

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

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13 **Author contributions**

14 GC, NMSP and HD developed the ideas presented in this viewpoint piece and wrote the
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16

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18 The authors of this preprint declare that they have no financial conflict of interest with the
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20

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23 **Abstract (332 words)**

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

49 spatio-temporal variation in carbon ~~biomass~~hydrate composition, fluxes and allocation in
50 relation to environmental drivers, (ii) the spatio-temporal variation in water content, water and
51 osmotic potentials, (iii) the modulation of phenological processes in response to
52 stress~~description of realistic organ temperature in relation to environment and phase transition.~~
53 This framework can help to improve the current process based models and to identify
54 interactions that needs to be better described in order to obtain~~Improving the descriptive range~~
55 ~~of these interrelations would subsequently allow a more~~ quantitative and dynamic ~~description~~
56 view of drought and frost ~~resistance~~vulnerabilities integrating the life history of the
57 treeindividual plant.

58

59 **Introduction**

60 Abiotic (*e.g.* temperature, water, light, nutrients) and biotic factors (*e.g.* intra and
61 interspecific competition, predation, parasitism) are the major drivers of plant distribution and,
62 therefore, evolutionary change (Erwin 2009; Klanderud *et al.*, 2015). Although biotic factors
63 drive the population dynamics in the ~~core~~entire range, abiotic factors ~~are more~~can be highly
64 relevant at the rear and leading edges of the distribution (Hampe & Petit, 2005). Within the
65 boreal, alpine, temperate and Mediterranean areas, plants are likely to be exposed to both
66 drought and frost stress, although it may not happen every year. At the rear edge, drought stress
67 is one of the critical abiotic factors (*e.g.* at low latitude and elevation in Europe; Loehle, 1998;
68 Lines *et al.*, 2010; Ruiz-Benito *et al.*, 2013). At the leading edge (high latitude and elevation),
69 cold and freezing temperatures usually limit the plant distribution (Gusta *et al.*, 1983; Körner,
70 1998; Larcher, 2005; Charrier *et al.*, 2013a). Along a latitudinal gradient within the niche of a
71 species~~-niche~~, drought and frost constraints are clearly ~~divided~~separated, *i.e.* episodes of mild
72 or severe drought ~~events are observed at~~on the rear edge during the summer, and frost stress ~~at~~
73 on the leading edge during the winter. This has led to define the autoecological approach to
74 predict the distribution of plant species within frost-exposed areas (boreal, alpine, temperate
75 and Mediterranean areas), considering individual limitations, such as minimum temperature at
76 the leading edge or water deficit at the rear edge (Guisan & Thuillier, 2005; Cheaib *et al.*, 2012).
77 However, drought and frost can co-occur at high elevation when, late in the winter, air
78 temperature increases while soil is still frozen, inducing the so-called winter drought
79 (Tranquillini, 1979; Mayr & Charra-Vaskou, 2007; Charrier *et al.*, 2017). An alternative
80 approach is thus required for taking the different involved processes into account, and, more
81 importantly, for addressing their interaction to improve the actual species distribution models.
82 This is even more crucial since dramatic changes in climate are likely to increase exposure
83 to abiotic constraints over all biomes (IPCC, 2012). Mean surface temperature increased at a
84 rate of 0.2°C per decade over the last decades, leading to species migration at higher latitudes

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

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

110 The risk of developing significant damages is only achieved at the crossing between climatic
111 hazards (*e.g.* drought or frost constraint), stress exposure (*e.g.* low water potential or organ
112 temperature) and tree vulnerability (*e.g.* low resistance to embolism or insufficient frost
113 hardiness; Breda-Bréda & Peiffer, 2014). The prediction of emerging risks therefore needs
114 accurate assessments of (i) the exposure to a given abiotic constraint (type, intensity, duration
115 and frequency) and (ii) the spatio-temporal patterns of vulnerability and subsequent damages.

116 The timing of critical phenological stages (*e.g.* bud burst date and leaf full expansion date with
117 respect to frost and drought, respectively) would thus modulate risk and subsequent damages.

118 ~~However, despite it can can significantly affect the probability of interaction between~~
119 ~~constraints, how How~~ the exposure to a given abiotic constraints at a given time instant would
120 influence the vulnerability to the same or a different constraint in the future is a critical issue
121 that has been only rarely investigated (Miao et al., 2009, Anderegg et al., 2013; Batlori et al.,
122 2017; Hossain et al., 2019) has not yet been characterized.

