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Guillaume Charrier[1], Nicolas Martin-StPaul[2], Claire Damesin[3], Nicolas Delpierre[3], Heikki Hänninen[4], Jose M. Torres-Ruiz[1], Hendrik Davi[2]

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

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

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

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

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ABSTRACT

In temperate, boreal and alpine areas, the edges of plant distribution are strongly affected by abiotic constraints. For example, heat waves and drought are major constraints at low latitude and elevation while cold and frost are key factors at high latitude and elevation. Over the next few decades, climate variability is expected to increase, enhancing the probability of extreme events and thus the potential stress imposed by abiotic constraints. Moreover, the likelihood of co-occurring and successive constraints, such as drought and frost, could increase in parallel. It is likely that initial exposure to a first constraint would affect the vulnerability to a subsequent one. Three integrative physiological processes, namely water status, carbon status and the timing of phenological stages, are crucial to understanding how trees will respond to these stress factors. Although these processes have largely been studied alone, in response to a single constraint, their interaction has rarely been investigated. In this paper, we have examined how water and carbon status interact with the growth cycle and affect both the vulnerability and the exposure to climatic constraints via two different focuses: (i) How would the interaction of frost and drought 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 frost and drought 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. This vulnerability can also be modulated by a shift in the annual phenological cycle induced by a previous constraint. Furthermore, we have identified significant gaps of knowledge in the ecophysiological tree response to interacting stresses based on three major points: (i) the spatio-temporal variation in carbohydrate composition, fluxes and allocation in relation to environmental drivers, (ii) the spatio-temporal variation in water content, water and osmotic potentials, (iii) the modulation of

phenological processes in response to stress. This framework can help to improve the current process based models and to identify interactions that needs to be better described in order to obtain a more quantitative and dynamic view of drought and frost vulnerabilities integrating the life history of the individual plant.

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

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 entire range, abiotic factors can be highly relevant at the rear and leading edges of the distribution (Hampe & Petit, 2005). Within the boreal, alpine, temperate and Mediterranean areas, plants are likely to be exposed to both drought and frost stress, although it may not happen every year. 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 usually limit the plant distribution (Gusta *et al.*, 1983; Körner, 1998; Larcher, 2005; Charrier *et al.*, 2013a). Along a latitudinal gradient within the niche of a species, drought and frost constraints are clearly separated, *i.e.* episodes of mild or severe drought are observed on the rear edge during the summer, and frost stress on the leading edge during the 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, 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 & Hänninen, 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 composition 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, ecologists 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 ultimately 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 climatic hazards (*e.g.* drought or frost constraint), stress exposure (*e.g.* low water potential or organ temperature) and tree vulnerability (*e.g.* low resistance to embolism or insufficient frost hardiness; Bréda & Peiffer, 2014). The prediction of emerging risks therefore needs accurate assessments of (i) the exposure to a given abiotic constraint (type, intensity, duration and frequency) and (ii) the spatio-temporal patterns of vulnerability and subsequent damages. The timing of critical phenological stages (*e.g.* bud burst date and leaf full expansion date with respect to frost and drought, respectively) would thus modulate risk and subsequent damages. How the exposure to a given abiotic constraint at a given time instant would influence the vulnerability to the same or a different constraint in the future is a critical issue that has been only rarely investigated (Miao *et al.*, 2009, Anderegg *et al.*, 2013; Batlori *et al.,* 2017; Hossain *et al.*, 2019).

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

This paper summarizes the state-of-the-art of tree responses to drought and frost constraints from the cellular to the individual scale and subsequent damages with the aim of emphasizing the undervalued role of their interactions at the short term scale (*i.e.* from the day to the year). Furthermore, different communities are interested in single process or sets of processes (*e.g.* hydraulic in response to drought, frost hardiness and damages, phenological cycles,...). The influence of previous stress factors on plant vulnerability, is mainly relevant on woody plants and will be mainly explored at the annual level through two main questions (i) How would the interaction of drought and frost constraints modulate the vulnerability to a subsequent constraint? (ii) How do vulnerability to a given constraint and phenology interact? Addressing these questions will provide novel information about the interaction between climate and trees from a wider, multifactorial and

temporal perspective. This framework would be crucial to understand and predict local mortality

