et al.*, 2017).

Trees have developed resistance mechanisms to avoid water stress (*i.e.* maintaining high water potential; Fig. 1) and related embolism formation by a tight control of water balance, such as stomatal closure, low cuticular transpiration, leaf shedding, capacitance and deep rooting (Choat *et al.*, 2018; Martin-StPaul *et al.*, 2017). Xylem vulnerability to embolism is also a key physiological trait representing the capacity of the tree to keep its hydraulic functioning under severe drought conditions (Fig. 1 #14; Sperry *et al.*, 1998). Therefore, the higher the difference between the minimum water potential experienced by the tree and the one leading to significant hydraulic dysfunctions (*i.e.* the hydraulic safety margin), the lower the risk of drought-induced mortality.

Given the narrow hydraulic safety margins within which most plant species operate (Choat *et al.*, 2012), the water potential at which stomata close and residual water losses after stomatal closure (measured as cuticular transpiration) appear to be more critical when evaluating extreme drought-induced tree mortality (Martin-StPaul *et al.*, 2017). Cuticular transpiration appears to be the ultimate driver of water loss when drought is combined with high temperature, which is often the case. In fact, recent studies have highlighted a significant



increase in cuticular transpiration above a temperature of phase transition that matches the range of temperatures known to trigger mortality during hot-droughts (leaf temperature between 30 and 39°C; Burghardt & Riederer, 2008).

On the longer term, closing the stomata to maintain the functionality of the hydraulic system leads to limited carbon assimilation during prolonged mild drought episodes (Fig. 2). As respiration is maintained and even increased during warm spells, carbon reserves steadily deplete ultimately leading to tree death by carbon starvation (McDowell *et al.*, 2008). As stress increase, leaf being more sensitive to drought than perennial organs (due to hydraulic vulnerability segmentation) usually fall (Fig. 1 #6 Tyree *et al.*, 1993) without recycling nutrients (Fig. 1 #5 Bréda *et al.*, 2006), although deciduous behavior may be preceded by nutrient resorption (Marchin *et al.*, 2010). Following leaf fall, the re-establishment of a new cohort of leaves would be even more detrimental to non-structural carbohydrate content. Therefore, hydraulic resistance to drought, directly and through its interaction with carbon availability, defines the tree capacity to cope with and survive to drought (Anderegg *et al.*, 2013).

The identified critical threshold to death thus varies across species and *phyla*. Until recently, water potential inducing 50% loss of hydraulic conductivity has been considered the point of no return from hydraulic failure for conifers (Brodribb & Cochard, 2009), grapevine (Charrier *et al.*, 2018a), the point being 88 to 99% for woody angiosperms (Barigah *et al.*, 2013a; Li *et al.*, 2016). However, recent studies have reported mean lethal thresholds higher than 60% loss of conductivity when comparing across species (Adams *et al.*, 2017), reaching up to 80% for some conifers (*P. taeda*; Hammond *et al.*, 2019). Such variation in the lethal thresholds for the different species highlights the importance of considering absolute instead of relative values for hydraulic conductivity when evaluating the minimum

xylem irrigation required to avoid the desiccation of the tree living tissues. Furthermore, other factors may modulate the tree's resistance, namely ontogenic changes across (Cavender Bares & Bazzaz, 2000) and within years (Charrier *et al.*, 2018a). Resilience to drought is also a crucial, although largely under-investigated, aspect characterized by an insulation of meristems (Barigah *et al.*, 2013b), re-sprouting ability (Schwilk & Ackerly, 2005) and embolism resorption (Nardini *et al.*, 2011; Charrier *et al.*, 2016). To which point significant dehydration of living tissues would affect the viability of the meristematic cells and, subsequently, the regrowth of new organs (leaves, stems, roots) after drought stress has been released is still unknown. It is therefore crucial to determine the spatio-temporal variability in drought resistance at both the vascular and cellular scales.

## **Frame#2 Mechanisms leading to frost-induced damages**

Although the actual predicted *scenarii* of climate change have prompted the scientific community to focus on abiotic constraints related with higher temperatures and drought, frost remains one of the major driver of the current tree distribution (Charrier *et al.*, 2015). The mechanisms by which low temperature drives tree species distribution are still unclear, including resistance to freezing temperature and to frost-induced embolism, and the time to complete the annual cycle and seedling survival (Koerner *et al.*, 2016).

When the organ temperature drops below 0°C, water molecules turn from liquid into ice lattice around a *nucleus* (Hacker & Neuner, 2008; Pramsohler *et al.*, 2012). The density of ice being lower than liquid water (917 vs 1000 kg m<sup>-3</sup> at 0°C; Hare & Sorensen, 1987; Holten *et al.*, 2012), mechanical strain can generate frost cracks in hydrated woody tissues (Kubler, 1983; Cinotti, 1991). If the temperature decreases further, the low chemical potential of ice pulls water molecules from the cells towards extracellular ice lattice, causing pronounced cell dehydration and shrinkage (Dowgert and Steponkus, 1984; Charra-Vaskou *et al.*, 2016).

At the individual scale, the location of ice nucleation event can have dramatic impacts on water relations, redistributing water towards nucleation sites (Ball *et al.*, 2006; Mayr & Charra-Vaskou, 2007) or insulating the trunk from further dehydration through enhanced embolism in the distal parts (Fig. 1 #15; Lemoine *et al.*, 1999; Charrier *et al.*, 2017).

The resistance to frost-induced embolism and to winter drought may be more critical when the root water absorption could not compensate the evaporative demand during periods of sunny days alternating with freezing nights (Tranquillini, 1979; Charrier *et al.*, 2017). At the interspecific level, maximal xylem embolism observed during winter was more tightly correlated than the frost hardiness of the living cells with the potential altitudinal limit (Charrier *et al.*, 2013a). Interestingly, higher embolism than 50% and, even 90%, is

frequently observed and recovered in over-wintering trees without impairing their survival suggesting that it does not constitute a lethal threshold *per se* (Sperry *et al.*, 1994; Mayr *et al.*, 2003; 2006; 2019; Charrier *et al.*, 2013b).

To cope with seasonal frost stress, trees have developed adaptive strategies to increase transiently their frost resistance (*i.e.* frost acclimation) in frost-exposed organs (Charrier *et al.*, 2013a). Non-structural carbohydrates content is tightly related to maximal frost resistance reached during winter (Palonen & Buszard, 1997; Morin *et al.*, 2007; Poirier *et al.*, 2010; Charrier *et al.*, 2013b; 2018b). Moreover, non-structural carbohydrates content usually increases with elevation suggesting that growth is rather limited by organ temperature (and related-meristematic activity) than by carbon availability (Hoch *et al.*, 2002; Shi *et al.*, 2008; Hoch & Koerner, 2009; 2012; Koerner 2015). ). Furthermore, the trade-off between growth and NSC at higher elevation results in a positive retroaction, as it would ensure sufficient frost resistance.

Trees uses various strategies to restore their hydraulic conductivity and supply growth in spring. Many conifer species seem able to recover from winter-embolism in late winter and spring although the involved mechanism remains to be clarified (Sperry & Sullivan 1992; Sperry *et al.*, 1994; Mayr *et al.*, 2003; 2014). In other (angiosperm) species, positive sap pressure being generated by the root system has been measured at the whole plant scale (Priestley 1920; Sperry *et al.*, 1987; Charrier *et al.*, 2016) or at the local (stem) scale (Améglio *et al.*, 2001; 2002; 2004). Contrarily to what has been observed following drought stress, high winter embolism rather seem to constitute an empirically correlated trait than a clear physiological lethal threshold (Mayr *et al.*, 2019).

### **Frame #3 A holistic modelling framework for tree stress physiology: a tentative outline**

Assessing ecological effects of climate change relies on models describing the response of one or several variables of interest to climatic drivers. The models can be conceptual or graphical descriptions of the link between the variable and the driver addressed through empirical relationships. However, as developed above, in order to achieve quantitative projections for ecological effects of climate change, accurate simulation of ecophysiological processes must be developed describing responses at the single tree level (Hänninen, 2016). Ecophysiological models can be readily used also at higher levels of organization as sub-models into stand and ecosystem models (Kramer & Hänninen, 2009), plant distribution models (Chuine and Beaubien, 2001; Morin *et al.*, 2007), and ultimately into global dynamic vegetation models (Guisan & Thuiller, 2005). Ecophysiological whole-tree models have been developed earlier separately for frost stress (Fuchigami *et al.*, 1982; Kellomäki *et al.*, 1992; 1995; Leinonen 1996; Charrier *et al.*, 2018c) and drought stress (Sperry *et al.*, 1998; Zweifel *et al.*, 2005; Martin-StPaul *et al.*, 2017). Different approaches have been developed which fall into two categories: growth models (relatively empirical models quantifying meristem activity and limited by relevant variables such as temperature and/or photoperiod, sometimes including inhibiting and inhibition-releasing factors) and Soil-Plant-Atmosphere models simulating carbon or water fluxes (photosynthesis, transpiration, respiration) and biomass allocation (reserves and growth) at the plant level. Here an attempt is made to develop a holistic modeling framework to address the interaction between drought and frost stress.