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

135 This paper summarizes the state-of-the-art of tree responses to drought and frost constraints
136 from the cellular to the individual scale and subsequent damages with the aim of emphasizing
137 the undervalued role of their interactions at the short term scale (i.e. from the day to the year).
138 Furthermore, different communities are interested in single process or sets of processes (e.g.
139 hydraulic in response to drought, frost hardiness and damages, phenological cycles,...).
140 ~~Another aim is therefore to bring scientists to make a step aside, having an integrative~~
141 ~~perspective of plant's response to abiotic constraints.~~ The influence of previous ~~damages stress~~
142 factors on plant vulnerability, is mainly relevant on woody plants and will be mainly explored
143 at the annual level through two main questions (i) How would the interaction of drought and
144 frost constraints modulate the vulnerability to a subsequent constraint? (ii) How do vulnerability
145 to a given constraint and phenology interact? Addressing these questions will provide novel
146 information about the interaction between climate and trees from a wider, multifactorial and
147 temporal perspective. This framework would be crucial to understand and predict local
148 mortality dynamics and ultimately to improve actual species distribution models.

149

150 **vulnerability to a subsequent constraint?**

151 Over the last decades, ecophysiological studies have led to a comprehensive understanding
152 on the direct relation between abiotic constraints and physiological processes (Frame #1 and
153 #2; Fig. 1). ~~The onset of drought induced damages is mainly based on the hydraulic~~
154 ~~component, whereas frost induced damages relies on the interaction between water and carbon~~
155 ~~availability.~~ From a physical perspective, both drought and frost constraints are related to a
156 limited liquid water availability. Similar damages are generated at both the and cellular levels
157 (*i.e.* plasmolysis and cell lysis; Levitt, 1980; Siminovitch & Cloutier, 1983); and vascular
158 levels (*i.e.* cavitation and embolism when a critical level of water potential is reached; Sperry
159 & Sullivan, 1992; Charrier *et al.*, 2014). A critical factor in the response to both stresses is the

160 ~~accumulation of solutes to maintain water and macromolecules and the cold hardiness~~ (Liu et al., 2009; Liu & Chen, 1993) Prashad has
161 developed similar molecular responses to drought and frost constraints (Beck *et al.*, 2007),
162 under the control of abscisic acid (ABA; Chandler & Robertson, 1994), ~~and~~-inducing, for
163 instance, the synthesis of dehydrins (Welling *et al.*, 2002); ~~or, the accumulation of solutes to~~
164 ~~maintain solvation layer around macromolecules.~~ Interestingly, the molecular response to both
165 constraint involves the same regulatory mechanisms (*e.g.* Dehydration Responsive Elements
166 containing Cold Binding Factors; Stockinger *et al.*, 1997; Baker *et al.*, 1994). The same
167 pathways are thus activated in both cold and drought responses (Yamaguchi-Shinozaki &
168 Shinozaki, 1994).

169 The onset of drought-induced damages is triggered by hydraulic failure and involves the
170 interaction between water and carbon status (Frame 1 and reviews from Choat *et al.*, 2018;
171 Martinez-Vilalta *et al.*, 2019, for extensive description of drought stress syndromes), as frost-
172 induced damages relies on (Charrier *et al.*, 2013b). At the vascular level, Tree species more
173 vulnerable to winter embolism seem to be also more vulnerable to summer embolism (Charrier
174 *et al.*, 2014). Finally This may be related to, the ability of air to propagate within xylem under
175 high frost- or drought-related tension if the vulnerability to embolism seems to be essentially
176 fixed phylogenetically, in relation to anatomy (through pit membrane membrane thickness;
177 (Cochard *et al.*, 1992) Li *et al.*, 2016), However, many tree species are able to restore their
178 hydraulic conductivity, for instance to supply growth in spring. One refilling mechanism
179 involves an osmoregulation via solutes compounds generating osmotic pressure in the lumen
180 of the vessels during winter (Ewers *et al.*, 2001; Améglio *et al.*, 2002), and eventually summer
181 (Nardini *et al.*, 2011). In conifers, the involved mechanism remains to be clarified, but many
182 species seem able to do so (Sperry & Sullivan 1992; Sperry *et al.*, 1994; Mayr *et al.*, 2003;
183 2014). Positive sap pressure has also been measured at the whole plant scale from the
184 pressurization of the root system, notably in woody lianas (Priestley 1920; Sperry *et al.*, 1987;
185 Charrier *et al.*, 2016).

186 Even if xylem conduits were completely refilled, residual bubbles within the xylem would
187 expand at lower tension if the tree is exposed again to drought after winter or at higher freezing
188 temperature occurring late in the winter (*i.e.* after the winter refilling process). Such a higher
189 vulnerability after the initial stress exposure and release would occur through physical or
190 chemical deformation of the pit ultrastructure (*i.e.* fatigue; Christensen-Dalsgaard & Tyree,
191 2014).

