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REVIEW PAPER

Interaction of drought and frost in tree ecophysiology: rethinking the timing of risks

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Abstract

• ***Key message*** **The increase in climate variability is likely to generate an increased occurrence of both frost-induced and drought-induced damages on perennial plants. We examined how these stress factors can potentially interact and would subsequently affect the vulnerability to each other. Furthermore, we discussed how this vulnerability could be modulated by shifts in the annual phenological cycle.**

Context The edges of plant distribution are strongly affected by abiotic constraints: heat waves and drought at low latitude and elevation, cold and frost at high latitude and elevation. The increase in climate variability will enhance the probability of extreme events and thus the potential interaction of stress factors. The initial exposure to a first constraint may affect the vulnerability to a subsequent one.

Aims Although three integrative physiological processes, namely water balance, carbon metabolism and the timing of phenological stages, have largely been studied in the response of trees to a single constraint, their interaction has rarely been investigated. How would the interaction of frost and drought constraints modulate the vulnerability to a subsequent constraint and how vulnerability to a given constraint and phenology interact?

Conclusion We suggest that the interaction between frost and drought constraints should in the short-term influence water balance and, in the longer term, carbon metabolism, both consequently affecting further vulnerability. However, this vulnerability can be modulated by shifts in the annual phenological cycle. Significant gaps of knowledge are reported in a mechanistic framework. This framework can help to improve the current process-based models integrating the life history of the individual plant.

Keywords Abiotic stress · Acclimation · Carbon availability · Drought · Frost · Phenology · Risk assessment · Tree ecophysiology

1 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 evolutionary change (Erwin 2009; Klanderud et al. 2015). Although biotic factors drive population dynamics in the entire range, abiotic factors can be highly relevant at the rear and leading edges of the distribution (Hampe and 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;

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Ruiz-Benito et al. 2013). At the leading edge (high latitude and elevation), cold and freezing temperatures usually limit plant distribution (Gusta et al. 1983; Koerner 1998; Larcher 2005; Charrier et al. 2013a). Along a latitudinal gradient within the niche of a species, drought and frost constraints are often separated; i.e., episodes of mild or severe drought are observed on the rear edge mostly during the summer, and frost stress on the leading edge during the autumn (early frosts), winter, or spring (late frosts). 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 and Thuiller 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 and Charra-Vaskou 2007; Charrier et al. 2017). Drought and frost may also take place successively at the same location, affecting plant health and resistance to following stress factor (Kreyling et al. 2012). 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 and 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 and Badeck 2005; Menzel et al. 2006; Fu et al. 2014; Keenan and Richardson 2015). On the other hand, a substantial deterioration in various physiological processes is expected to be induced by 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 frost events (Leinonen and 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, 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 (IPCC 2014; Ummenhofer and Meehl 2017). 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 and 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 (e.g., perennial tissues facing early and winter frosts vs. flowers and flushing buds facing late frosts). 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; Batllori 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 and 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 and Trumbore 2016). The individual responses of each tree ecophysiological process have been integrated into process-based models such as PHENOFIT (Morin and Chuine 2005), SUREAU (Martin-StPaul et al. 2017), or CASTANEA (Dufrêne 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 and subsequent damages from the cellular to the individual scale with the aim of emphasizing the undervalued role of their interactions at the short-term scale (i.e., from day to year). In fact, so far, the different scientific communities have only focused in one of these processes at a time (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 perennial 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 will be crucial to understand and predict local mortality dynamics and ultimately to improve current species distribution models.