A living tree is a functionally holistic system although including constantly interacting growth units. Accordingly, rather than taking place in isolation from each other, the various physiological processes are more or less closely linked to each other. The principle of functionally holistic system has an important implication: whenever measuring two different

146 physiological variables *eg.* water potential and frost hardiness, one most probably measures, at  
147 least partially, different manifestations of the same physiological phenomena although being  
148 measured from different standpoints (as described by the relations between (i) frost hardiness  
149 and water content and (ii) water content and water potential). However, even though the focus  
150 on various quantities in this way is somewhat artificial, or insufficient, it is nevertheless needed  
151 in operational ecophysiological experimentation and simulation. The categories are also needed  
152 in ecophysiological modeling, where one needs to decide which quantities are represented in  
153 the model by their respective explicit state variables. After that crucial decision the other crucial  
154 issue is to determine, based on experimental data, how the different quantities (state variables)  
155 depend on environmental drivers, and possibly interact with another one.

156 By addressing the major seasonal alternation of growth and dormancy, the annual  
157 phenological cycle also reflects major changes in the physiology of trees that could enhance or  
158 mitigate the stress level experienced by the tree. This has been the starting point for developing  
159 the so-called integrated models of frost hardiness, where the environmental responses of frost  
160 hardening and dehardening change according to the prevailing phase of the annual phenological  
161 cycle (Fuchigami *et al.*, 1982; Kellomäki *et al.*, 1992; 1995; Leinonen 1996; Charrier *et al.*,  
162 2018c). The used approach consists of the following steps and could be generalized to address  
163 the interactions between stresses.

164 (i) Quantitatively describe the interesting variable(s) *e.g.* loss of hydraulic conductivity, frost  
165 damage.

166 (ii) Identify the internal physiological drivers that are relevant, with special attention dedicated  
167 to the one that would affect more than one of the interesting variables, *e.g.* water or  
168 carbohydrate content.

169 (ii) Develop a model predicting the progress of the interesting variable in relation with external  
170 climatic drivers and internal physiological drivers based on experimental studies, *e.g.*

171 relation between frost hardiness, tissue water content, carbohydrate and temperature  
172 (Poirier *et al.*, 2010).

173 (iii) Describe the responses of the physiological drivers to external climatic drivers. For each  
174 experiment, the interesting variable is quantified according to Step (i).

175 (iv) Develop a model predicting the progress of the internal physiological driver in relation with  
176 external climatic drivers *e.g.* carbohydrate content depending on air temperature (Charrier  
177 *et al.*, 2018c).

178 (v) Coupling the models obtained at Steps (ii) and (iv), develop a model predicting the  
179 interesting variable with input data being climatic, state variables (such as specific  
180 parameters or initial values) and intermediate physiological drivers.

181 (vi) Simulate the interesting variable and compare with stress related variable such as frost  
182 hardiness vs daily minimum temperature (Charrier *et al.*, 2018b).

183 Frost hardiness models have been developed under such an approach, simulating changes in  
184 frost hardiness depending on the state of dormancy and air temperature. We suggest to broaden  
185 the use of that integrated modeling approach to the holistic studies addressing simultaneously  
186 the effects of frost and drought stress on trees. The main identified scientific lockers to resolve  
187 are the following:

188 1) Spatio-temporal variation in carbon biomass (structural vs annual), fluxes (leaf and stem  
189 photosynthesis, respiration) and allocation (reserve vs growth), in relation with potential  
190 drivers, such as nitrogen and water contents, temperature, *etc.*. Especially, does an increase in  
191 carbohydrates at mild drought stress, as predicted by Mc Dowell (2011) result in increasing the  
192 level of reserves or supply other processes?

193 2) Explicitate the relation between water content and water potential (as modeled by van  
194 Genuchten, 1980), osmotic potential and ultimately lethal thresholds.

195 3) Accurately describe organ temperature (depending on radiation, wind, relative humidity  
196 and air temperature) and latent heat absorbed or released via phase transition (from liquid to  
197 gas or solid).

198 4) Spatio-temporal variation in drought and frost resistance. Drought damage is modeled in  
199 an analogous way, addressing the spatio-temporal variability in the vulnerability to drought  
200 during the annual phenological cycle (Charrier *et al.*, 2018a) and along the xylem water column  
201 (Charrier *et al.*, 2016).

202 5) Finally, the effect of drought exposure on subsequent development of seasonality of frost  
203 hardiness can be addressed through water and NSC content, whereas the effect of frost exposure  
204 on drought vulnerability is approached through water conductance, transpiration, water and  
205 osmotic potentials, as a first approach.

206 However, other interesting variables may still be introduced such as nutrient status, induced  
207 changes on the annual phenological cycle (such as advanced or delayed bud dormancy) or  
208 epigenetic phenomena, although the identified challenge is already substantial.

209



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

212 Over the last decades, ecophysiological studies have led to a comprehensive understanding  
213 on the direct relation between abiotic constraints and physiological processes (Frame #1 and  
214 #2; Fig. 1). The onset of drought-induced damages is mainly based on the hydraulic component,  
215 whereas frost-induced damages relies on the interaction between water and carbon availability.  
216 From a physical perspective, both drought and frost constraints are related to a limited liquid  
217 water availability. Similar damages are generated at both the vascular (*i.e.* cavitation and  
218 embolism when a critical level of water potential is reached; Sperry & Sullivan, 1992; Charrier  
219 *et al.*, 2014) and cellular levels (*i.e.* plasmolysis and cell lysis; Levitt, 1980; Siminovitch &  
220 Cloutier, 1983). Plants have thus developed similar molecular responses to drought and frost  
221 constraints (Beck *et al.*, 2007), under the control of abscisic acid (ABA; Chandler & Robertson,  
222 1994), and inducing, for instance, the synthesis of dehydrins (Welling *et al.*, 2002), or the  
223 accumulation of solutes to maintain solvation layer around macromolecules. Interestingly, the  
224 molecular response to both constraint involves the same regulatory mechanisms (*e.g.*  
225 Dehydration Responsive Elements containing Cold Binding Factors; Stockinger *et al.*, 1997;  
226 Baker *et al.*, 1994). The same pathways are thus activated in both cold and drought responses  
227 (Yamaguchi-Shinozaki & Shinozaki, 1994). Tree species more vulnerable to winter embolism  
228 seem to be also more vulnerable to summer embolism (Charrier *et al.*, 2014). Finally, if the  
229 vulnerability to embolism seems to be essentially fixed phylogenetically, in relation to anatomy  
230 (pit membrane thickness; Li *et al.*, 2016), an osmo-regulation via carbon compounds allows the  
231 resorption of the embolism during winter (via stem pressure; Fig. 1 #3 Ewers *et al.*, 2001;  
232 Améglio *et al.*, 2002) and eventually in summer (Nardini *et al.*, 2011).

233 Although, drought and frost constraints affect similarly many physiological processes, it is  
234 unclear how the response to a repeated exposure would affect the vulnerability to a given

235 constraint. As a first approach, we could expect that a stress that affects the carbon balance  
236 would makes the tree more vulnerable to the subsequent stresses, *e.g.* defoliated oaks would  
237 decline within two years (Wargo, 1981), or carbon-deprived spruces would die faster from  
238 drought (Hartmann *et al.*, 2013). These effects have indeed been hypothesized as promoting  
239 tree decline (Wargo, 1996; Breda & Peiffer, 2014), but, to date, have not been properly  
240 investigated in ecophysiological studies.