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

198 an osmoregulation via carbon compounds allows the resorption of the embolism during
199 winter (via stem pressure; Fig. 1 #3 Ewers *et al.*, 2001; Améglio *et al.*, 2002) and eventually in
200 summer (Nardini *et al.*, 2011).

201 Two alternative hypotheses hypothesis, although not self-mutually exclusive, can should be
202 taken into account to predict the interaction between stress factors be introduced: A legacy, is
203 considered as a passive change of physiological status in response to previous stress exposure.
204 We suggest that the modulation of either carbon and/or water pools would resulting in the
205 modulation in-of vulnerability (Mc-Dowell *et al.*, 2008). On the one hand, a Altered water and
206 carbon status would generate potential feedback physiological loops and trade-offs during
207 successive abiotic constraint stress exposures (legacy effect). Mand memory, which is also
208 called priming in plant defense facing biotic and also abiotic stress (Savvides *et al.*, 2016), is ,
209 considered as an active process through stress memory, or facilitated acclimation shifting
210 biological processes enhancing a basal level of resistance at the cost of reducing primary

211 metabolism such as growth (Bruce *et al.*, 2007; Walter *et al.*, 2013; Martinez-Medina *et al.*,
212 2016). It requires pre exposure to the stress factor in contrast with acclimation that occurs in
213 anticipation. On the one hand, altered water and carbon status would generate potential
214 feedback physiological loops and trade-offs during successive abiotic constraint exposures
215 (legacy effect). On the other hand, In long living organisms such as trees, the concept of
216 memory is still unclear common because most of the studies dealing with memory have focused
217 on short-term memory in annual plants. Some studies have evaluated how the vulnerability to
218 a given constrain, *i.e.* frost or drought, is affected by a repeated exposure of the trees to it (Mayr
219 *et al.*, 2003; Tomasella *et al.*, 2019). However, studies evaluating the feedback between
220 constraints and vulnerability (*i.e.* the effect of drought on vulnerability to frost and vice versa)
221 are very few (*e.g.* Kreyling, *et al.*, 2014; Sierra-Almeida *et al.*, 2016). We attempted to draw a
222 generic picture as both constraints affect the same physiological processes (Fig. 1).

223 This interaction is likely to occur under montane/boreal climate. A first path of interaction
224 between drought and frost is through water and solute content that both play a role at the organ
225 level. Indeed, drought constraint will reduce water content in all tree compartments, including
226 living cells (symplastic) and xylem conduits (apoplastic). Such reduction in water content
227 would increase in the solute concentration (*i.e.* lower osmotic potential) that, consequently,
228 would decrease the freezing point (-1.86°C.mol⁻¹.kg⁻¹; Hansen & Beck, 1988) in both living
229 cells (Charrier *et al.*, 2013b) and the apoplasm (Lintunen *et al.*, 2018). Soil water deficits can
230 indeed initiate the early stages of frost hardiness in Douglas-fir (Timmis & Tanaka, 1976).
231 However, it should be noticed that This effect is likely to be canceled during the transition from
232 drought- to frost-exposed period, in case of a wet autumn period. However, -changes in the
233 water regime, as predicted by future climate predictions, could cause this dry summer and
234 autumn conjunction to occur more -regularly.

235 Lower frost vulnerability of trees pre-exposed to drought is thus expected through two

236 potential side-effects (i) lower probability of ice formation under similar sub-zero temperatures
237 and (ii) higher probability of ice nucleation within the apoplasm, pulling symplasmic water
238 towards extracellular ice lattice (~~when cryoprotective solutes can protect different~~
239 ~~macromolecules as generally observed during frost acclimation, see above~~). However, this
240 effect may be balanced by a decrease in non-structural carbohydrates, due to photosynthesis
241 limitation by stomatal closure, leading to similar, or even lower solute concentration in drought-
242 exposed trees. In fact, both effects have been observed in winter frost damages following
243 summer drought. Increasing frost hardiness is thus expected for relatively moderate dehydration
244 (~~<30% drought stress intensity~~; Fig. 3 as observed in Benzoni *et al.*, 1992; Kreyling *et al.*,
245 2012; Sierra-Almeida *et al.*, 2016). It should also be noted that growth-related processes being
246 more sensitive to water stress than photosynthesis (Fig. 2A), mild water stress would also
247 promote transient increase in non-structural carbohydrates (McDowell, 2011; Granda &
248 Camarero, 2017). However, would this transient increase result in higher reserves (potentially
249 enhancing frost acclimation) or be allocated to other processes such as belowground growth?
250 Finally, lower frost hardiness would be observed for high ~~water stress level (>50%~~-drought stress
251 ~~level intensity~~) in relation to carbon depletion (Fig. 3 right Wong *et al.*, 2009; Galvez *et al.*,
252 2013; Fig. 3).