dynamics and ultimately to improve actual species distribution models.
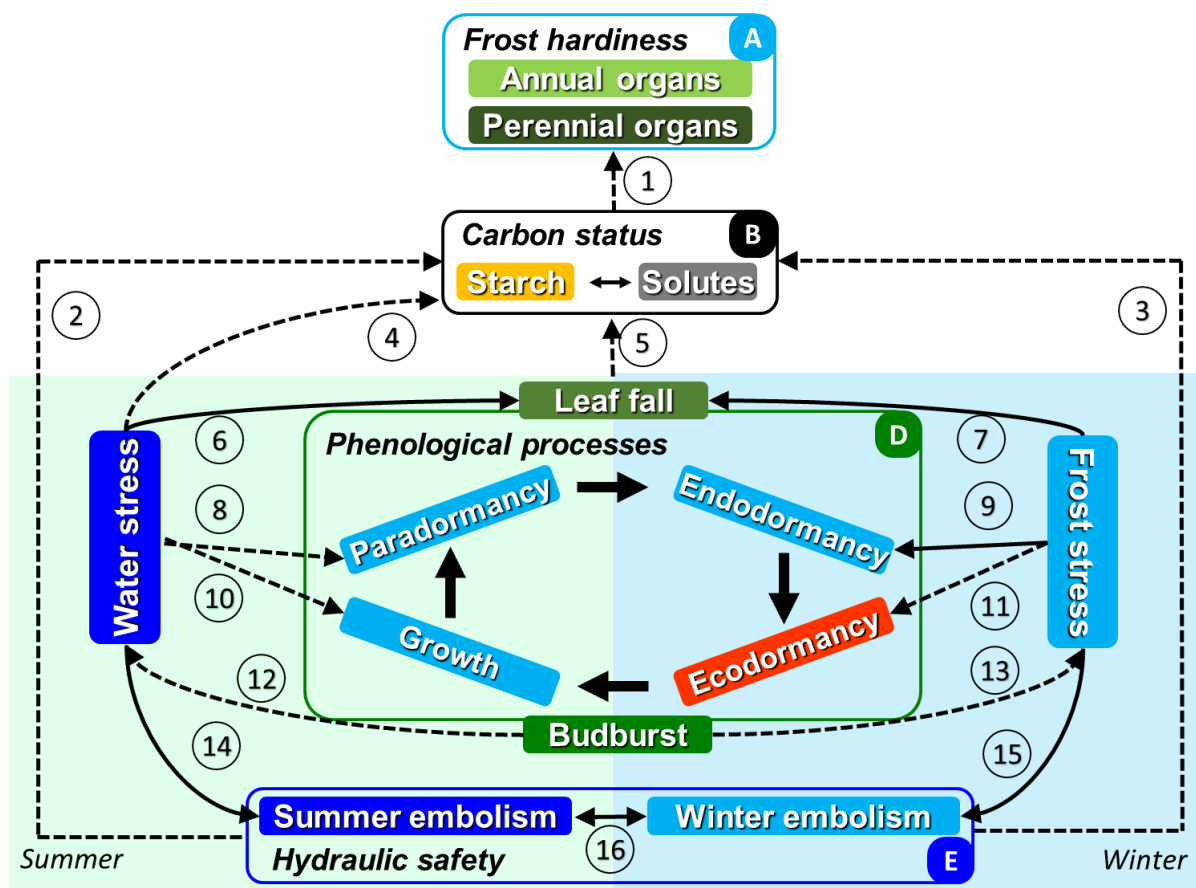
Figure 1. Involved processes affected by water (mainly during summer period) and frost stress (mainly during winter period). Positive (solid) and negative (dashed) effects of stresses are expected on three functional components, namely carbon status, phenological processes and hydraulic safety. Positive relations between timing events (phenological stages such as leaf fall and budburst) and other processes indicate that earlier event induce higher level, and vis-versa). All represented processes are interrelated either directly and indirectly. Both winter and summer stresses affect the same processes either synergistically or antagonistically. Main effects are reported, although non-linear and thresholds could make the response more complex. 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. Hänninen, 1991; 14. Sperry *et al.*, 1998; 15. Charra-Vaskou *et al.*, 2016; 16. Charrier *et al.*, 2014).