241 Two alternative hypotheses, although not self-exclusive, can be introduced: legacy,  
242 considered as a change of either carbon and/or water pools resulting in modulation in  
243 vulnerability (Mc Dowell *et al.*, 2008), and memory, considered as an active process through  
244 stress memory, or facilitated acclimation (Bruce *et al.*, 2007; Walter *et al.*, 2013). On the one  
245 hand, altered water and carbon status would generate potential feedback physiological loops  
246 and trade-offs during successive abiotic constraint exposures (legacy effect). On the other hand,  
247 in long living organisms such as trees, the concept memory is still unclear because most of the  
248 studies dealing with memory have focused on short-term memory in annual plants. Some  
249 studies have evaluated how the vulnerability to a given constrain, *i.e.* frost or drought, is  
250 affected by a repeated exposure of the trees to it (Mayr *et al.*, 2003; Tomasella *et al.*, 2019).  
251 However, studies evaluating the feedback between constraints and vulnerability (*i.e.* the effect  
252 of drought on vulnerability to frost and vice versa) are very few. We attempted to draw a generic  
253 picture as both constraints affect the same physiological processes (Fig. 1).

#### 254 *Effect of drought on vulnerability to frost*

255 This interaction is likely to occur under montane/boreal climate. A first path of interaction  
256 between drought and frost is through water and solute content that both play a role at the organ  
257 level. Indeed, drought constraint will reduce water content in all tree compartments, including  
258 living cells (symplastic) and xylem conduits (apoplastic). Such reduction in water content  
259 would increase the solute concentration (*i.e.* lower osmotic potential) that, consequently, would

260 decrease the freezing point ( $-1.86^{\circ}\text{C}\cdot\text{mol}^{-1}\cdot\text{kg}^{-1}$ ; Hansen & Beck, 1988) in both living cells  
261 (Charrier *et al.*, 2013b) and the apoplasm (Lintunen *et al.*, 2018). However, it should be noticed  
262 that this effect is likely to be canceled during the transition from drought- to frost-exposed  
263 period, in case of a wet autumn period.

264 Lower frost vulnerability of trees pre-exposed to drought is thus expected through two  
265 potential side-effects (i) lower probability of ice formation under similar sub-zero temperatures  
266 and (ii) higher probability of ice nucleation within the apoplasm, pulling symplasmic water  
267 towards extracellular ice lattice (when cryoprotective solutes can protect different  
268 macromolecules as generally observed during frost acclimation, see above). However, this  
269 effect may be balanced by a decrease in non-structural carbohydrates, due to photosynthesis  
270 limitation by stomatal closure, leading to similar, or even lower solute concentration in drought-  
271 exposed trees. In fact, both effects have been observed in winter frost damages following  
272 summer drought. Increasing frost hardiness is thus expected for relatively moderate dehydration  
273 (<30% drought stress intensity; Fig.3 as observed in Benzioni *et al.*, 1992; Kreyling *et al.*, 2012;  
274 Sierra-Almeida *et al.*, 2016). It should also be noted that growth-related processes being more  
275 sensitive to water stress than photosynthesis (Fig. 2A), mild water stress would also promote  
276 transient increase in non-structural carbohydrates (McDowell, 2011; Granda & Camarero,  
277 2017). However, would this transient increase result in higher reserves (potentially enhancing  
278 frost acclimation) or be allocated to other processes such as belowground growth? Finally,  
279 lower frost hardiness would be observed for higher stress level (>50% drought stress intensity)  
280 in relation to carbon depletion (Wong *et al.*, 2009; Galvez *et al.*, 2013; Fig. 3).

281 From the xylem/hydraulic point of view, frost-induced embolism is only generated when sap  
282 is under moderate tension (Mayr *et al.*, 2007). Freeze-thaw cycles will thus exacerbate the pre-  
283 existing tension promoting air seeding from vessels to vessels in dehydrated trees (Fig. 2B;  
284 Tyree & Sperry, 1989; Mayr *et al.*, 2007; Kasuga *et al.*, 2015). Drought episodes during the

285 growing season lead to the reduction in vessel diameter (Lovisolo & Schubert, 1998; Beikircher  
286 & Mayr, 2009) that would result in higher resistance to FT embolism. However, a reduced level  
287 of non-structural carbohydrates would limit the ability of the tree to refill embolized vessels  
288 during winter via active mechanism (*e.g.* stem pressure; Améglio *et al.*, 2001). Even if xylem  
289 conduits were completely refilled, residual bubbles within the xylem would expand at lower  
290 tension if the tree is exposed again to drought after winter or at higher freezing temperature  
291 occurring late in the winter (*i.e.* after the winter refilling process), *via* the so-called fatigue  
292 (Christensen-Dalsgaard & Tyree, 2014). The main positive effect (*i.e.* decreasing the  
293 vulnerability to frost-induced embolism) therefore would lie in the higher ability of sap to  
294 supercool and therefore avoid the phase shift from liquid to ice and the resulting formation of  
295 air bubbles (Lintunen *et al.*, 2018).

#### 296 *Effect of frost on vulnerability to drought*

297 This interaction is likely to occur under temperate climate. Although we have a relatively  
298 clear vision of the potential effect of drought exposure on frost risks (cf. Fig. 2), major gaps of  
299 knowledge remain with respect to frost exposure. Overall, frost damages before drought  
300 exposure would mainly have negative effects for the trees, through limited hydraulic  
301 conductivity and/or biomass destruction although the affected organs as well as the  
302 consequences for the tree can be various. However, in our literature review we did not find a  
303 single study that specifically explored the physiological consequences of frost damages during  
304 the following growing season and after, although Charrier *et al.* (2018c) highlighted a  
305 significant negative correlation between autumnal frost damages and fruit yield the following  
306 summer in walnut.

307 Freeze/thaw-induced embolism and frost cracks increase the volume of air within the xylem  
308 tissue, facilitating thus not only the entry of air into the conduits, but also the spreading from  
309 conduit to conduit, through the punctuations of the vessels, leading to major losses in hydraulic

310 conductivity (Lens *et al.*, 2011; Li *et al.*, 2016). Lower hydraulic conductivity would also limit  
311 plant transpiration, which should result in increased water use efficiency. Depleting soil water  
312 content more slowly should thus delay drought onset and intensity. However, at the stand scale,  
313 the competition to water resources from other tree individuals or other plant species may delete  
314 this potential benefit.

315 Changes in the density and porosity of the pit membrane micro-fibrils that connect  
316 neighboring xylem conduits induced by frost have been observed for different species when  
317 evaluating defrosted wood samples (Li *et al.*, 2016). Whether such changes in the pit  
318 membranes affect the vulnerability to drought-induced embolism formation is still unclear.  
319 These conditions are typically observed under high elevation during clear nights and days, when  
320 minimum night temperatures co-occur with high daily transpiration (Charrier *et al.*, 2017).  
321 Furthermore, when the winter precipitation regimes change from solid to liquid, the soil will  
322 reach lower temperature, damaging the root system more frequently. This would alter the whole  
323 tree hydraulic architecture by decreasing water supply and decreasing the ability to recover,  
324 ultimately increasing xylem embolism (Cox & Malcom, 1997; Zhu *et al.*, 2000). This syndrome  
325 has been identified as pre-disposing dieback for Yellow birch (Cox & Zhu, 2003).

326 One important aspect to consider regarding frost damages is the temporality, higher damages  
327 being observed during the elongation period of new growth units in spring (Chaar & Colin,  
328 1999). By destroying the developing organs late frost damage (leaf, flowers and new shoots)  
329 would immediately reduce the transpiration (water output) and the photosynthesis (carbon  
330 input), but, on a longer term, the remobilization of carbon reserves to reconstruct annual organs  
331 may result in a significant carbon depletion (Wargo 1996). Although under non-stressing  
332 circumstances carbon reserves are quickly restored, under drought stress we could expect a  
333 significant limitation in the ability of the tree to maintain the stomata open and related carbon  
334 input in depleted trees (O'Brien *et al.*, 2014). Furthermore, assuming an increase in resistance

335 to drought-induced embolism along the growing season, the newly formed xylem will be more  
336 vulnerable whereas drought exposure will be higher (Charrier *et al.*, 2018a). Furthermore,  
337 leaves would expand later in the season, when the probability of drought exposure (*i.e.* high  
338 evaporative demand combined with limited soil water availability) is higher although earlier  
339 soil water uptake has been limited.

### 340 **How vulnerability to a given constraint and phenology interact?**

341 The annual phenological cycle consists of developmental events related to the alternation of  
342 growth and dormancy of the trees. Longer growing seasons, such as predicted by vegetation  
343 models due to climate change, are expected to increase the carbon uptake and the ecosystem  
344 net primary production (Angert *et al.*, 2005, Delpierre *et al.*, 2009; Wolf *et al.*, 2016). However,  
345 this would be at the cost of longer periods of effective transpiration that would, ultimately,  
346 deplete soil water content and thus increase the exposure to drought stress. Although timing is  
347 a crucial parameter in the exposure to a seasonal abiotic constraint, the models predicting tree  
348 seasonality developed so far mostly consider non-stressing conditions (see Lang *et al.*, 1987;  
349 Delpierre *et al.*, 2016).