253 From the xylem/hydraulic point of view, the resulting vulnerability is frost-induced
254 embolism is only generated when sap is under moderate tension (Mayr *et al.*, 2007). Freeze-
255 thaw cycles will thus exacerbate the pre-existing tension promoting air seeding from vessels to
256 vessels in dehydrated trees (Fig. 2B; Tyree & Sperry, 1989; Mayr *et al.*, 2007; Kasuga *et al.*,
257 2015). Drought episodes during the growing season lead to the reduction in vessel diameter
258 (Lovisolo & Schubert, 1998; Beikircher & Mayr, 2009) that would result in higher resistance
259 to ~~FT-freeze-thaw induced~~ embolism. However, a reduced level of non-structural carbohydrates
260 would limit the ability of the tree to refill embolized vessels during winter via active mechanism
261 (e.g. stem pressure; Améglio *et al.*, 2001). ~~Even if xylem conduits were completely refilled,~~

262 ~~will likely have little impact on drought resistance (cf. Fig. 1, Lintunen et al., 2018)~~ To predict drought resistance
263 would lie in the higher ability of sap to supercool and therefore avoid the phase shift from liquid
264 to ice and the resulting formation of air bubbles (Lintunen *et al.*, 2018).

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

266 This interaction is likely to occur under temperate climate. ~~Although we have a relatively~~
267 ~~clear vision of the potential effect of drought exposure on frost risks (cf. Fig. 2), major gaps~~
268 of knowledge remain with respect to frost exposure onto drought vulnerability, although
269 assumptions can be made. Overall, frost damages before drought exposure would mainly have
270 negative effects for the trees, through limited hydraulic conductivity and/or biomass destruction
271 although the affected organs as well as the consequences for the tree can be various. However,
272 in our literature review, we did not find a single study that specifically explored the
273 physiological consequences of frost damages during the following growing season and after,
274 although Charrier *et al.* (2018e2018a) highlighted a significant negative correlation
275 between autumnal frost damages and fruit yield the following summer in walnut.

276 When Low, but not necessarily frozen, soil temperature is too low (but not necessarily
277 frozen), the limits root water uptake becomes very limited (Améglio *et al.*, 2002). Thanks to
278 thermal inertia, the combination of cold soil and warm and dry air can thus promote the
279 aboveground dehydration and hydraulic failure. This type of phenomenon, called winter
280 drought, is typical of late winter conditions at high altitudes (Mayr *et al.*, 2006; Charrier *et al.*,
281 2017; Earles *et al.*, 2018). Winter drought- and Furthermore, when the winter precipitation
282 regimes change from solid to liquid, the soil will reach lower temperature, damaging the root
283 system more frequently. This would alter the whole tree hydraulic architecture by decreasing
284 water supply and decreasing the ability to recover, ultimately increasing xylem embolism (Cox
285 & Maleom, 1997; Zhu *et al.*, 2000). This syndrome has been identified as pre-disposing dieback
286 for Yellow birch (Cox & Zhu, 2003). Freeze/thaw-induced embolism and frost cracks increase

287 the volume of ~~air~~gas within the xylem tissue conduits, therefore facilitating thus not only the entry spreading of air into through
288 ~~the~~and the pit membrane but also feeding into the hydraulic conductivity (Law & D'Amato 2011). ~~For~~If the ~~tree~~birch twigs
289 thaw events has been observed for different species when evaluating defrosted wood samples
290 (Li et al., 2016). Such changes in the pit membrane thickness is likely to increase drought-
291 vulnerability through air seeding (Charrier et al., 2014; ~~Li et al., 2016).~~ Such an increased
292 vulnerability would only remain if the tree is still living during the winter period, which is limited due to any
293 When the winter precipitation regimes change from solid to liquid, the shorter snow cover
294 duration is likely to expose soil to lower temperature, damaging the root system more frequently
295 (Francon et al., 2020). This would alter the whole tree hydraulic architecture by decreasing
296 water supply and decreasing the ability to recover, ultimately increasing xylem embolism (Cox
297 & Malcom, 1997; Zhu et al., 2000). This syndrome has been identified as pre-disposing dieback
298 for Yellow birch (Cox & Zhu, 2003).

299 Lower hydraulic conductivity, from winter embolism and limited spring refilling would limit
300 plant transpiration, which should result in lower leaf water potential and stomatal conductance.
301 As partially open stomata allow sufficient CO₂ diffusion while limiting the amount of transpired
302 water, it is likely that water use efficiency would be increased. Depleting ~~S~~oil water content
303 would be depleted more slowly which should thus delay drought onset and intensity. The same
304 dynamic is expected However, at the stand scale, the competition to water resources from other
305 tree individuals or other plant species may delete this potential benefit after late frost damages,
306 as Furthermore leaves would leaves would expand later in the season, when the probability of
307 drought exposure (i.e. high evaporative demand combined with limited soil water availability)
308 is higher although earlier soil water uptake has been limited. However, at the stand scale, the
309 competition for water resources from other tree individuals or other plant species (less
310 vulnerable to winter embolism or frost damages) may delete this potential benefit.