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). From a physical perspective, both drought and frost constraints are related to a limited liquid water availability. Similar damages are generated at both the cellular (*i.e.* plasmolysis and cell lysis; Levitt, 1980; Siminovitch & Cloutier, 1983) and vascular levels (*i.e.* cavitation and embolism when a critical level of water potential is reached; Sperry & Sullivan, 1992; Charrier *et al.*, 2014). A critical factor in the response to both stresses is the accumulation of solutes to maintain a solvation layer around macromolecules. 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), inducing, for instance, the synthesis of dehydrins (Welling *et al.*, 2002). Interestingly, the molecular response to both constraints 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).

The onset of drought-induced damages is triggered by hydraulic failure and involves the interaction between water and carbon status (Frame 1 and reviews from Choat *et al.*, 2018; Martinez-Vilalta *et al.*, 2019, for extensive description of drought stress syndromes), as frost-induced damages relies on (Charrier *et al.*, 2013b). At the vascular level, species more vulnerable to winter embolism seem to be also more vulnerable to summer embolism (Charrier *et al.*, 2014). This may be related to the ability

of air to propagate within xylem under high frost- or drought-related tension through bordered pits; Cochard *et al.,* 1992). Despite current controversies on the ability of plant to restore their hydraulic conductivity under tension (*e.g.* Zwieniecki & Holbrook, 2006; Brodersen *et al.*, 2010; Lamarque *et al.*, 2018), many tree species are able to restore their hydraulic conductivity under positive pressure, for instance to supply growth in spring (Hacke & Sauter, 1996; Cochard *et al.*, 2001). One refilling mechanism involves osmoregulation via solutes compounds generating low osmotic potential in the lumen of the vessels during winter (Ewers *et al.,* 2001; Améglio *et al.,* 2002), and eventually summer (Nardini *et al.,* 2011). A refilling mechanism has not yet been identified for conifers, but there is evidence that refilling likely occurs within several species (Sperry & Sullivan 1992; Sperry *et al.,* 1994; Mayr *et al.,* 2003; 2014). Positive sap pressure has also been measured at the whole plant scale from the pressurization of the root system, notably in woody lianas (Priestley 1920; Sperry *et al.,* 1987; Charrier *et al.,* 2016) and herbs (Gleason *et al.,* 2017).

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 (maintaining high water potential; Fig. 1) by a tight control of both inwards (*e.g.* deep rooting) and outward water fluxes (*e.g.* stomatal closure, leaf shedding, low cuticular transpiration; Choat *et al.*, 2018; Martin-StPaul *et al.*, 2017). Maintaining xylem hydraulic function under high tension is also a critical trait avoiding dehydration, and ultimately desiccation, of living tissues (Fig. 1 #14; Sperry *et al.*, 1998, Brodribb & Cochard, 2009). However, ontogenic changes in xylem vulnerability to embolism may modulate thus the tree's resistance across seasons (Charrier *et al.*, 2018b).

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

Frame 2: Mechanisms leading to frost-induced damages

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

Embolism arising from the freezing of xylem sap and high tension arising from drought may interact. Such repeated freeze-thaw and drought events may lead to reduced embolism resistance (Mayr *et al.*, 2003; 2007). This is because the initial exposure to freezing temperatures may result in the deformation of the ultrastructure of bordered pit membranes, which are critical for preventing the spread of gas from one conduit into another (Christensen-Dalsgaard & Tyree 2014).

However, despite high xylem embolism has been suggested to cause plant death (Brodribb & Cochard, 2009), higher embolism than 50% and, even 90%, is frequently observed and recovered in over-wintering trees without impairing their survival, which suggests that it does not constitute a lethal threshold by itself (Sperry *et al.*, 1994; Mayr *et al.*, 2003; 2006; 2019; Charrier *et al.*, 2013a). High xylem embolism may be an empirical correlate with plant death, rather than a physiological cause (Mayr *et al.*, 2019).