350 In spring, ecodormancy release and growth (both primary and secondary) are accelerated by  
351 warm temperature, in some species in interaction with photoperiod (Laube *et al.*, 2014). At the  
352 end of the growing season, growth cessation is mainly controlled by decreasing photoperiod,  
353 whereas budset and dormancy by warm and low night temperatures, respectively (Svystun *et*  
354 *al.*, 2019). Endodormancy is subsequently released by chilling temperature. Among these  
355 different stages, we can distinguish two different processes: temperature-promoted processes  
356 (*i.e.* occurring at a rate proportional to temperature such as ecodormancy release, primary and  
357 secondary growth, and budset) and signal-limited processes (*i.e.* occurring after a specific  
358 threshold has been reached such as growth cessation, endodormancy induction, leaf fall), which  
359 are indirectly affected by photoperiod and temperature. However, the effect of abiotic stress on

360 the different phenological processes and, furthermore, how carry-over effects can modulate  
361 pluri-annual dynamics, have not been explored yet (Fu *et al.*, 2014). Thus, depending on the  
362 timing of the previous stage, the onset of the following ones will be affected, leading to  
363 unpredictable behavior (Hänninen & Tanino, 2010). For instance, an increase in temperature  
364 would hasten or delay growth cessation depending on the diurnal dynamics (see Rohde *et al.*,  
365 2011 and Kalcsits *et al.*, 2009, respectively), affecting the subsequent stages (budset,  
366 endodormancy and budburst; Fig. 4). Leaf senescence timing is positively correlated with  
367 budburst timing once removing the influence of autumn temperature (Fu *et al.*, 2014). This  
368 carry-over effect is, however, of second order (Liu *et al.*, 2019) and potentially hidden by the  
369 prominent role of environmental variables such as temperature and photoperiod (Vitasse *et al.*,  
370 2009). Such an interacting process has been incorporated in a leaf senescence model (Delpierre  
371 *et al.*, 2009) by modulating the cold-temperature sum leading to leaf senescence by the budburst  
372 date (Kennan & Richardson, 2015).

373 Drought stress affects radial (*i.e.* secondary) growth but its effects on primary growth is  
374 relatively unexplored. Drought exposure can thus significantly hasten the primary growth onset  
375 in *Erica multiflora*, although not in *Globularia alipum* (Bernal *et al.*, 2011). However, also no  
376 effect on growth cessation has been reported (Bernal *et al.*, 2011). One would expect that earlier  
377 growth onset would favor drought avoidance during springtime, but it could hasten soil water  
378 depletion and this may be at the cost of the alteration of the development of shoot, leaves and  
379 buds (Misson *et al.*, 2011). Autumnal drought is expected to induce earlier endodormancy,  
380 probably through the induction of ABA (Maurya & Bhalerao, 2017; Tylewicz *et al.*, 2018).  
381 Furthermore, higher temperatures associated to drought events would induce deeper dormancy  
382 (Heide, 2003; Tanino *et al.*, 2010; Rohde *et al.*, 2011). As this would result in later budburst  
383 the following year, these trees are likely to be more drought-exposed since they would expand  
384 their leaves during a period of more pronounced water deficit. Delayed dormancy and budburst

385 are thus expected through synergistic combination between drought exposure and carry-over  
386 effect (Xie *et al.*, 2015).

387 The impact of frost event on phenology has essentially been reported in spring when it affects  
388 developing organs such as flushing buds, flowers and new leaves. After a single damaging  
389 event, the resulting leaf area (*i.e.* post growth) can be reduced (up to more than 50%) and leaf  
390 full expansion delayed (16 to 34 days; Augspurger, 2013), exposing the tree to summer  
391 constraints, although leaf area and carbon reserves can be reduced (Menzel *et al.*, 2015;  
392 d'Andrea *et al.*, 2019). During summer, after growth cessation and dormancy induction, frost  
393 exposure promotes the dormancy release and, as cold temperature, induces leaf fall (Rinne *et*  
394 *al.*, 1997). So depending on the timing, frost damages could delay or hasten the annual cycle  
395 (later leaf full expansion or earlier endodormancy release, after spring and autumn frost  
396 damages, respectively). However, frost events may induce both cellular and vascular damages  
397 in the distal organs, resulting in re-growth from more basal buds. After several years, the whole  
398 tree architecture may be affected resulting in smaller and denser canopy, which would be less  
399 frost exposed, but at the cost of canopy light transmittance and subsequent photosynthesis.

## 400 **Conclusion and perspectives**

401 Exposure to different constraints has a potential feedback on the sensitivity to future constraints  
402 by affecting physiological components such as non-structural carbohydrates and water balance  
403 (Fig. 2). However, previous exposure may also alter the rate of the future response through  
404 memory effect via accumulation of regulatory proteins, transcription factors or histone  
405 methylation (Bruce *et al.*, 2007; Walter *et al.*, 2013). Although woody plants have to face multi-  
406 annual constraints, these mechanisms have been more thoroughly studied at relatively short  
407 time scale (up to one week) and considering only one constraint (*i.e.* drought or frost). To  
408 unravel the mechanisms of tree mortality and adaptation under a challenging environment, we  
409 need to i) develop a systemic approach at the plant scale integrating ontogenic and histological



410 differences as well as the different physiological processes involved (water use, carbon uptake,  
411 annual cycle); and ii) develop a multicollinearity approach aimed to evaluate the crossing  
412 effects between different constraints in the tree survival capacity both at short and a long time  
413 scale. Interesting insights have been brought by integrative studies, for instance, focusing on  
414 carbon availability and hydraulic failure facing drought (McDowell *et al.*, 2008). It is especially  
415 relevant to develop this type of approaches on different species exhibiting contrasted  
416 combinations of drought and frost tolerance, including provenances originating from the entire  
417 species' distribution range (core and edges) to unravel local adaptations (Kreyling *et al.*, 2014).  
418 The effect of different successive and concomitant constraints at different periods of the year  
419 should help to develop deterministic relationships between different physiological variables and  
420 processes in response to each of them. This is a pre-requisite to improve mechanistic models  
421 simulating these interacting processes in order to predict accurately the effect of cumulative  
422 stress on tree physiology and survival as mentioned Frame 3.