311

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

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

322 Photoperiod and temperature are key signals regulating plant phenology (Maurya &
323 Bhalearao, 2017). In spring, ecodormancy release and growth (both primary and secondary) are
324 accelerated by warm temperature, in some species in interaction with photoperiod (Laube *et al.*,
325 2014). At the end of the growing season, growth cessation, bud set and endodormancy –is–are
326 mainly controlled by decreasing photoperiod and temperature through two separate, but
327 temporally connected processes: one photosensitive (short day) and one thermosensitive (low
328 temperature) process (Tanino et al., 2010), whereas budset and dormancy by warm and low
329 night temperatures, respectively (Svystun et al., 2019). Endodormancy is subsequently released
330 by chilling temperature. Among these different stages, we can distinguish two different
331 processes: temperature promoted processes (*i.e.* occurring at a rate proportional to temperature
332 such as ecodormancy release, primary and secondary growth, and budset) and signal-limited
333 processes (*i.e.* occurring after a specific threshold has been reached such as growth cessation,
334 endodormancy induction, leaf fall), which are indirectly affected by photoperiod and
335 temperature. However, the effect of abiotic stress on the different phenological processes and,
336 furthermore, how carry-over effects can modulate pluri-annual dynamics, have not been
337 explored yet (Fu *et al.*, 2014). Thus, depending on the timing of the previous stage, the onset of

338 the following ones will be affected, leading to unpredictable behavior (Hänninen & Tanino,
339 ~~2010~~2011). For instance, an increase in temperature would hasten or delay growth cessation
340 depending on the diurnal dynamics of temperature (see Rohde *et al.*, 2011 and Kalcsits *et al.*,
341 2009, respectively), affecting the subsequent stages (budset, endodormancy and budburst; Fig.
342 4). Leaf senescence timing is positively correlated with budburst timing once removing the
343 influence of autumn temperature (Fu *et al.*, 2014). This carry-over effect is, however, of second
344 order (Liu *et al.*, 2019) and potentially hidden by the prominent role of environmental variables
345 such as temperature and photoperiod (Vitasse *et al.*, 2009). Such an interacting process has been
346 incorporated in a leaf senescence model (Delpierre *et al.*, 2009) by modulating the cold
347 temperature sum leading to leaf senescence by the budburst date (~~Kennan~~Keenan &
348 Richardson, 2015).

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

363 The impact of frost events~~s~~ on phenology has essentially been reported in spring when it

364 affects developing organs such as flushing buds, flowers and new leaves. After a single
365 damaging event, the resulting leaf area (*i.e.* post growth) can be reduced (up to more than 50%)
366 and leaf full expansion delayed (16 to 34 days; Augspurger, 2013), exposing the tree to summer
367 constraints, although leaf area and carbon reserves are reduced (Menzel *et al.*, 2015; d'Andrea
368 *et al.*, 2019; [2020](#)). During late summer, after growth cessation and dormancy induction, frost
369 exposure ~~may~~ promotes the dormancy release and, as cold temperature, induces leaf fall (Rinne
370 *et al.*, 1997). So depending on the timing, frost damages could delay or hasten the annual cycle
371 (later leaf full expansion or earlier endodormancy release, after spring and autumn frost
372 damages, respectively). However, frost events may induce both cellular and vascular damages
373 in the distal organs, resulting in re-growth from more basal buds. After several years, the whole
374 tree architecture may be affected resulting in smaller and denser canopy, which would be less
375 frost exposed, but at the cost of canopy light transmittance and subsequent photosynthesis.

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

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

382 Ecophysiological models have been developed separately for frost stress (Fuchigami *et al.*,
383 1982; Leinonen 1996; Charrier *et al.*, 2018a) and drought stress (Sperry *et al.*, 1998; Zweifel *et*
384 *al.*, 2005; Martin-StPaul *et al.*, 2017). By addressing the seasonal alternation of growth and
385 dormancy, the annual phenological cycle also reflects major changes in the physiology of trees
386 that could enhance or mitigate the vulnerability to stress factors. Accordingly, the integrated
387 models of frost hardiness simulates the environmental responses of changes in frost hardiness
388 according to the phenological stage (Kellomäki *et al.*, 1992; 1995; Leinonen 1996; Charrier *et*