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

Two alternative hypotheses, although not mutually exclusive, should be taken into account to predict the interaction between stress factors. Legacy is considered as a passive change of physiological status in response to previous stress exposure. We suggest that the modulation of either carbon or water pools would result in the modulation of vulnerability (McDowell *et al.*, 2008). Altered water and carbon status would generate potential feedback physiological loops and trade-offs during successive abiotic stress exposures (legacy effect). Memory (aka priming) relates to a defensive plant response to either biotic or abiotic stress (Savvides *et al.,* 2016), and is considered an active process that shifts or enhances the basal of resistance, but at the cost of reducing primary metabolism such as growth (Bruce *et al.*, 2007; Walter *et al.,* 2013; Martinez-Medina *et al.,* 2016). Memory requires pre exposure to the stress factor in contrast with acclimation, which occurs prior to stress exposure. In long living organisms such as trees, the concept of memory is uncommon 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. Such an increase in solute concentration (*i.e.* lower osmotic potential) would decrease the freezing point ($-1.86°C.mol^{-1}.kg^{-1}$;

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 frost hardiness in Douglas-fir (Timmis & Tanaka, 1976). This effect is likely to be canceled during the transition from drought- to frost-exposed period, in case of a wet autumn period. However, changes in the water regime, as predicted by future climate predictions, could cause this dry summer and autumn conjunction to occur more regularly.