423

## 424 References

- 425 Adams HD, Zeppel MJ, Anderegg WR, Hartmann H, Landhausser SM, Tissue DT, Huxman  
426 TE, Hudson PJ, Franz TE, Allen CD *et al.*, 2017. A multispecies synthesis of physiological  
427 mechanisms in drought-induced tree mortality. *Nature Ecology and Evolution* 1: 1285
- 428 Allen, C. D., Macalady, A. K., Chenchouni, H. *et al.*, (2010). A global overview of drought and  
429 heat-induced tree mortality reveals emerging climate change risks for forests. *Forest  
430 Ecology and Management*, 259: 660-684.
- 431 Améglio, T., Ewers, F. W., Cochard, H., Martignac, M., Vandame, M., Bodet, C., & Cruiziat,  
432 P. (2001). Winter stem xylem pressure in walnut trees: effects of carbohydrates, cooling  
433 and freezing. *Tree Physiology*, 21: 387-394.
- 434 Améglio, T., Bodet, C., Lacoite, A., & Cochard, H. (2002). Winter embolism, mechanisms of  
435 xylem hydraulic conductivity recovery and springtime growth patterns in walnut and peach  
436 trees. *Tree Physiology*, 22: 1211-1220.
- 437 Améglio, T., Decourteix, M., Alves, G. *et al.*, (2004). Temperature effects on xylem sap  
438 osmolarity in walnut trees: evidence for a vitalistic model of winter embolism repair. *Tree  
439 Physiology*, 24: 785-793.
- 440 Anderegg, W. R., Plavcová, L., Anderegg, L. D., Hacke, U. G., Berry, J. A., & Field, C. B.  
441 (2013). Drought's legacy: multiyear hydraulic deterioration underlies widespread aspen  
442 forest die-off and portends increased future risk. *Global change biology*, 19(4), 1188-1196.
- 443 Anderegg, W. R., Flint, A., Huang, C. Y. *et al.*, (2015). Tree mortality predicted from drought-  
444 induced vascular damage. *Nature Geoscience*, 8: 367-371.
- 445 Angert, A., Biraud, S., Bonfils, C. *et al.*, (2005). Drier summers cancel out the CO<sub>2</sub> uptake  
446 enhancement induced by warmer springs. *Proceedings of the National Academy of  
447 Sciences of the United States of America*, 102: 10823-10827.
- 448 Augspurger, C. K. (2013). Reconstructing patterns of temperature, phenology, and frost  
449 damage over 124 years: spring damage risk is increasing. *Ecology*, 94: 41-50.
- 450 Baker SS, Wilhelm KS, Thomashow MF (1994) The 50- region of *Arabidopsis thaliana* cor15a  
451 has cis-acting elements that confer cold, drought, and ABA-regulated gene expression.  
452 *Plant Molecular Biology* 24: 701–713.
- 453 Ball, M. C., Canny, M. J., Huang, C. X., Egerton, J. J. G., & Wolfe, J. (2006). Freeze/thaw-  
454 induced embolism depends on nadir temperature: the heterogeneous hydration hypothesis.  
455 *Plant, Cell & Environment*, 29: 729-745.
- 456 Barigah, T. S., Charrier, O., Douris, M. *et al.*, (2013a). Water stress-induced xylem hydraulic  
457 failure is a causal factor of tree mortality in beech and poplar. *Annals of Botany*, 112: 1431-  
458 1437.
- 459 Barigah, T. S., Bonhomme, M., Lopez, D. *et al.*, (2013b). Modulation of bud survival in  
460 *Populus nigra* sprouts in response to water stress-induced embolism. *Tree Physiology*, 33:  
461 261-274.
- 462 Bartholomeus, R. P., Witte, J. P. M., van Bodegom, P. M., van Dam, J. C., & Aerts, R. (2011).  
463 Climate change threatens endangered plant species by stronger and interacting water-  
464 related stresses. *Journal of Geophysical Research: Biogeosciences*, 116(G4).
- 465 Beck, E. H., Fettig, S., Knake, C., Hartig, K., & Bhattarai, T. (2007). Specific and unspecific  
466 responses of plants to cold and drought stress. *Journal of Biosciences*, 32: 501-510.
- 467 Beikircher B, Mayr S (2009) Intraspecific differences in drought tolerance and acclimation in  
468 hydraulics of *Ligustrum vulgare* and *Viburnum lantana*. *Tree Physiol* 29:765–775
- 469 Benzioni, A., Palzkill, D. A., & Nelson, J. M. (1992). Flower bud dormancy, ABA  
470 concentration, and survival during frost of jojoba genotypes under water stress. *Journal of  
471 the American Society for Horticultural Science*, 117: 976-980.

472 Bernal, M., Estiarte, M., & Peñuelas, J. (2011). Drought advances spring growth phenology of  
473 the Mediterranean shrub *Erica multiflora*. *Plant Biology*, 13: 252-257.

474 Bréda, N., Huc, R., Granier, A., & Dreyer, E. (2006). Temperate forest trees and stands under  
475 severe drought: a review of ecophysiological responses, adaptation processes and long-  
476 term consequences. *Annals of Forest Science*, 63: 625-644.

477 Bréda, N., & Peiffer, M. (2014). Vulnerability to forest decline in a context of climate changes:  
478 new prospects about an old question in forest ecology. *Annals of Forest Science*, 71: 627-  
479 631.

480 Brodribb, T. J., & Cochard, H. (2009). Hydraulic failure defines the recovery and point of death  
481 in water-stressed conifers. *Plant physiology*, 149: 575-584.

482 Burghardt, M., & Riederer, M. (2008). Cuticular transpiration. *Annual Plant Reviews, Biology  
483 of the Plant Cuticle*. Blackwell publishing, 23: 292.

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

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

489 Cavender-Bares, J., & Bazzaz, F. A. (2000). Changes in drought response strategies with  
490 ontogeny in *Quercus rubra*: implications for scaling from seedlings to mature trees.  
491 *Oecologia*, 124: 8-18.

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

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

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

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

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

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

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

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

513 Charrier, G., Torres-Ruiz, J. M., Badel, E. *et al.*, (2016). Evidence for hydraulic vulnerability  
514 segmentation and lack of xylem refilling under tension. *Plant Physiology*, 172: 1657-1668.

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

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

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

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

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

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

531 Choat, B., Brodribb, T. J., Brodersen, C. R., Duursma, R. A., López, R., & Medlyn, B. E.  
532 (2018). Triggers of tree mortality under drought. *Nature*, 558: 531.

533 Christensen-Dalsgaard, K. K., & Tyree, M. T. (2014). Frost fatigue and spring recovery of  
534 xylem vessels in three diffuse-porous trees in situ. *Plant, Cell & Environment*, 37: 1074-  
535 1085.

536 Chuine, I., Bonhomme, M., Legave, J. M., García de Cortázar-Atauri, I., Charrier, G., Lacoïnte,  
537 A., & Améglio, T. (2016). Can phenological models predict tree phenology accurately in  
538 the future? The unrevealed hurdle of endodormancy break. *Global Change Biology*. 22:  
539 3444-3460.

540 Chuine, I., & Beaubien, E. G. (2001). Phenology is a major determinant of tree species range.  
541 *Ecology Letters*, 4: 500-510.

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

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

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

550 Cox, R. M., & Zhu, X. B. (2003). Effects of simulated thaw on xylem cavitation, residual  
551 embolism, spring dieback and shoot growth in yellow birch. *Tree Physiology*, 23: 615-624.

552 D'Andrea, E., Rezaie, N., Battistelli, A. *et al.* (2019). Winter's bite: Beech trees survive  
553 complete defoliation due to spring late-frost damage by mobilizing old C reserves. *New*  
554 *Phytologist*.

555 Delpierre, N., Soudani, K., Francois, C. *et al.*, (2009). Exceptional carbon uptake in European  
556 forests during the warm spring of 2007: a data–model analysis. *Global Change Biology*,  
557 15: 1455-1474.

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

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

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

566 Erwin, D. H. (2009). Climate as a driver of evolutionary change. *Current Biology*, 19: R575–  
567 R583.

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

570 Fu, Y. S., Campioli, M., Vitasse, Y. *et al.*, (2014). Variation in leaf flushing date influences  
571 autumnal senescence and next year's flushing date in two temperate tree species.  
572 Proceedings of the National Academy of Sciences, 111: 7355-7360.

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

576 Galvez, D. A., Landhäusser, S. M., & Tyree, M. T. (2013). Low root reserve accumulation  
577 during drought may lead to winter mortality in poplar seedlings. New Phytologist, 198:  
578 139-148.

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

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

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

586 Hacker, J., & Neuner, G. (2008). Ice propagation in dehardened alpine plant species studied by  
587 infrared differential thermal analysis (IDTA). Arctic, Antarctic, and Alpine Research, 40:  
588 660-670.

589 Hammond, W. M., & Adams, H. D. (2019). Dying on time: traits influencing the dynamics of  
590 tree mortality risk from drought. Tree Physiology.

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

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

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

597 Hänninen, H. (2016). Boreal and temperate trees in a changing climate. Biometeorology.  
598 Springer, Dordrecht.

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

602 Hare, D. E., & Sorensen, C. M. (1987). The density of supercooled water. II. Bulk samples  
603 cooled to the homogeneous nucleation limit. The Journal of Chemical Physics, 87: 4840-  
604 4845.

605 Hartmann, H. (2015). Carbon starvation during drought-induced tree mortality—are we chasing  
606 a myth?. Journal of Plant Hydraulics, 2, e005.

607 Hartmann, H., & Trumbore, S. (2016). Understanding the roles of nonstructural carbohydrates  
608 in forest trees—from what we can measure to what we want to know. New Phytologist, 211:  
609 386-403.

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

612 Hoch, G., & Körner, C. (2009). Growth and carbon relations of tree line forming conifers at  
613 constant vs. variable low temperatures. Journal of Ecology, 97: 57-66.

614 Hoch, G., & Körner, C. (2012). Global patterns of mobile carbon stores in trees at the high-  
615 elevation tree line. Global Ecology and Biogeography, 21: 861-871.

616 Hoch, G., Popp, M., & Körner, C. (2002). Altitudinal increase of mobile carbon pools in *Pinus*  
617 *cembra* suggests sink limitation of growth at the Swiss treeline. Oikos, 98: 361-374.

618 Holten, V., Bertrand, C. E., Anisimov, M. A., & Sengers, J. V. (2012). Thermodynamics of  
619 supercooled water. The Journal of Chemical Physics, 136: 094507.