389 *al., 2018a). Seasonality is indeed located at the core of any modelling framework related to*
390 *seasonal frost or drought stress factors. We first propose that existing ecophysiological models*
391 *explicitly integrate seasonality weighing relevant parameters by the variables describing*
392 *phenological processes (e.g. sum of growth degree days, sum of chilling units,...). Although*
393 *not being mechanistic, these variables would unify the framework of the models, allowing*
394 *further research into the deterministic relations between three highlighted processes*
395 *(phenological, carbon and hydraulics). Such an integrated modeling approach should be used*
396 *to the interaction between stresses factors through the following steps:*

397 (i) *Quantitative description of the variable(s) of interest e.g. loss of hydraulic conductivity,*
398 *cellular lysis.*

399 (ii) *Identification of the relevant physiological drivers with special attention dedicated to the*
400 *ones that interact with several variables of interest e.g. water or carbohydrate content.*

401 (iii) *Description of the relation between the drivers and the variable of interest e.g. relation*
402 *between frost hardiness, tissue water content, carbohydrate and temperature (Poirier *et**
403 *al., 2010).*

404 (iv) *Experimentally-based description of the relation between physiological drivers and*
405 *external climatic drivers to ensure realistic behavior.*

406 (v) *Mathematical description of the relationship between physiological driver and external*
407 *climatic drivers e.g. carbohydrate content depending on air temperature (Charrier *et al.*,*
408 *2018c).*

409 (vi) *Coupling the models obtained at Steps (ii) and (iv) and development of a model predicting*
410 *the variable of interest with input data being climatic, state variables (such as specific*
411 *parameters or initial values) and intermediate physiological drivers.*

412 (vii) Simulate the tree response and compare with stress-related variable such as frost
413 hardness vs daily minimum temperature (Charrier *et al.*, 2018a).

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

416

417 Exposures to drought and frost constraints has exerted potential feedbacks on the sensitivity
418 to future constraints by affecting physiological components such as non-structural
419 carbohydrates and water balance (*i.e.* legacy Fig. 2). Phenological processes has been for long
420 only studied in non-stressed plants, although physiological seasonality is altered by stress (Fig.
421 4). Major advances are needed in characterizing environmental control of phenological
422 processes in trees during or after stress. Notably do critical sums of temperature (e.g. chilling
423 or forcing temperature) vary with stress intensity, potentially explaining the residual variance
424 in phenological predictions?

425 Phenological processes are likely to exhibit legacy through carbon balance e.g. trophic
426 limitation of meristem growth (Bonhomme *et al.*, 2009), disturbed glycan deposition onto
427 plasmodesmata (Rinne *et al.*, 2001). However, previous exposure to stress factors may also
428 alter the rate of the future ecophysiological response through memory effect via accumulation
429 of regulatory proteins, transcription factors or histone methylation (Bruce *et al.*, 2007; Walter
430 *et al.*, 2013). As already performed in annual plants, there is a clear need for multi-constrained
431 and longer term studies. Although in woody plants have to face multi-annual constraints, these
432 mechanisms have been more thoroughly studied at relatively short time scale (up to one week)
433 and considering only one constraint (*i.e.* drought or frost).

434 To specifically deal with the interaction between constraints, we need to i) develop a systemic
435 approach at the plant scale integrating ontogenetic and histological differences as well as carbon

436 ~~and water coupled with hydraulic and different physiological processes in the tree at multiple scales and developmental~~
437 approach aimed to evaluate the ~~crossing effects interactions~~ between different constraints in the tree survival
438 capacity both at short and a long time scale. Interesting insights have been brought by
439 integrative studies, for instance, focusing on carbon availability and hydraulic failure facing
440 drought (*e.g.* McDowell *et al.*, 2008). It is especially relevant to develop this type of approaches
441 on different species exhibiting contrasted combinations of drought and frost tolerance,
442 including provenances originating from the entire species' distribution range (core and edges)
443 to unravel local adaptations (Kreyling *et al.*, 2014). The effect of different successive and
444 concomitant constraints at different periods of the year should help to develop deterministic
445 relationships between different physiological variables and processes in response to each of
446 them. [It would simulate the life history of the tree and modulated response through legacy and](#)
447 [memory effects as a function of previous level of damages, water and carbon contents.](#)
448 Improving the descriptive range of these interrelations [at the individual and population scales](#)
449 would subsequently allow quantitative and dynamic description of drought and frost resistance
450 [integrating in interaction the life history of the tree.](#) This [is a pre requisite to would](#) improve
451 [existing](#) mechanistic models simulating these interacting processes in order to predict
452 accurately the effect of cumulative stress on tree physiology and survival [as mentioned Frame](#)
453 [3.](#)
454

