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

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15 **Abstract (332 words)**

16 The edges of plant distribution are mainly defined by abiotic constraints. For example, in
17 temperate, boreal and alpine area, heatwaves and drought are major constraints at low latitude
18 and elevation whereas cold and frost are key factors at high latitude and elevation. Over next
19 decades, climate variability is expected to increase, enhancing the probability of extreme
20 events and therefore, the potential stress imposed by abiotic constraints. Moreover, the
21 probability of co-occurring and successive constraints, such as drought and frost, could
22 increase in parallel. It is likely that an initial exposure to a first constraint would affect the
23 vulnerability to a subsequent one. Three integrative physiological processes, namely water
24 status, carbon status and the timing of phenological stages, are crucial to maintain tree
25 survival when facing these abiotic constraints. Although these processes have been
26 extensively studied alone, in response to a single constraint, their interaction has rarely been
27 investigated. In this paper, we explored how plant water and carbon status interact with
28 growth cycle and affect both the vulnerability and the exposure to climatic constraints via two
29 different focuses: (i) How would the interaction of drought and frost constraints modulate the
30 vulnerability to a subsequent constraint? (ii) How vulnerability to a given constraint and
31 phenology interact? In the light of numerous papers, we suggest that the interaction between
32 frost and drought constraints should in the short-term influence water status and, in the longer
33 term, the carbon status, both consequently affecting further vulnerability, potentially leading
34 to a decline. However, annual cycle could also be affected by a constraint exposure and
35 therefore modulate this direct mechanistic response. Furthermore, we identified significant
36 gaps and therefore propose a framework for building a new generation of process-based
37 models through three focus, (i) spatio-temporal variation in carbon biomass, fluxes and
38 allocation in relation to environmental drivers, (ii) spatio-temporal variation in water content,
39 water and osmotic potentials, (iii) description of realistic organ temperature in relation to
40 environment and phase transition. Improving the descriptive range of these interrelations

41 would subsequently allow quantitative and dynamic description of drought and frost
42 resistance integrating the life history of the tree.

43

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, abiotic factors are more relevant at the rear and leading edges of the distribution (Hampe & Petit, 2005). At the rear edge, drought stress is one of the critical abiotic factors (*e.g.* at low latitude and elevation 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; Körner, 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 within frost exposed areas (boreal, alpine, temperate and Mediterranean areas), considering individual limitations, such as minimum 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). An alternative approach is thus required for taking the different involved processes 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, 2012). 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 elevation (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, increased productivity is expected in relation to longer growing season (early flushing dates and delayed senescence; Schaber & Badeck, 2005; Menzel *et al.*, 2006; Fu *et al.*, 2014; Keenan & Richardson, 2015). However, on the other hand, a substantial deterioration in various physiological processes is expected to be induced by *e.g.* an insufficient winter chilling that would alter plant development (Chuine *et al.*, 2016; Delpierre *et al.*, 2016), or increased climatic hazards such as drought (Porporato *et al.*, 2004; Allen *et al.*, 2010; Carnicer *et al.*, 2012) or late frosts events (Leinonen & Hanninen, 2002; Augspurger, 2013).

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

The risk of developing significant damages is only achieved at the crossing between

94 climatic hazards (e.g. drought or frost constraint), stress exposure (e.g. low water potential or
95 organ temperature) and tree vulnerability (e.g. low resistance to embolism or insufficient frost
96 hardiness; Breda & Peiffer, 2014). The prediction of emerging risks therefore needs accurate
97 assessments of (i) the exposure to a given abiotic constraint (type, intensity, duration and
98 frequency) and (ii) the spatio-temporal patterns of vulnerability and subsequent damages. The
99 timing of critical phenological stages (e.g. bud burst date and leaf full expansion date with
100 respect to frost and drought, respectively) would thus modulate risk and subsequent damages.
101 However, despite it can significantly affect the probability of interaction between
102 constraints, how the exposure to a given abiotic constraints at a given time instant would
103 influence the vulnerability to the same or a different constraint in the future has not yet been
104 characterized.