- 620 Intergovernmental Panel on Climate Change. (2012). Managing the Risks of Extreme Events  
621 and Disasters to Advance Climate Change Adaptation. A Special Report of Working  
622 Groups I and II of the Intergovernmental Panel on Climate Change [Field, C.B., V. Barros,  
623 T.F. Stocker, D. Qin, D.J. Dokken, K.L. Ebi, M.D. Mastrandrea, K.J. Mach, G.-K. Plattner,  
624 S.K. Allen, M. Tignor, and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge,  
625 UK, and New York, NY, USA, 582 pp.
- 626 Intergovernmental Panel on Climate Change. (2014). Climate Change 2014–Impacts,  
627 Adaptation and Vulnerability: Regional Aspects. Cambridge University Press.
- 628 Kalcsits, L. A., Silim, S., & Tanino, K. (2009). Warm temperature accelerates short  
629 photoperiod-induced growth cessation and dormancy induction in hybrid poplar (*Populus*×  
630 spp.). *Trees*, 23: 971-979.
- 631 Kasuga, J., Charrier, G., Uemura, M., & Améglio, T. (2015). Characteristics of ultrasonic  
632 acoustic emissions from walnut branches during freeze–thaw-induced embolism  
633 formation. *Journal of Experimental Botany*, 66: 1965-1975.
- 634 Keenan, T. F., & Richardson, A. D. (2015). The timing of autumn senescence is affected by the  
635 timing of spring phenology: implications for predictive models. *Global Change Biology*,  
636 21: 2634-2641.
- 637 Kellomäki, S., Väisänen, H., Hänninen, H., Kolström, T., Lauhanen, R., Mattila, U., & Pajari,  
638 B. (1992). A simulation model for the succession of the boreal forest ecosystem.
- 639 Kellomäki, S., Hanninen, H., & Kolstrom, M. (1995). Computations on frost damage to Scots  
640 pine under climatic warming in boreal conditions. *Ecological Applications*, 5: 42-52.
- 641 Klanderud, K., Vandvik, V., & Goldberg, D. (2015). The importance of biotic vs. abiotic drivers  
642 of local plant community composition along regional bioclimatic gradients. *PloS one*, 10:  
643 e0130205.
- 644 Knapp, A. K., Fay, P. A., Blair, J. M. *et al.*, (2002). Rainfall variability, carbon cycling, and  
645 plant species diversity in a mesic grassland. *Science*, 298: 2202-2205.
- 646 Koerner, C. (2015). Paradigm shift in plant growth control. *Current Opinion in Plant Biology*,  
647 25, 107-114.
- 648 Koerner, C., Basler, D., Hoch, G. *et al.*, (2016). Where, why and how? Explaining the low-  
649 temperature range limits of temperate tree species. *Journal of Ecology*, 104: 1076-1088.
- 650 Koerner, C. (1998). A re-assessment of high elevation treeline positions and their explanation.  
651 *Oecologia* 115: 445–459.
- 652 Kramer, K., & Hänninen, H. (2009). The annual cycle of development of trees and process-  
653 based modelling of growth to scale up from the tree to the stand. In *Phenology of ecosystem*  
654 *processes* (pp. 201-227). Springer, New York, NY.
- 655 Kreyling, J., Buhk, C., Backhaus, S. *et al.*, (2014). Local adaptations to frost in marginal and  
656 central populations of the dominant forest tree *Fagus sylvatica* L. as affected by  
657 temperature and extreme drought in common garden experiments. *Ecology and Evolution*,  
658 4: 594-605.
- 659 Kreyling, J., Wiesenberg, G. L., Thiel, D. *et al.*, (2012). Cold hardiness of *Pinus nigra* Arnold  
660 as influenced by geographic origin, warming, and extreme summer drought. *Environmental*  
661 *and Experimental Botany*, 78: 99-108.
- 662 Kubler, H. (1983). Mechanism of frost crack formation in trees—a review and synthesis. *Forest*  
663 *Science*, 29: 559-568.
- 664 Lang, G.A., Early, J.D., Martin, G.C., Darnell, R.L. (1987). Endo-, para- and ecodormancy:  
665 physiological terminology and classification for dormancy research. *Hortscience* 22: 371–  
666 377
- 667 Larcher, W. (2005). Climatic constraints drive the evolution of low temperature resistance in  
668 woody plants. *Journal of Agricultural Meteorology*, 61: 189–202.
- 669 Laube, J., Sparks, T. H., Estrella, N., Höfler, J., Ankerst, D. P., & Menzel, A. (2014). Chilling

670 outweighs photoperiod in preventing precocious spring development. *Global Change*  
671 *Biology*, 20: 170-182.

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

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

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

678 Lenoir, J., Gégout, J. C., Marquet, P. A., De Ruffray, P., & Brisse, H. (2008). A significant  
679 upward shift in plant species optimum elevation during the 20th century. *Science*, 320:  
680 1768-1771.

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

684 Levitt, J. (1980). *Responses of Plants to Environmental Stress, Volume 1: Chilling, Freezing,*  
685 *and High Temperature Stresses.* Academic Press.

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

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

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

693 Liu, G., Chen, X., Fu, Y., & Delpierre, N. (2019). Modelling leaf coloration dates over  
694 temperate China by considering effects of leafy season climate. *Ecological modelling*, 394:  
695 34-43.

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

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

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

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

704 Maurya, J.P., & Bhalerao, R.P. (2017). Photoperiod-and temperature-mediated control of  
705 growth cessation and dormancy in trees: a molecular perspective. *Annals of Botany*, 120:  
706 351-360.

707 Mayr, S., & Charra-Vaskou, K. (2007). Winter at the alpine timberline causes complex within-  
708 tree patterns of water potential and embolism in *Picea abies*. *Physiologia plantarum*, 131:  
709 131-139.

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

712 Mayr, S., Hacke, U., Schmid, P., Schwienbacher, F., & Gruber, A. (2006). Frost drought in  
713 conifers at the alpine timberline: xylem dysfunction and adaptations. *Ecology*, 87: 3175-  
714 3185.

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

717 Mayr, S., Schmid, P., Laur, J., Rosner, S., Charra-Vaskou, K., Dämon, B., & Hacke, U. G.  
718 (2014). Uptake of water via branches helps timberline conifers refill embolized xylem in  
719 late winter. *Plant Physiology*, 164: 1731-1740.

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

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

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

727 Menzel, A., Helm, R., & Zang, C. (2015). Patterns of late spring frost leaf damage and recovery  
728 in a European beech (*Fagus sylvatica* L.) stand in south-eastern Germany based on repeated  
729 digital photographs. *Frontiers in Plant Science* 6.

730 Menzel, A., Sparks, T. H., Estrella, N. *et al.* (2006). European phenological response to climate  
731 change matches the warming pattern. *Global Change Biology*, 12: 1969-1976.

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

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

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

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

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

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

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

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

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

754 Pramsohler, M., Hacker, J., & Neuner, G. (2012). Freezing pattern and frost killing temperature  
755 of apple (*Malus domestica*) wood under controlled conditions and in nature. *Tree*  
756 *Physiology*, 32: 819-828.

757 Rinne, P., Hänninen, H., Kaikuranta, P., Jalonen, J. E., & Repo, T. (1997). Freezing exposure  
758 releases bud dormancy in *Betula pubescens* and *B. pendula*. *Plant, Cell & Environment*,  
759 20: 1199-1204.

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

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

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

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

769 Schaber, J., & Badeck, F. W. (2005). Plant phenology in Germany over the 20th century.



770 Regional Environmental Change, 5: 37-46.

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

774 Schwilk, D. W., & Ackerly, D. D. (2005). Is there a cost to resprouting? Seedling growth rate  
775 and drought tolerance in sprouting and nonsprouting *Ceanothus* (*Rhamnaceae*). American  
776 Journal of Botany, 92: 404-410.

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

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

783 Sierra-Almeida, A., Reyes-Bahamonde, C., & Cavieres, L. A. (2016). Drought increases the  
784 freezing resistance of high-elevation plants of the Central Chilean Andes. Oecologia, 1-13.

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

787 Sperry, J. S., & Sullivan, J. E. (1992). Xylem embolism in response to freeze-thaw cycles and  
788 water stress in ring-porous, diffuse-porous, and conifer species. Plant Physiology, 100:  
789 605-613.

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

792 Sperry, J. S., Nichols, K. L., Sullivan, J. E., & Eastlack, S.E. (1994). Xylem embolism in ring-  
793 porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska. Ecology,  
794 75: 1736-1752.

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

798 Sperry, J. S., Hacke, U. G., Oren, R., & Comstock, J. P. (2002). Water deficits and hydraulic  
799 limits to leaf water supply. Plant, Cell & Environment, 25: 251-263.

