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Abstract (332 words)

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

Introduction

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

This is even more crucial since dramatic changes in climate are likely to increase exposure to abiotic constraints over all biomes (IPCC, 2014). Mean surface temperature increased at a rate of 0.2°C per decade over the last decades, leading to species migration at higher latitudes and altitudes (Parmesan & Yohe, 2003; Lenoir *et al.*, 2008). Ecosystem functioning is likely to 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   thererefore 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 extend on the tree capacity to retain xylem hydraulic functioning, therefore avoiding desiccation of living tissues (Brodribb & 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 depletes 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.

119

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^{-3} 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).

120

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

physiological variables *eg.* water potential and frost hardiness, one most probably measures, at

least partially, different manifestations of the same physiological phenomena although being

measured from different standpoints (as described by the relations between (i) frost hardiness

and water content and (ii) water content and water potential). However, even though the focus

on various quantities in this way is somewhat artificial, or insufficient, it is nevertheless needed

in operational ecophysiological experimentation and simulation. The categories are also needed

in ecophysiological modeling, where one needs to decide which quantities are represented in

the model by their respective explicit state variables. After that crucial decision the other crucial

issue is to determine, based on experimental data, how the different quantities (state variables)

depend on environmental drivers, and possibly interact with another one.

By addressing the major seasonal alternation of growth and dormancy, the annual

phenological cycle also reflects major changes in the physiology of trees that could enhance or

mitigate the stress level experienced by the tree. This has been the starting point for developing

the so-called integrated models of frost hardiness, where the environmental responses of frost

hardening and dehardening change according to the prevailing phase of the annual phenological

cycle (Fuchigami *et al.,* 1982; Kellomäki *et al.,* 1992; 1995; Leinonen 1996; Charrier *et al.,*

2018c). The used approach consists of the following steps and could be generalized to address

the interactions between stresses.

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

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

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

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

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

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

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

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

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

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

2) Explicitate the relation between water content and water potential (as modeled by van 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

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

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

Although, drought and frost constraints affect similarly many physiological processes, it is 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 ($-1.86°C.mol^{-1}.kg^{-1}$; 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

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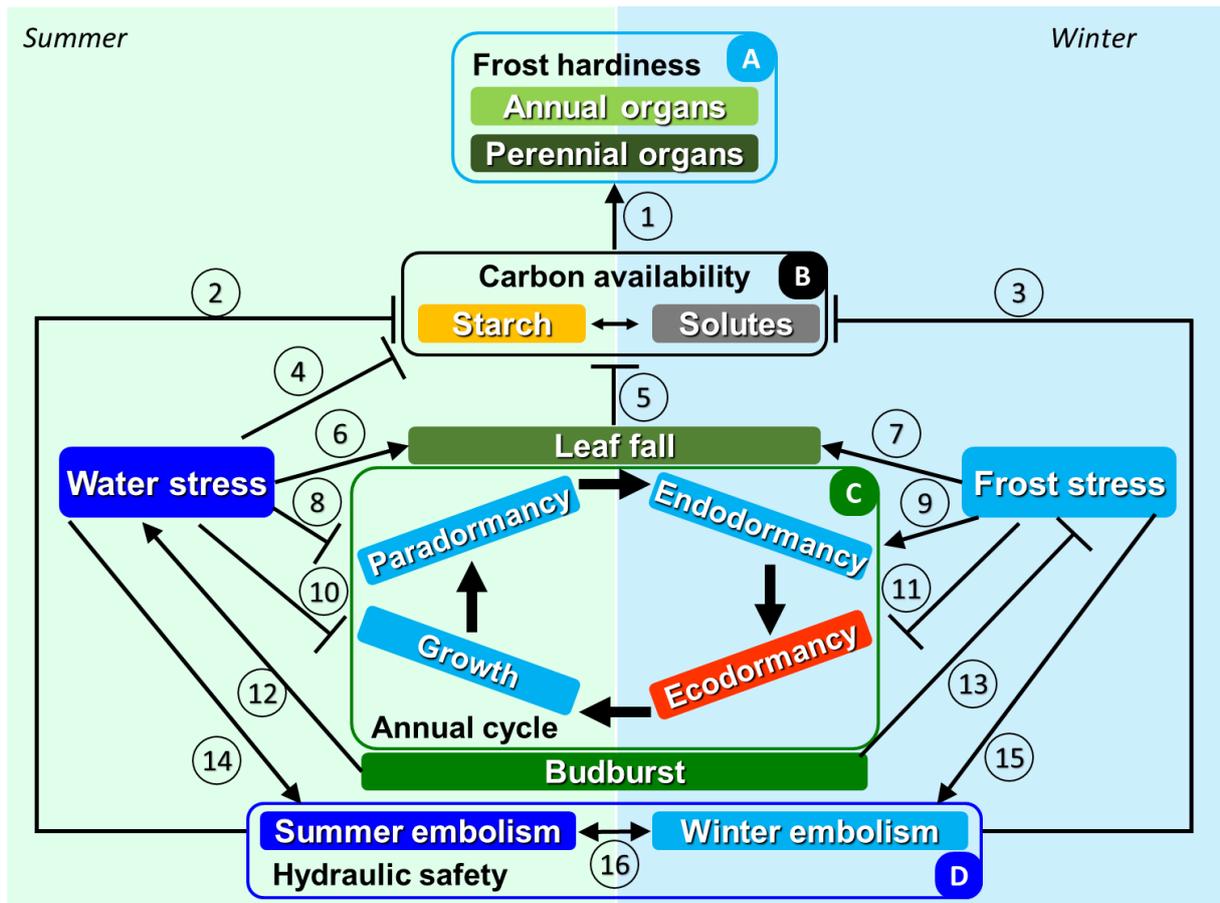
Figure 1. Positive (arrow) and negative (bars) effects of water stress (mainly during summer period) and frost stress (mainly during winter period) on three functional components, namely carbon status, annual cycle and hydraulic architecture. The numbers refer to studies that document these effects (1.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