105 The vulnerability to abiotic constraints (which is the susceptibility to develop damages
106 facing a given stress intensity) has been studied for decades via three different focuses,
107 namely phenology (Fig. 1 Frame C; Hänninen & Tanino, 2011), water use (Fig. 1 Frame D,
108 Choat *et al.*, 2012; Anderegg *et al.*, 2015) and carbon availability (Fig.1 Frame B, Sala *et al.*,
109 2012; Hartmann & Trumbore, 2016). The individual responses of each tree eco-physiological
110 process has been integrated into process-based models such as PHENOFIT (Morin & Chuine,
111 2005), SUREAU (Martin-StPaul *et al.*, 2017) or CASTANEA (Dufrene *et al.*, 2005), for
112 phenology, water use and carbon availability, respectively. Facing constraints, the response of
113 each process may not be linear. Therefore, the response to simultaneous or successive
114 constraints may generate chaotic behavior. Integrating the physiological response to abiotic
115 constraints is therefore needed to predict various forms of emergent behavior under new
116 conditions imposed by climate change (Bartholomeus *et al.*, 2011).

117 This paper summarizes the state-of-the-art of tree responses to drought and frost
118 constraints from the cellular to the individual scale and subsequent damages with the aim of

119 emphasizing the undervalued role of their interactions. Furthermore, different communities
120 are interested in single process or sets of processes (e.g. hydraulic in response to drought,
121 frost hardiness and damages, phenological cycles,...). Another aim is therefore to bring
122 scientists to make a step aside, having an integrative perspective of plant's response to abiotic
123 constraints. The influence of previous damages on plant vulnerability, is mainly relevant on
124 woody plants and will be mainly explored at the annual level through two main questions (i)
125 How would the interaction of drought and frost constraints modulate the vulnerability to a
126 subsequent constraint? (ii) How vulnerability to a given constraint and phenology interact?
127 Addressing these questions will provide novel information about the interaction between
128 climate and trees from a wider, multifactorial and temporal perspective. This framework
129 would be crucial to understand local mortality dynamics and ultimately to improve actual
130 species distribution models.

131

Frame #1 Mechanisms leading to drought-induced damages

Water stress results from an imbalance between inwards (root water absorption) and outwards water fluxes (transpiration and evaporation). Trees have developed resistance mechanisms to avoid water stress (*i.e.* maintaining high water potential; Fig. 1) by a tight control of water fluxes, both inwards (*e.g.* deep rooting) and outward fluxes (*e.g.* stomatal closure, leaf shedding, low cuticular transpiration; Choat *et al.*, 2018; Martin-StPaul *et al.*, 2017).

The main drivers of drought-induced tree mortality revolve 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, tree survival under extreme drought depends to a large extent on the tree capacity to retain xylem hydraulic functioning, therefore avoiding desiccation of living tissues (Brodribb & Cochard, 2009; Adams *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), modulated by hydraulic capacitance. Therefore, the higher the difference between the minimum water potential experienced by the tree and the one leading to significant hydraulic dysfunctions (*i.e.* the hydraulic safety margin), the lower the risk of drought-induced mortality.

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

high temperature, which is often the case. In fact, recent studies have highlighted a significant increase in cuticular transpiration above a temperature of phase transition that matches the range of temperatures known to trigger mortality during hot-droughts (leaf temperature between 30 and 39°C; Burghardt & Riederer, 2008).

On the longer term, closing the stomata to maintain the functionality of the hydraulic system leads to limited carbon assimilation during prolonged mild drought episodes (Fig. 2). As respiration is maintained and even increased during warm spells, carbon reserves steadily deplete ultimately leading to tree death by carbon starvation (McDowell *et al.*, 2008). As stress increases, leaves 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 the level of non-structural carbohydrate reserves. 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 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 aspect through *e.g.* hydric insulation of meristems (Barigah *et al.*, 2013b), maintenance of re-sprouting ability (Schwilk & Ackerly, 2005) and resorption of embolism (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 is most likely the main point controlling spatio-temporal variability in drought mortality/resilience.