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

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

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

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

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

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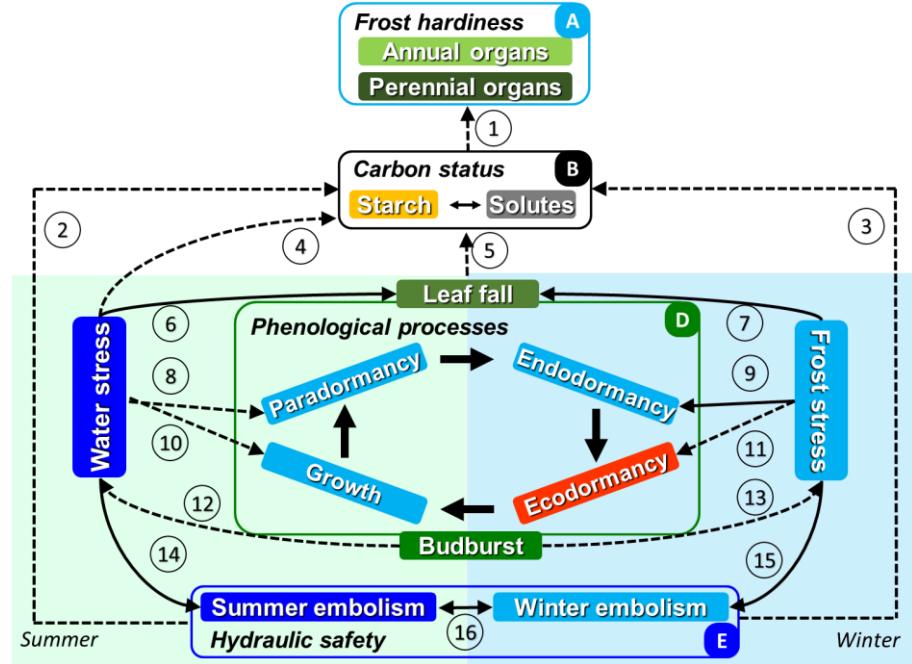
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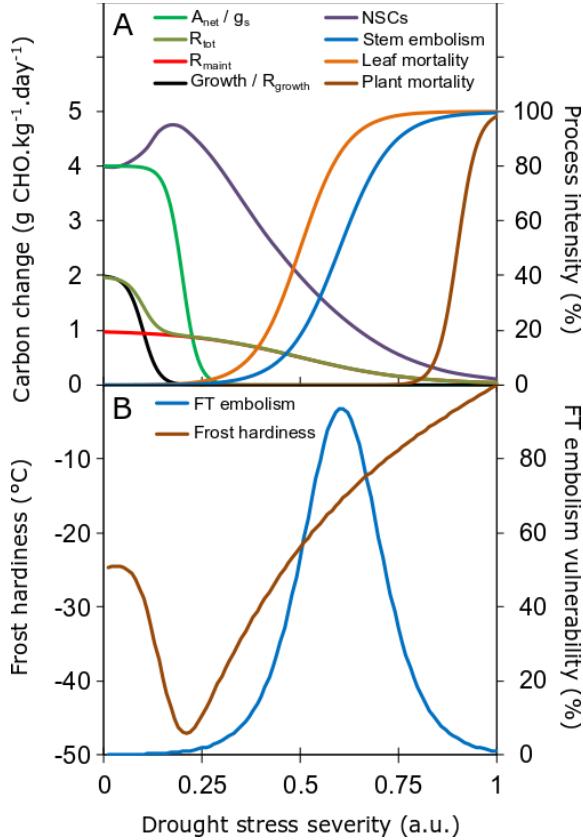