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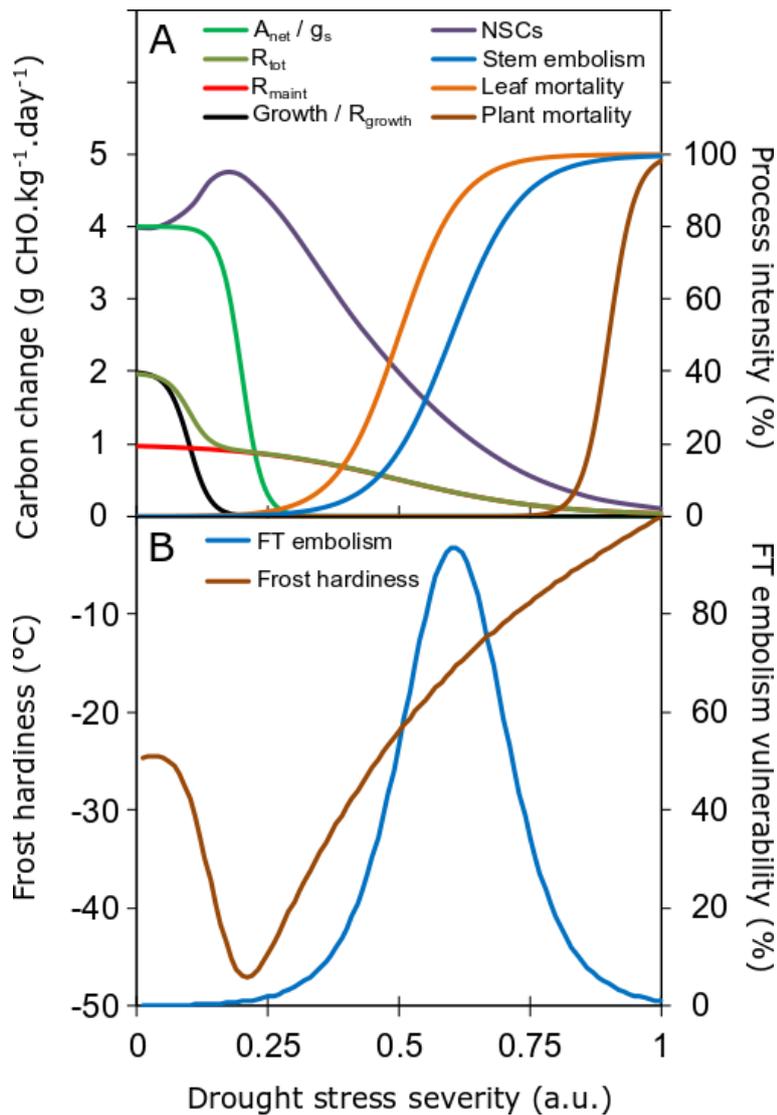
**Figure 2. A.** Processes affected by drought stress severity (Photosynthesis A_{net}, stomatal conductance gs, respiration (growth R_{growth}, maintenance R_{maint} and total R_{tot}), non structural carbohydrates (NSCs), stem embolism, leaf and plant mortality. Growth being more sensitive to water stress than photosynthesis, and respiration, the NSCs pool initially increases (McDowell, 2011). After photosynthesis declines, NSCs decline whereas leaf mortality, embolism and plant mortality increase (Charrier et al., 2018). **B.