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

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

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

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

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 variable(s) of interest *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 variables of interest, *e.g.* water or carbohydrate content.

(ii) Develop a model predicting the progress of the variable of interest in relation to 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 variable of interest is quantified according to Step (i).

(iv) Develop a model predicting the progress of the internal physiological driver in relation to 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 variable of interest 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 keys 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 to 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) Making explicit the relation between water content and water potential (as modeled by

van Genuchten, 1980), osmotic potential and ultimately lethal thresholds.

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

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

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

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

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

Two alternative hypotheses, although not self-exclusive, can be introduced: legacy, considered as a change of either carbon and/or water pools resulting in modulation in vulnerability (Mc Dowell *et al.*, 2008), and memory, considered as an active process through stress memory, or facilitated acclimation (Bruce *et al.*, 2007; Walter *et al.*, 2013). On the one hand, altered water and carbon status would generate potential feedback physiological loops and trade-offs during successive abiotic constraint exposures (legacy effect). On the other hand, in long living organisms such as trees, the concept memory is still unclear because most of the studies dealing with memory have focused on short-term memory in annual plants. Some studies have evaluated how the vulnerability to a given constrain, *i.e.* frost or drought, is affected by a repeated exposure of the trees to it (Mayr *et al.*, 2003; Tomasella *et al.*, 2019). However, studies evaluating the feedback between constraints and vulnerability (*i.e.* the effect of drought on vulnerability to frost and vice versa) are very few (*e.g.* Kreyling, *et al.*, 2014; Sierra-Almeida *et al.*, 2016). We attempted to draw a generic picture as both constraints affect the same physiological processes (Fig. 1).

Effect of drought on vulnerability to frost

This interaction is likely to occur under montane/boreal climate. A first path of interaction between drought and frost is through water and solute content that both play a role at the organ level. Indeed, drought constraint will reduce water content in all tree compartments,

including living cells (symplastic) and xylem conduits (apoplastic). Such reduction in water content would increase the solute concentration (*i.e.* lower osmotic potential) that, consequently, would decrease the freezing point ($-1.86^{\circ}\text{C}.\text{mol}^{-1}.\text{kg}^{-1}$; Hansen & Beck, 1988) in both living cells (Charrier *et al.*, 2013b) and the apoplasm (Lintunen *et al.*, 2018). Soil water deficits can indeed initiate the early stages of hardiness in Douglas-fir (Timmis & Tanaka 1976). However, it should be noticed that this effect is likely to be canceled during the transition from drought- to frost-exposed period, in case of a wet autumn period.

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

From the xylem/hydraulic point of view, frost-induced embolism is only generated when sap is under moderate tension (Mayr *et al.*, 2007). Freeze-thaw cycles will thus exacerbate the pre-existing tension promoting air seeding from vessels to vessels in dehydrated trees (Fig. 2B; Tyree & Sperry, 1989; Mayr *et al.*, 2007; Kasuga *et al.*, 2015). Drought episodes during the growing season lead to the reduction in vessel diameter (Lovisolo & Schubert, 1998; Beikircher & Mayr, 2009) that would result in higher resistance to FT embolism. However, a reduced level of non-structural carbohydrates would limit the ability of the tree to refill embolized vessels during winter via active mechanism (*e.g.* stem pressure; Améglio *et al.*, 2001). Even if xylem conduits were completely refilled, residual bubbles within the xylem would expand at lower tension if the tree is exposed again to drought after winter or at higher freezing temperature occurring late in the winter (*i.e.* after the winter refilling process), *via* the so-called fatigue (Christensen-Dalsgaard & Tyree, 2014). The main positive effect (*i.e.* decreasing the vulnerability to frost-induced embolism) therefore would lie in the higher ability of sap to supercool and therefore avoid the phase shift from liquid to ice and the resulting formation of air bubbles (Lintunen *et al.*, 2018).