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. 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 (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 drought stress level in relation to carbon depletion (Fig. 3 right Wong *et al.*, 2009; Galvez *et al.*, 2013; Fig. 3).
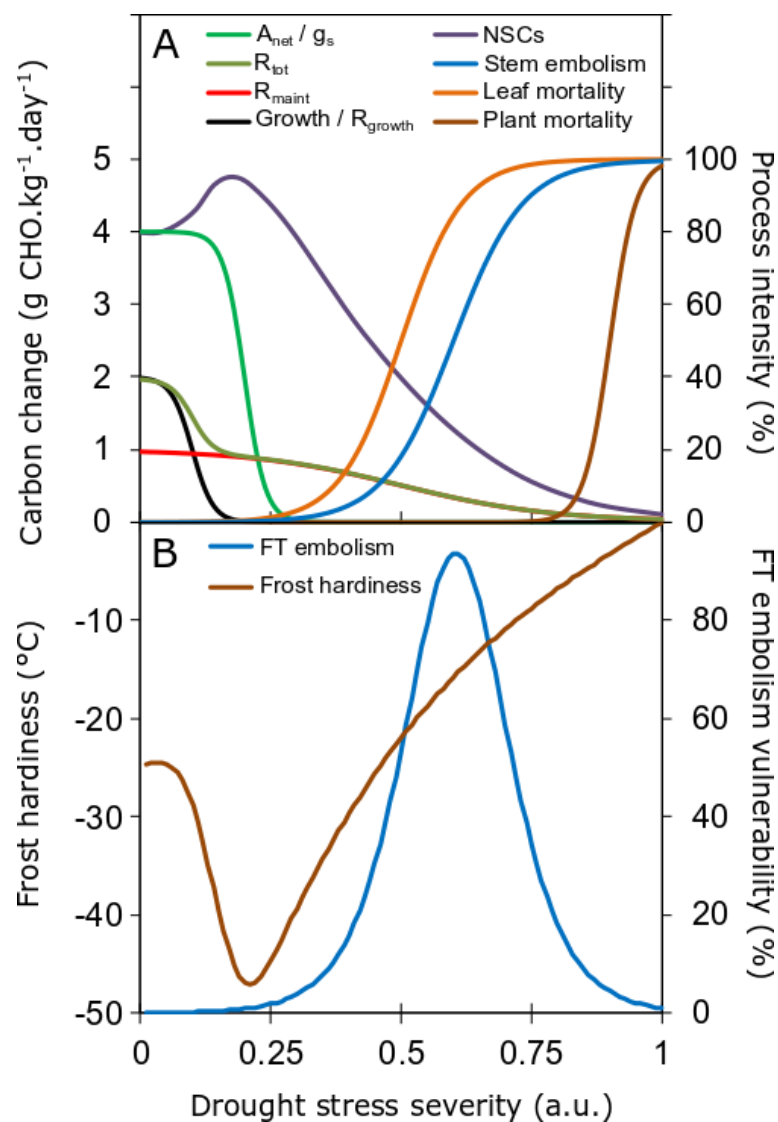
Figure 2. A. Processes and pools affected by drought stress intensity (Photosynthesis A_{net}, stomatal conductance gs, respiration (growth R_{growth}, maintenance R_{maint} and total R_{tot}), non structural carbohydrates (NSCs), stem embolism, leaf and plant mortality. Growth being more sensitive to 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.*, 2018b). **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.
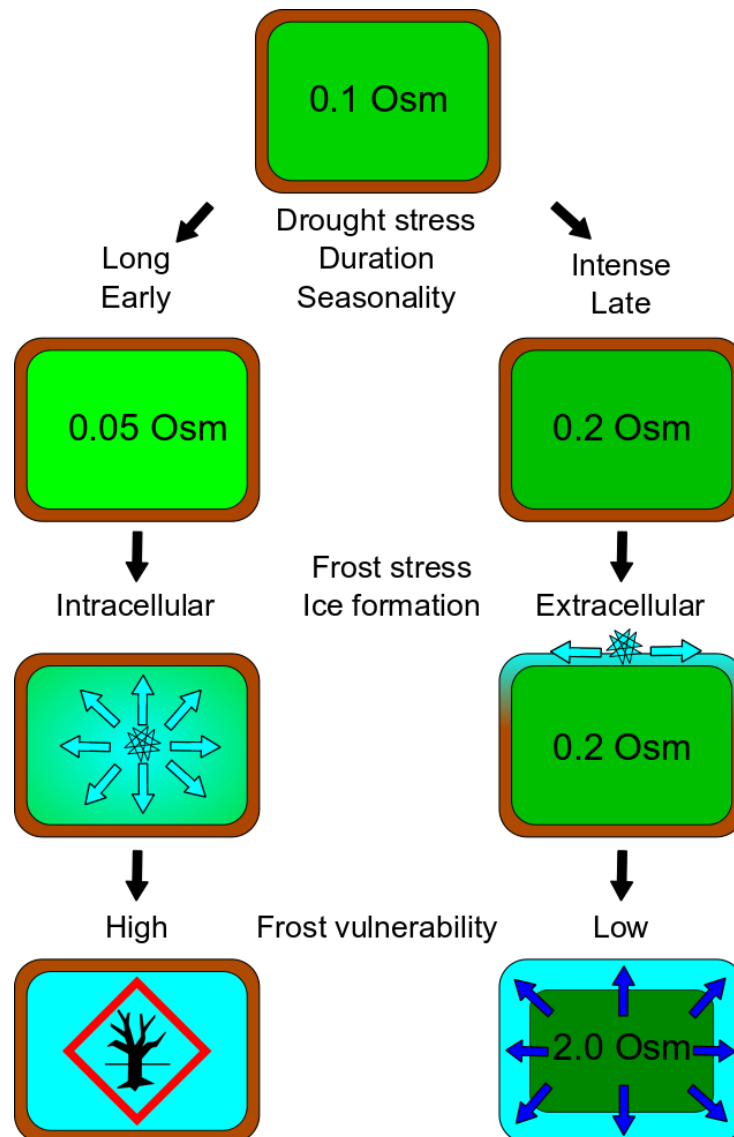
Figure 3. Alternative pathways that would explain why contrasted frost vulnerabilities are observed after previous drought exposure. Osmolarity of intracellular sap, controlled notably by the ratio between soluble carbohydrates and water content, could be considered as the main driver. On the right path, intense and/or late drought is expected to concentrate cell sap, increasing the probability of extra cellular ice nucleation. The low chemical potential of ice would pull water, further increasing cell osmolarity. On the left path, long and/or early drought prevents timely increase in solutes, through reduction in carbon reserves. Intracellular freezing through is expected to happen more often and at higher freezing temperature, inducing cellular damages.