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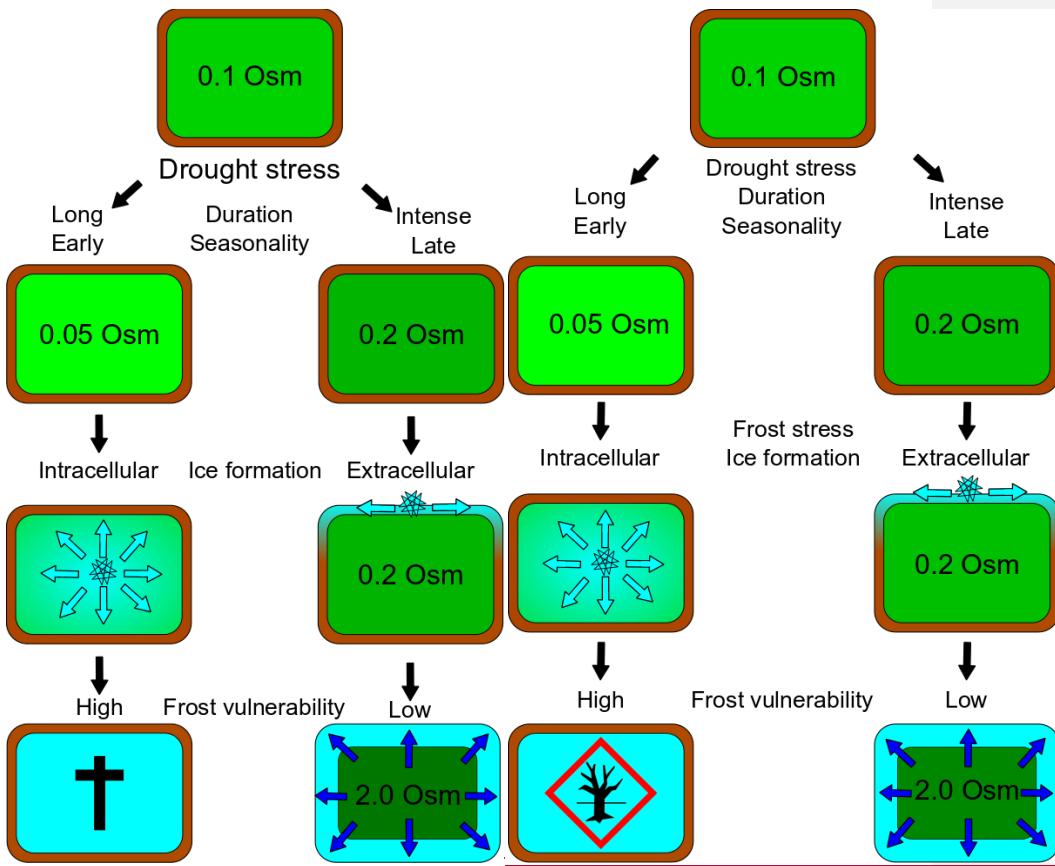
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(mainly during winter period). Positive (arrowsolid) and negative (barsdashed) effects of water stress (mainly during summer period) and frost stresses (mainly during winter period) are expected on three functional components, namely carbon status, annual cyclephenological processes and hydraulic architecturesafety. Positive relations between timing events (phenological stages such as leaf fall and budburst) and other processes indicate that earlier event induce higher level, and vis-versa). All represented processes are interrelated either



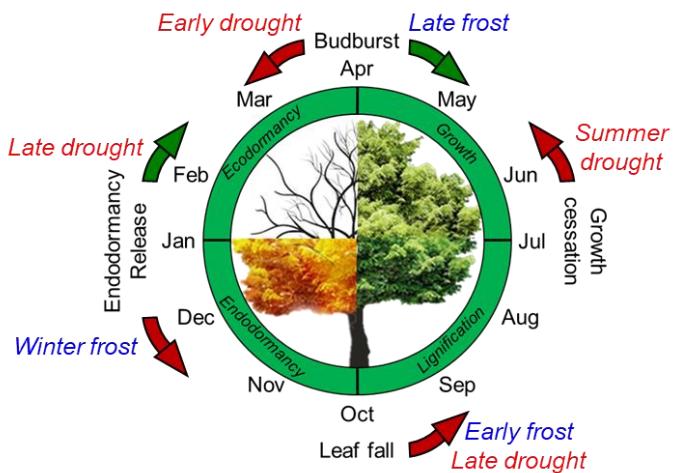
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939 **Figure 2. A.** Processes and pools affected by drought stress severity intensity (Photosynthesis
940 A_{net} , stomatal conductance g_s , respiration (growth R_{growth} , maintenance R_{maint} and total R_{tot}),
941 non structural carbohydrates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



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948 **Figure 3.** Alternative pathways that would explain why contrasted frost vulnerability
 949 vulnerabilities may differentially be affected by are observed after previous drought exposure.
 950 depending on how Osmolarity of intracellular sap, controlled notably by the ratio between
 951 soluble carbohydrates and water content, could be considered as the main driver the ratio
 952 between soluble carbohydrates and water content. On the right path, intense and/or late drought
 953 is expected to concentrate cell sap, increasing the probability of extra cellular ice nucleation.
 954 The low chemical potential of ice would pull water, further increasing cell osmolarity. have
 955 been affected On the left path, long and/or early drought prevents timely increase in solutes,
 956 through reduction in carbon reserves. Intracellular freezing through is expected to happen more
 957 often and at higher freezing temperature, inducing cellular damages.
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Figure 4. Hastening (brown arrow) or delaying (green arrow) phenological stages in response to drought and frost events. At the center is presented the Typical seasonal phenological stages in a deciduous tree in Northern ~~hemisphere~~^{hemisphere} and, outside the potential effects of drought and frost stress on hastening (brown arrow) or delaying (green arrow) phenological stages depending on their timing. It should be noted that stress factors can have a lagged effect onto phenology (e.g. late drought in late summer delaying winter dormancy release). Early and late drought typically happen in May-June and September, respectively. Early and late frost typically happen in September-October and April-May, respectively.