Effect of frost on vulnerability to drought

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

324 summer in walnut.

325 Freeze/thaw-induced embolism and frost cracks increase the volume of air within the
326 xylem tissue, facilitating thus not only the entry of air into the conduits, but also the spreading
327 from conduit to conduit, through the punctuations of the vessels, leading to major losses in
328 hydraulic conductivity (Lens *et al.*, 2011; Li *et al.*, 2016). Lower hydraulic conductivity
329 would also limit plant transpiration, which should result in increased water use efficiency.
330 Depleting soil water content more slowly should thus delay drought onset and intensity.
331 However, at the stand scale, the competition to water resources from other tree individuals or
332 other plant species may delete this potential benefit.

333 Changes in the density and porosity of the pit membrane micro-fibrils that connect
334 neighboring xylem conduits induced by frost have been observed for different species when
335 evaluating defrosted wood samples (Li *et al.*, 2016). Whether such changes in the pit
336 membranes affect the vulnerability to drought-induced embolism formation is still unclear.
337 These conditions are typically observed at high elevation during clear nights and days, when
338 minimum night temperatures co-occur with high daily transpiration (Charrier *et al.*, 2017).
339 Such conditions may induce the red belt syndrome in sensitive conifer species. When soil
340 temperature is too low (but not necessarily frozen), the water uptake becomes very limited
341 (Améglio *et al.*, 2002). Warm and dry air can thus promote the aboveground dehydration and
342 hydraulic failure. This type of phenomenon is typical of late winter conditions at high
343 altitudes (Mayr *et al.*, 2006; Charrier *et al.*, 2017; Earles *et al.*, 2018). Furthermore, when the
344 winter precipitation regimes change from solid to liquid, the soil will reach lower
345 temperature, damaging the root system more frequently. This would alter the whole tree
346 hydraulic architecture by decreasing water supply and decreasing the ability to recover,
347 ultimately increasing xylem embolism (Cox & Malcom, 1997; Zhu *et al.*, 2000). This
348 syndrome has been identified as pre-disposing dieback for Yellow birch (Cox & Zhu, 2003).

One important aspect to consider regarding frost damages is the temporality, higher damages being observed during the elongation period of new growth units in spring (Chaar & Colin, 1999). By destroying the developing organs late frost damage (leaf, flowers and new shoots) would immediately reduce the transpiration (water output) and the photosynthesis (carbon input), but, on a longer term, the remobilization of carbon reserves to reconstruct annual organs may result in a significant carbon depletion (Wargo 1996). Although under non-stressing circumstances carbon reserves are quickly restored, under drought stress we could expect a significant limitation in the ability of the tree to maintain the stomata open and related carbon input in depleted trees (O'Brien *et al.*, 2014). Furthermore, assuming an increase in resistance to drought-induced embolism along the growing season, the newly formed xylem will be more vulnerable whereas drought exposure will be higher (Charrier *et al.*, 2018a). Furthermore, leaves would expand later in the season, when the probability of drought exposure (*i.e.* high evaporative demand combined with limited soil water availability) is higher although earlier soil water uptake has been limited.