From the xylem/hydraulic point of view, the resulting vulnerability from 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 freeze-thaw induced 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). 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. Major gaps of knowledge remain with respect to frost exposure onto drought vulnerability, although assumptions can be made. 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.* (2018a) highlighted a significant negative correlation between autumnal frost damages and fruit yield the following summer in walnut.

Low, but not necessarily frozen, soil temperature limits root water uptake (Améglio *et al.*, 2002). Thanks to thermal inertia, the combination of cold soil and warm and dry air can promote aboveground dehydration and hydraulic failure. This phenomenon, called winter drought, is typical

of late winter conditions at high altitudes (Mayr *et al.*, 2006; Charrier *et al.*, 2017; Earles *et al.*, 2018). Winter drought- and freeze/thaw-induced embolism increase the volume of gas within the xylem conduits, therefore facilitating the spreading of air through conduits (Lens *et al.*, 2011). Furthermore, higher porosity of the pit membrane following freeze-thaw events has been observed for different species when evaluating defrosted wood samples (Li *et al.*, 2016). Such changes in the pit membrane thickness is likely to increase drought-vulnerability through air seeding (Charrier *et al.*, 2014; Li *et al.*, 2016). Such an increased vulnerability would only remain if the embolism is not refilled.

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

Lower hydraulic conductivity, from winter embolism and limited spring refilling would limit hydraulic conductance of the whole plant. Under relatively high evaporative demand (high VPD), it should result in lower leaf water potential and stomatal conductance. As partially open stomata allow sufficient CO_2 diffusion while limiting the amount of transpired water, it is likely that water use efficiency would be increased. Soil water content would be depleted more slowly which should thus delay drought onset and intensity. The same dynamic is expected after late frost damages, as leaves would expand later in the season. However, at the stand scale, the competition for water resources

from other tree individuals or other plant species (less vulnerable to winter embolism or frost damages) may eliminate this potential benefit.

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.*, 2018b).

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).

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

role of environmental variables such as temperature and photoperiod (Vitasse *et al.*, 2009). Such an interacting process has been incorporated in a leaf senescence model (Delpierre *et al.*, 2009) by modulating the cold temperature sum leading to leaf senescence by the budburst date (Keenan & Richardson, 2015).
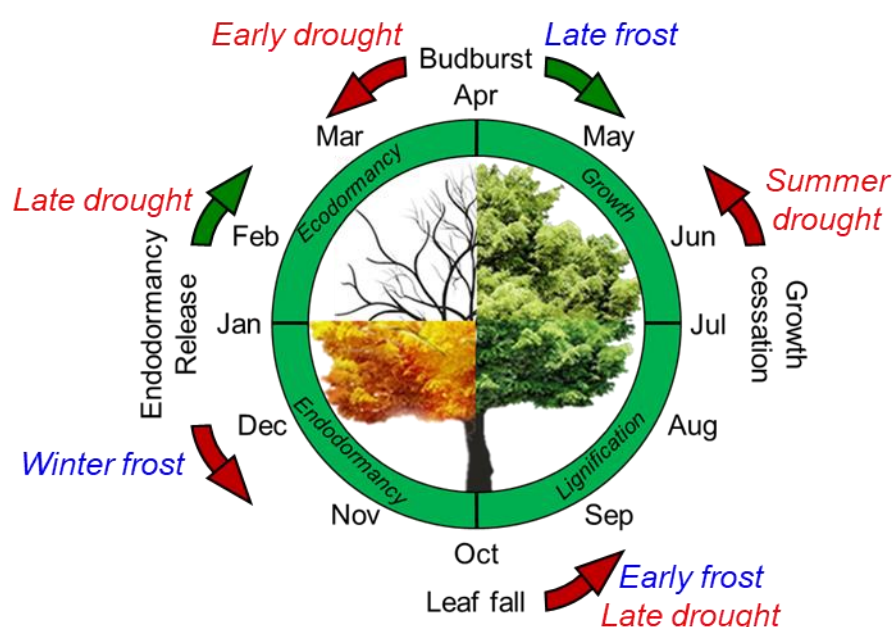
Figure 4. Hastening (brown arrow) or delaying (green arrow) phenological stages in response to drought and frost events. At the center is presented the typical seasonal phenological stages in a deciduous tree in Northern hemisphere and, outside the potential effects of drought and frost stress depending on their timing. It should be noted that stress factors can have a lagged effect onto phenology (*e.g.* late drought in late summer delaying winter dormancy release). Early and late drought typically happen in May-June and September, respectively. Early and late frost typically happen in September-October and April-May, respectively.

Drought stress affects radial (*i.e.* secondary) growth but its effects on primary growth is relatively unexplored. Drought exposure can 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 events 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; 2020). During late summer, after growth cessation and dormancy induction, frost exposure may promote 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.

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

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

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

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

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

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

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

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

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

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

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

Conclusion and perspectives

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

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

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 carbon and water use coupled with the phenological dynamic; and ii) develop a multi-colinearity approach aimed to evaluate the interactions 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 (*e.g.* 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. It would simulate the life history of the tree and modulated response through legacy and memory effects as a function of the previous level of damages, water and carbon contents. Improving the descriptive range of these interrelations at the individual and population scales would subsequently allow quantitative and dynamic description of drought and frost resistance. This would improve existing mechanistic models simulating these interacting processes in order to predict accurately the effect of cumulative stress on tree physiology and survival.

Author contributions

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

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Conflict of interest disclosure

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

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