** Potential effect generated by drought stress on frost hardiness of living cell (through the non-linear relation between NSC and water content) and vulnerability to freeze-thaw induced embolism.
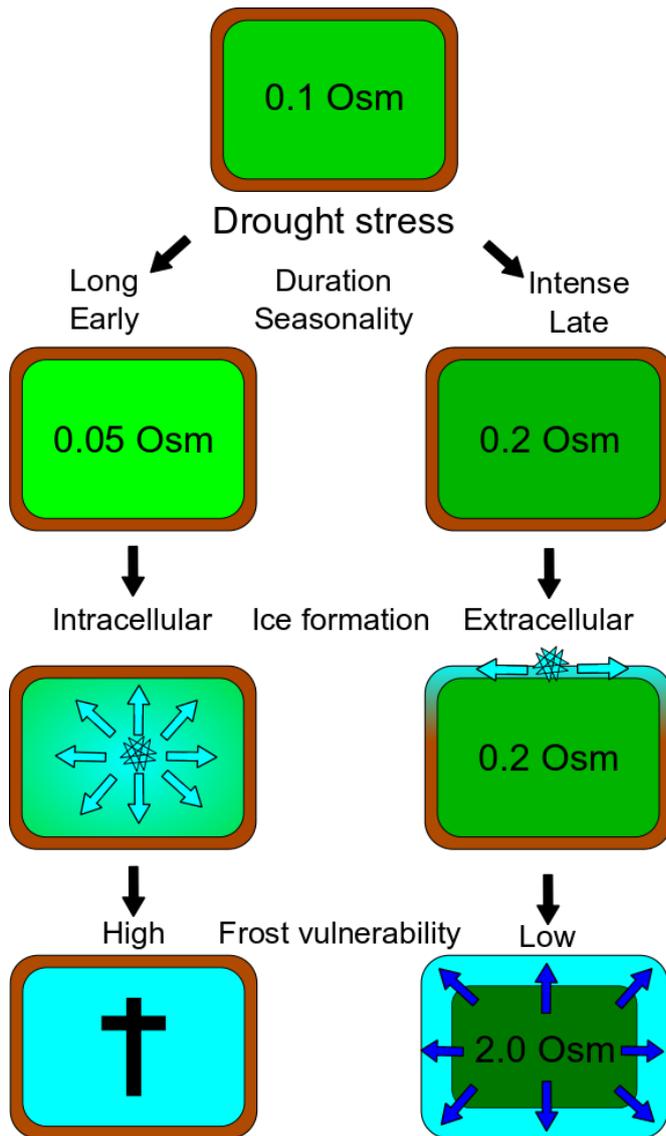
886
887 **Figure 3.** Alternative pathways that would explain why frost vulnerability may differentially
888 be affected by previous drought exposure depending on how the ratio between soluble
889 carbohydrates and water content have been affected.
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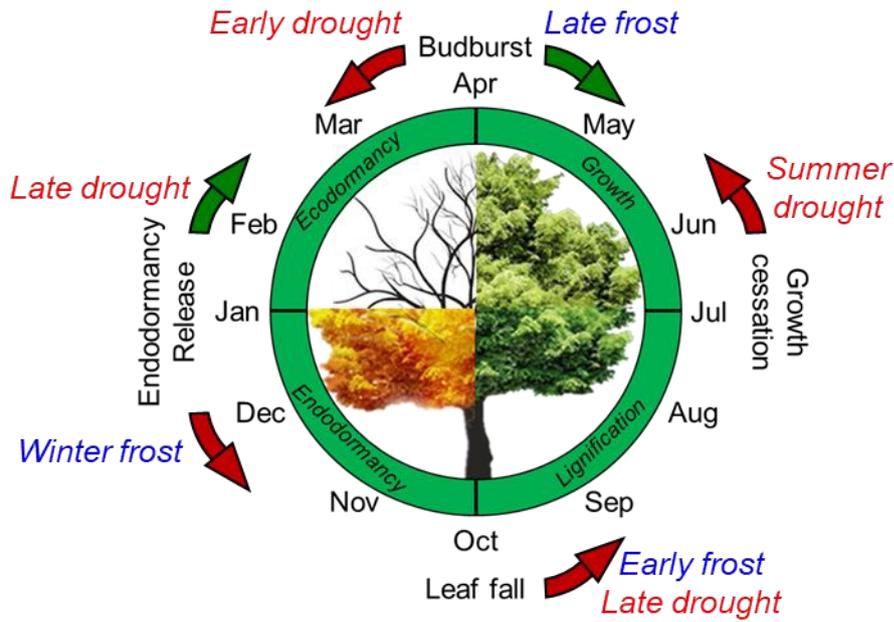
891
Figure 4. Typical seasonal phenological stages in a deciduous tree in Northern hemisphere
and potential effect of drought and frost stress on hastening (brown arrow) or delaying (green
arrow) phenological stages depending on the timing.