Potential interaction between vulnerability to constraints and phenology

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

In spring, ecodormancy release and growth (both primary and secondary) are accelerated

374 by warm temperature, in some species in interaction with photoperiod (Laube *et al.*, 2014). At
375 the end of the growing season, growth cessation is mainly controlled by decreasing
376 photoperiod, whereas budset and dormancy by warm and low night temperatures, respectively
377 (Svystun *et al.*, 2019). Endodormancy is subsequently released by chilling temperature.
378 Among these different stages, we can distinguish two different processes: temperature-
379 promoted processes (*i.e.* occurring at a rate proportional to temperature such as ecodormancy
380 release, primary and secondary growth, and budset) and signal-limited processes (*i.e.*
381 occurring after a specific threshold has been reached such as growth cessation, endodormancy
382 induction, leaf fall), which are indirectly affected by photoperiod and temperature. However,
383 the effect of abiotic stress on the different phenological processes and, furthermore, how
384 carry-over effects can modulate pluri-annual dynamics, have not been explored yet (Fu *et al.*,
385 2014). Thus, depending on the timing of the previous stage, the onset of the following ones
386 will be affected, leading to unpredictable behavior (Hänninen & Tanino, 2010). For instance,
387 an increase in temperature would hasten or delay growth cessation depending on the diurnal
388 dynamics (see Rohde *et al.*, 2011 and Kalcsits *et al.*, 2009, respectively), affecting the
389 subsequent stages (budset, endodormancy and budburst; Fig. 4). Leaf senescence timing is
390 positively correlated with budburst timing once removing the influence of autumn
391 temperature (Fu *et al.*, 2014). This carry-over effect is, however, of second order (Liu *et al.*,
392 2019) and potentially hidden by the prominent role of environmental variables such as
393 temperature and photoperiod (Vitasse *et al.*, 2009). Such an interacting process has been
394 incorporated in a leaf senescence model (Delpierre *et al.*, 2009) by modulating the cold-
395 temperature sum leading to leaf senescence by the budburst date (Kennan & Richardson,
396 2015).

397 Drought stress affects radial (*i.e.* secondary) growth but its effects on primary growth is
398 relatively unexplored. Drought exposure can thus significantly hasten the primary growth

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

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

subsequent photosynthesis.

Conclusion and perspectives

Exposure to drought and frost constraints has a potential feedback on the sensitivity to future constraints by affecting physiological components such as non-structural carbohydrates and water balance (Fig. 2). However, previous exposure may also alter the rate of the future response through memory effect via accumulation of regulatory proteins, transcription factors or histone methylation (Bruce *et al.*, 2007; Walter *et al.*, 2013). Although woody plants have to face multi-annual constraints, these mechanisms have been more thoroughly studied at relatively short time scale (up to one week) and considering only one constraint (*i.e.* drought or frost). To specifically deal with the interaction between constraints, we need to i) develop a systemic approach at the plant scale integrating ontogenic and histological differences as well as the different physiological processes involved (water use, carbon uptake, annual cycle); and ii) develop a multi-colinearity approach aimed to evaluate the crossing effects between different constraints in the tree survival capacity both at short and a long time scale. Interesting insights have been brought by integrative studies, for instance, focusing on carbon availability and hydraulic failure facing drought (McDowell *et al.*, 2008). It is especially relevant to develop this type of approaches on different species exhibiting contrasted combinations of drought and frost tolerance, including provenances originating from the entire species' distribution range (core and edges) to unravel local adaptations (Kreyling *et al.*, 2014). The effect of different successive and concomitant constraints at different periods of the year should help to develop deterministic relationships between different physiological variables and processes in response to each of them. Improving the descriptive range of these interrelations would subsequently allow quantitative and dynamic description of drought and frost resistance integrating the life history of the tree. This is a pre-requisite to improve mechanistic models simulating these interacting processes in order to predict accurately the

449 effect of cumulative stress on tree physiology and survival as mentioned Frame 3..