800 Stockinger, E. J., Gilmour, S. J., & Thomashow, M. F. (1997). Arabidopsis thaliana CBF1  
801 encodes an AP2 domain-containing transcriptional activator that binds to the C-  
802 repeat/DRE, a cis-acting DNA regulatory element that stimulates transcription in response  
803 to low temperature and water deficit. Proceedings of the National Academy of Sciences,  
804 94: 1035-1040.

805 Svystun, T., Bhalerao, R. P., & Jönsson, A. M. (2019). Modelling *Populus autumn* phenology:  
806 The importance of temperature and photoperiod. Agricultural and Forest Meteorology,  
807 271: 346-354.

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

812 Tomasella, M., Nardini, A., Hesse, B. D., Machlet, A., Matyssek, R., Häberle, K. H. (2019).  
813 Close to the edge: effects of repeated severe drought on stem hydraulics and non-structural  
814 carbohydrates in European beech saplings. Tree Physiology

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

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

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

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

824 van Genuchten, M.T. (1980). A closed-form equation for predicting the hydraulic conductivity  
825 of unsaturated soils. *Soil science society of America journal*, 44: 892–898.

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

829 Vanoni, M., Bugmann, H., Nötzli, M., & Bigler, C. (2016). Drought and frost contribute to  
830 abrupt growth decreases before tree mortality in nine temperate tree species. *Forest*  
831 *Ecology and Management*, 382: 51-63.

832 Vitasse, Y., Porté, A. J., Kremer, A., Michalet, R., & Delzon, S. (2009). Responses of canopy  
833 duration to temperature changes in four temperate tree species: relative contributions of  
834 spring and autumn leaf phenology. *Oecologia*, 161: 187-198.

835 Walter, J., Jentsch, A., Beierkuhnlein, C., & Kreyling, J. (2013). Ecological stress memory and  
836 cross stress tolerance in plants in the face of climate extremes. *Environmental and*  
837 *Experimental Botany*, 94, 3-8.

838 Wargo, P. M. (1981). Defoliation, dieback and mortality. The gypsy moth: research toward  
839 integrated pest management. Edited by CC Doane and ML McManus. US Dep. Agric.  
840 Tech. Bull, 1584, 240-248.

841 Wargo, P. M. (1996). Consequences of environmental stress on oak: predisposition to  
842 pathogens. *Annales des Sciences Forestières*, 53: 359-368.

843 Welling, A., Moritz, T., Palva, E. T., & Junttila, O. (2002). Independent activation of cold  
844 acclimation by low temperature and short photoperiod in hybrid aspen. *Plant Physiology*,  
845 129: 1633-1641.

846 Wolf, S., Keenan, T. F., Fisher, J. B., Baldocchi, D. D., Desai, A. R., Richardson, A. D., ... &  
847 Peters, W. (2016). Warm spring reduced carbon cycle impact of the 2012 US summer  
848 drought. *Proceedings of the National Academy of Sciences*, 201519620.

849 Wong, B. L., Baggett, K. L., & Rye, A. H. (2009). Cold-season patterns of reserve and soluble  
850 carbohydrates in sugar maple and ice-damaged trees of two age classes following drought.  
851 *Botany*, 87: 293-305.

852 Xie, Y., Wang, X., & Silander, J. A. (2015). Deciduous forest responses to temperature,  
853 precipitation, and drought imply complex climate change impacts. *Proceedings of the*  
854 *National Academy of Sciences*, 112: 13585-13590.

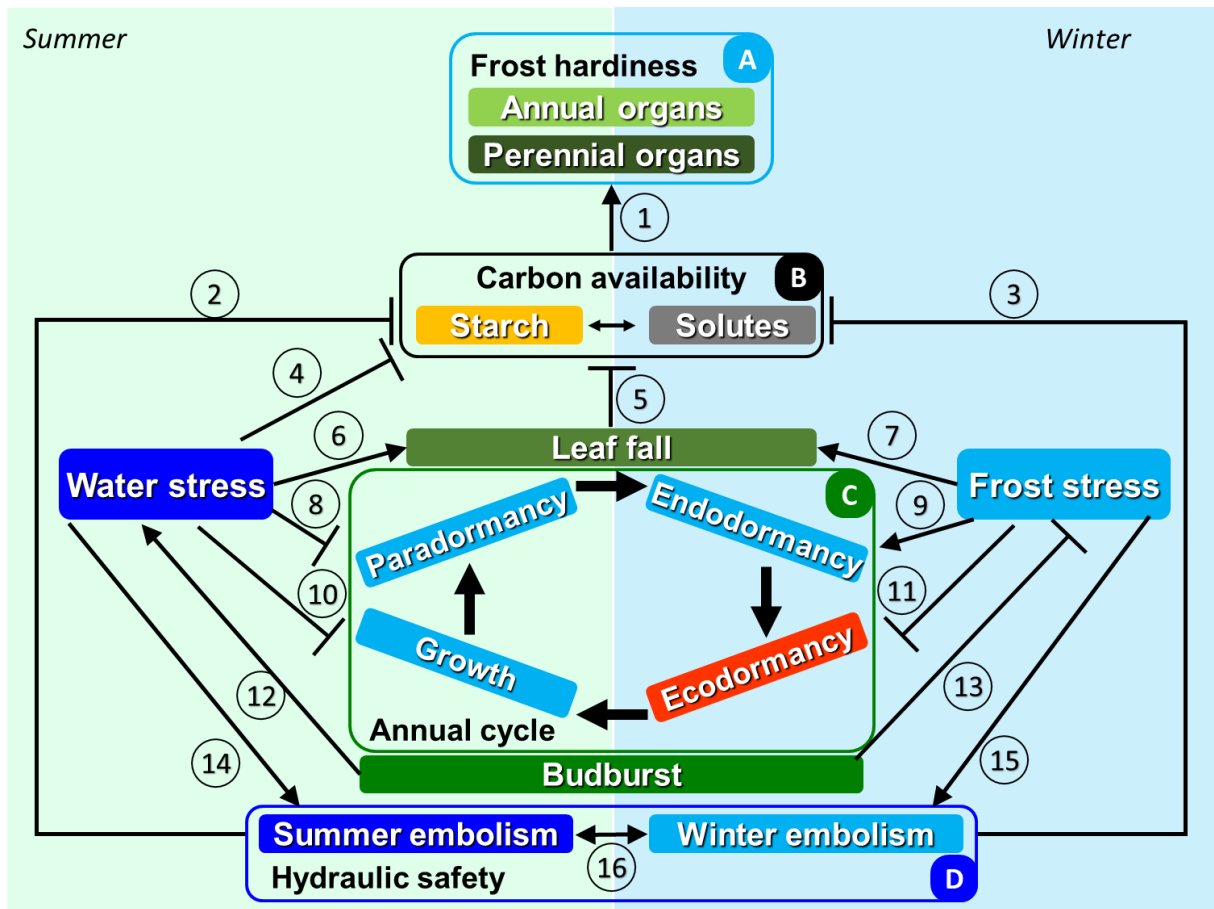
855 Yamaguchi-Shinozaki, K., & Shinozaki, K. (1994). A novel cis-acting element in an  
856 *Arabidopsis* gene is involved in responsiveness to drought, low-temperature, or high-salt  
857 stress. *The Plant Cell*, 6: 251-264.

858 Zhu, X. B., Cox, R. M., & Arp, P. A. (2000). Effects of xylem cavitation and freezing injury  
859 on dieback of yellow birch (*Betula alleghaniensis*) in relation to a simulated winter thaw.  
860 *Tree Physiology*, 20: 541-547.