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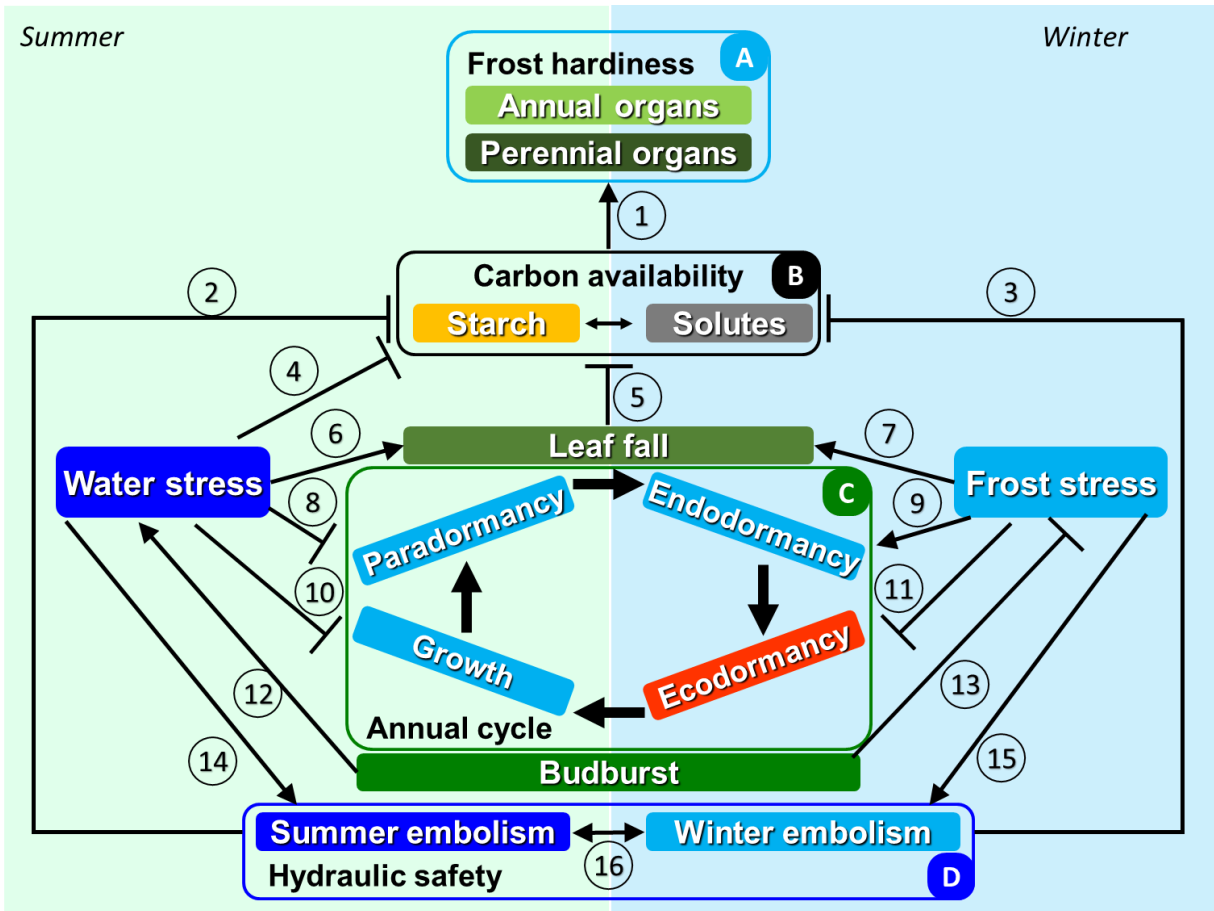
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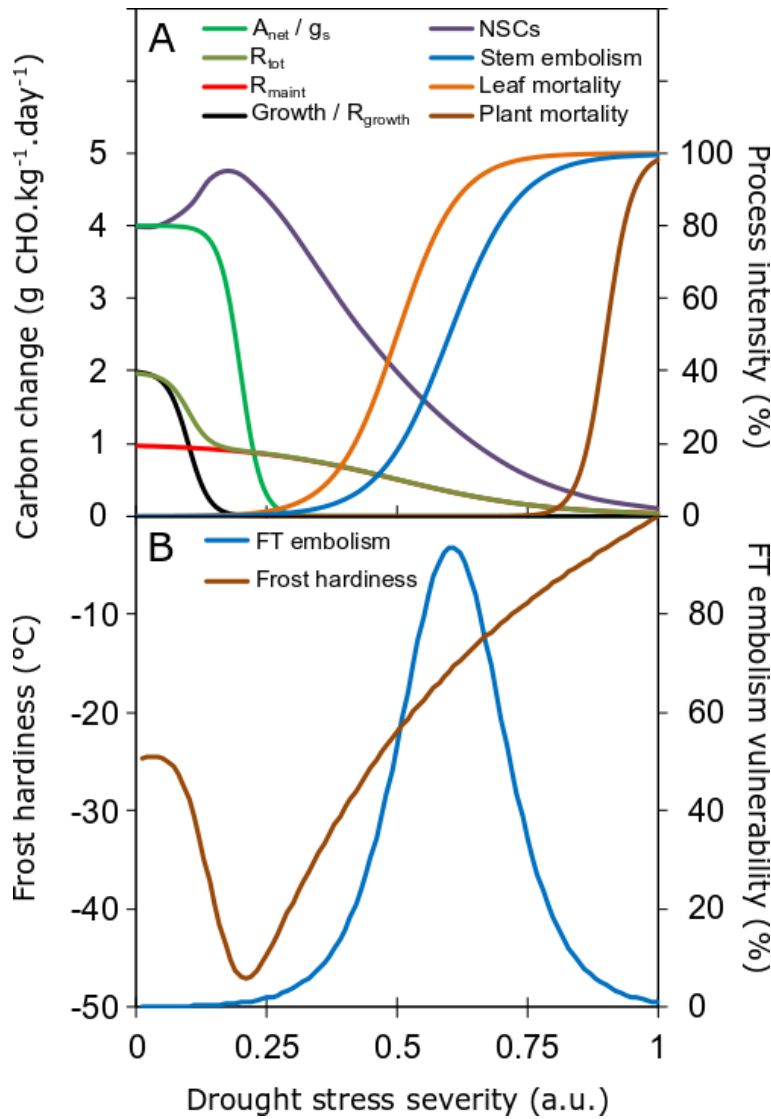
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Figure 1. Positive (arrow) and negative (bars) effects of water stress (mainly during summer period) and frost stress (mainly during winter period) on three functional components, namely carbon status, annual cycle and hydraulic architecture. The numbers 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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916 **Figure 2. A.** Processes affected by drought stress severity (Photosynthesis A_{net} , stomatal
 917 conductance g_s , respiration (growth R_{growth} , maintenance R_{maint} and total R_{tot}), non structural
 918 carbohydrates (NSCs), stem embolism, leaf and plant mortality. Growth being more sensitive
 919 to water stress than photosynthesis, and respiration, the NSCs pool initially increases
 920 (McDowell, 2011). After photosynthesis declines, NSCs decline whereas leaf mortality,
 921 embolism and plant mortality increase (Charrier et al., 2018). **B.** Potential effect generated by
 922 drought stress on frost hardiness of living cell (through the non-linear relation between NSC
 923 and water content) and vulnerability to freeze-thaw induced embolism.