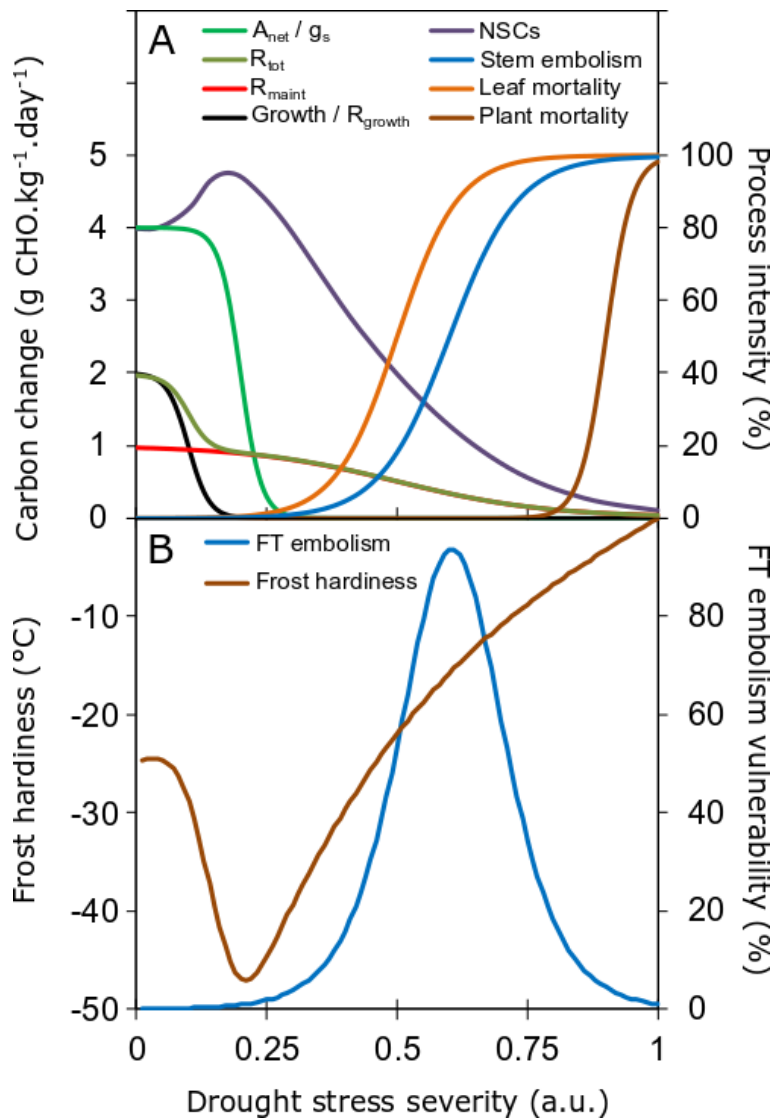
861 Zweifel, R., Zimmermann, L., & Newbery, D. M. (2005). Modeling tree water deficit from  
862 microclimate: an approach to quantifying drought stress. *Tree Physiology*, 25: 147-156.

863

864

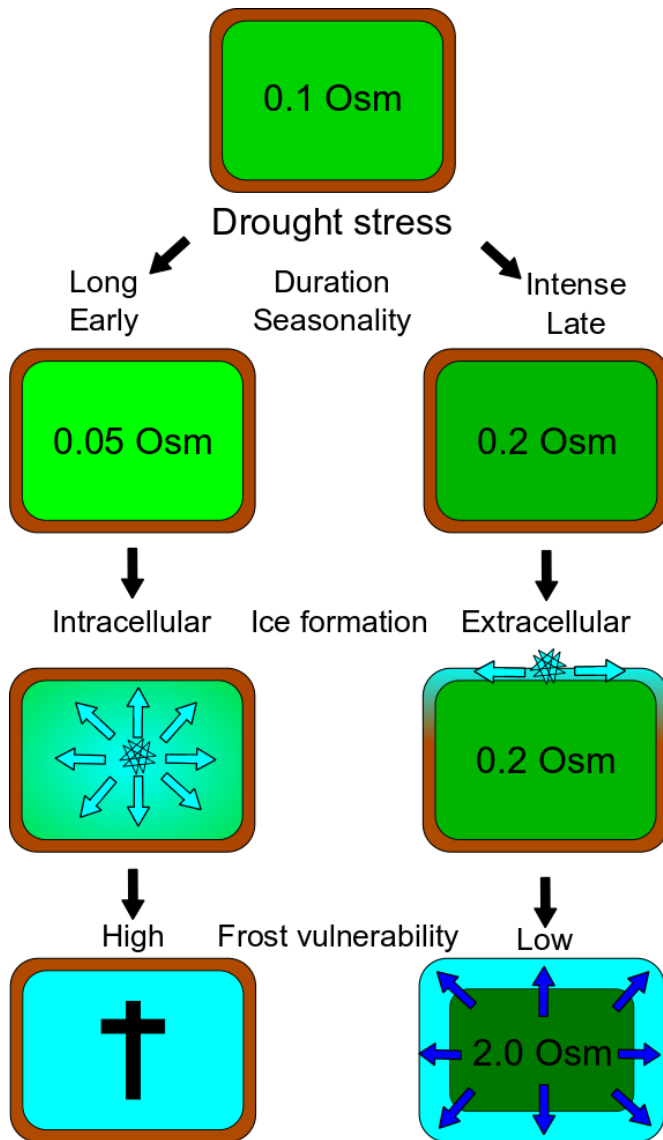


866  
 867 **Figure 1.** Positive (arrow) and negative (bars) effects of water stress (mainly during summer  
 868 period) and frost stress (mainly during winter period) on three functional components, namely  
 869 carbon status, annual cycle and hydraulic architecture. The numbers refer to studies that  
 870 document these effects (1. Morin *et al.*, 2007; 2. O'Brien *et al.*, 2014; 3. Améglio *et al.*, 2004;  
 871 4. McDowell *et al.*, 2008; 5. Bréda *et al.*, 2006; 6. Tyree *et al.*, 1993; 7. Schuster *et al.*, 2014;  
 872 8. Xie *et al.*, 2015; 9. Rinne *et al.*, 1997; 10. Chaves *et al.*, 2002; 11. Charrier *et al.*, 2011; 12.  
 873 Ghesquière *et al.*, 2014; 13. Hanninen, 1991; 14. Sperry *et al.*, 1998; 15. Charra-Vaskou *et al.*,  
 874 2015; 16. Charrier *et al.*, 2014). Both winter and summer stresses affect the same processes  
 875 either synergistically or antagonistically.

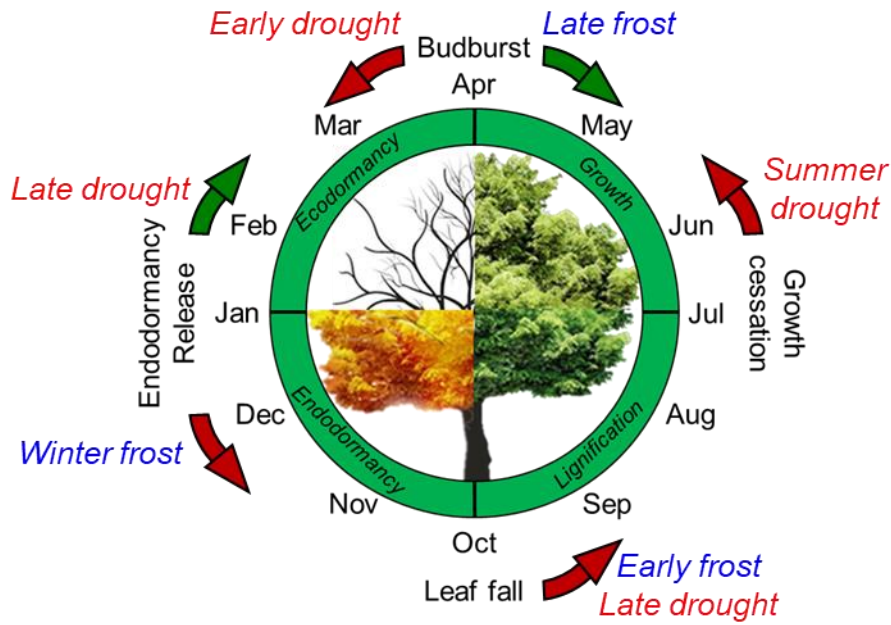


877

878 **Figure 2. A.** Processes affected by drought stress severity (Photosynthesis  $A_{net}$ , stomatal  
 879 conductance  $g_s$ , respiration (growth  $R_{growth}$ , maintenance  $R_{maint}$  and total  $R_{tot}$ ), non structural  
 880 carbohydrates (NSCs), stem embolism, leaf and plant mortality. Growth being more sensitive  
 881 to water stress than photosynthesis, and respiration, the NSCs pool initially increases  
 882 (McDowell, 2011). After photosynthesis declines, NSCs decline whereas leaf mortality,  
 883 embolism and plant mortality increase (Charrier et al., 2018). **B.** Potential effect generated by  
 884 drought stress on frost hardiness of living cell (through the non-linear relation between NSC  
 885 and water content) and vulnerability to freeze-thaw induced embolism.



886  
 887 **Figure 3.** Alternative pathways that would explain why frost vulnerability may differentially  
 888 be affected by previous drought exposure depending on how the ratio between soluble  
 889 carbohydrates and water content have been affected.  
 890



891  
 892 **Figure 4.** Typical seasonal phenological stages in a deciduous tree in Northern hemisphere  
 893 and potential effect of drought and frost stress on hastening (brown arrow) or delaying (green  
 894 arrow) phenological stages depending on the timing.