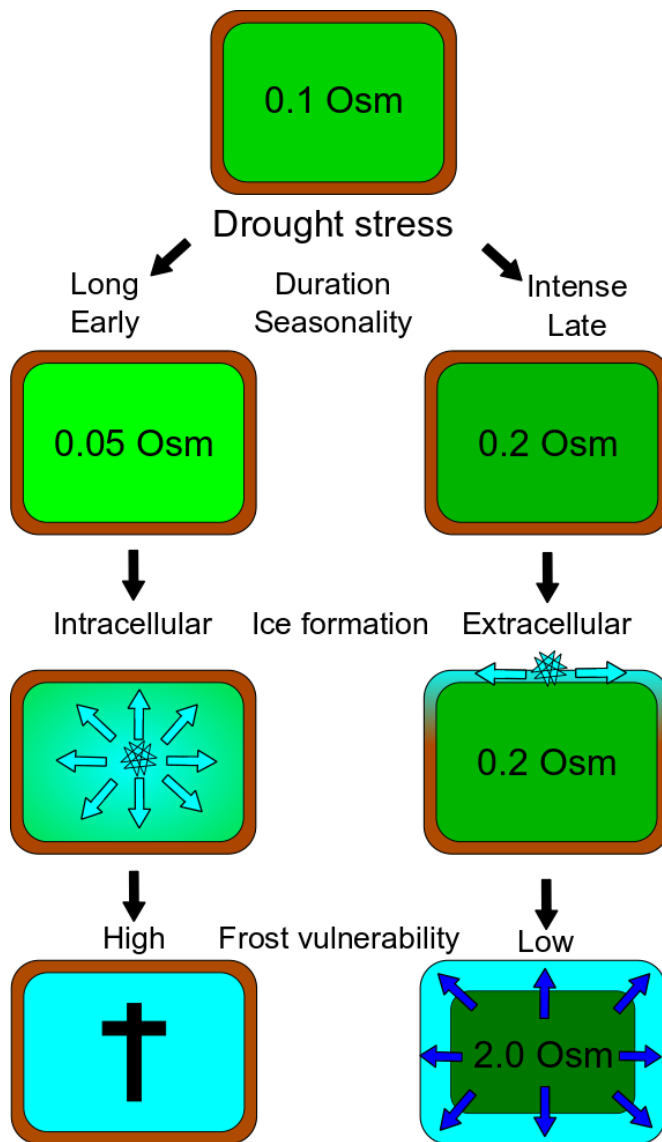


Figure 3. Alternative pathways that would explain why frost vulnerability may differentially be affected by previous drought exposure depending on how the ratio between soluble carbohydrates and water content have been affected.

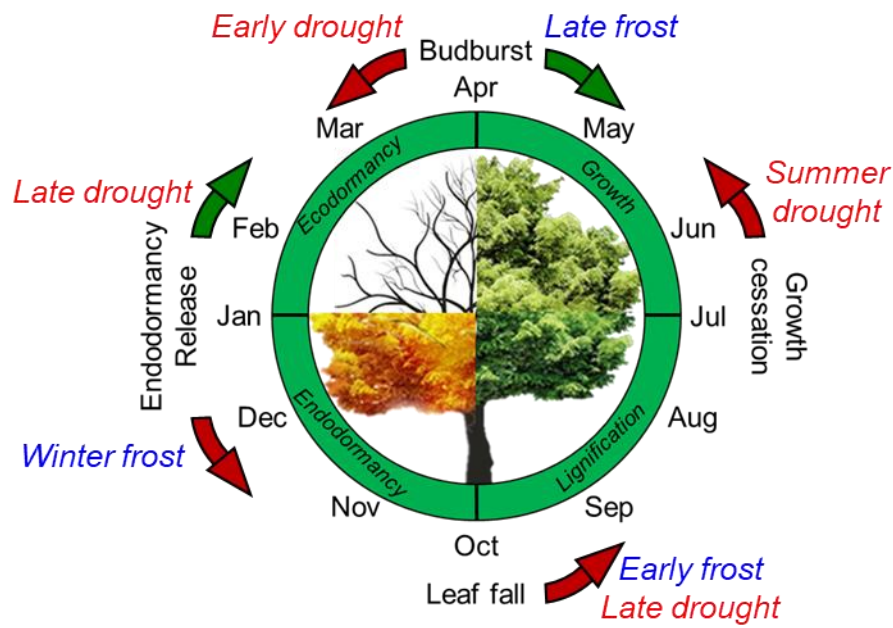


Figure 4. Typical seasonal phenological stages in a deciduous tree in Northern hemisphere and potential effect of drought and frost stress on hastening (brown arrow) or delaying (green arrow) phenological stages depending on the timing.