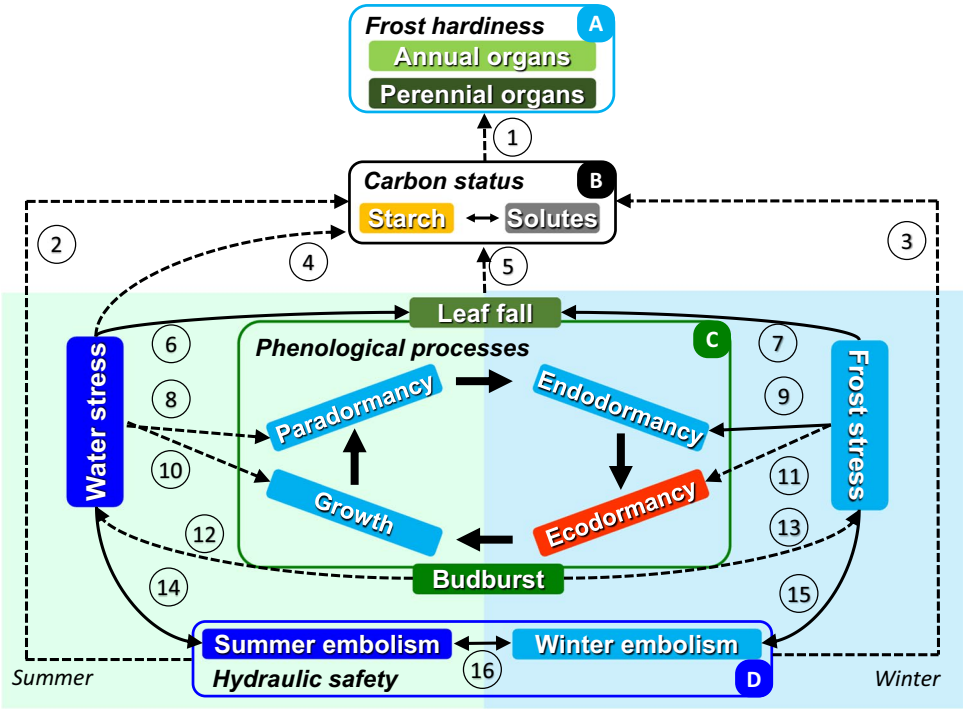

Fig. 1 Involved processes affected by water (mainly during the summer period) and frost stress (mainly during the winter period). Positive (solid) and negative (dashed) effects of stresses are expected on three functional components, namely carbon metabolism (B), phenological processes (C), and hydraulic safety (D). Positive relations between timing events (phenological stages such as leaf fall and budburst) and other processes indicate that earlier event induces higher level, and vice 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)

2 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 (Frames #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 and Cloutier 1983) and vascular levels (i.e., cavitation and embolism when a critical level of water potential is reached; Sperry and 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 and 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 and Shinozaki 1994).

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 to avoid dehydration, and ultimately desiccation, of living tissues (Fig. 1 #14; Sperry et al. 1998, Brodribb and Cochard 2009). However, ontogenic changes in xylem vulnerability to embolism may modulate tree 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 the 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 deplete (Fig. 2; McDowell et al. 2008). Finally, two pools, namely solutes, including carbohydrates, and water, interact to maintain a turgor and a solvation layer around biomolecules avoiding critical denaturation and related cellular death (Bowman and Roberts 1985; 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), 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 redistribute water towards nucleation sites (Ball et al. 2006; Mayr and 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 cannot 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 them. Being the main substrate and energetic source, non-structural carbohydrate content in the autumn is thus tightly related to maximum frost resistance reached during the winter (Fig. 1 #1; Palonen and Buszard 1997; Morin et al. 2007; Charrier et al. 2013a; 2018c). As non-structural carbohydrate 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 the winter.

The onset of drought-induced damages is triggered by hydraulic failure and involves the interaction between water balance and carbon metabolism (Frame 1 and reviews from Choat et al. 2018; Martinez-Vilalta et al. 2019, for extensive description of drought stress syndromes), as for frost-induced damages (Charrier et al. 2013b; 2015). 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-related or drought-related tension through bordered pits (Cochard et al. 1992). Despite current controversies on the ability of plant to restore its hydraulic conductivity under tension (e.g., Zwieniecki and Holbrook 2009; 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 the spring (Hacke and Sauter 1996; Cochard et al. 2001). In angiosperms, one refilling mechanism involves osmoregulation via solute compounds generating low osmotic potential in the lumen of the vessels during the winter (Ewers et al. 2001; Améglio et al. 2002), and eventually the 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 and 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).

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 and Tyree 2014). However, despite high xylem embolism has been suggested to cause plant death (Brodribb and 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 may make the tree more vulnerable to subsequent stresses; e.g., defoliated oaks would decline within 2 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 may cause trees to decline (Wargo 1996; Bréda and Peiffer 2014). Wood growth has been used as an integrative marker following frost and drought stress (Vanoni et al. 2016; d'Andrea et al. 2020). However, due to the difficulty of conducting long-term studies through the development of project-based funding, few studies have been able to accurately characterize the affected ecophysiological processes.

Two alternative processes, although not mutually exclusive, may help to predict the interaction between stress factors. Legacy is considered a passive change of physiological status in response to previous stress exposure. We suggest that the modulation of either carbon or water pools may result in the modulation of vulnerability (McDowell et al. 2008). Altered water balance and carbon metabolism would generate potential feedback physiological loops and trade-offs during successive abiotic stress exposures (legacy effect). Memory (also known as 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 resistance 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 that will modulate the rate of plant response through the accumulation of regulatory proteins, transcription factors, or histone methylation. In contrast, acclimation occurs in response to a change in environmental conditions prior to stress exposure or after 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 trees to it (Mayr et al. 2003; Tomasella et al. 2019; Zweifel et al. 2020). 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; Feichtinger et al. 2015; Sierra-Almeida et al. 2016). We attempted to draw a generic picture as both constraints affect the same physiological processes (Fig. 1).

3 Effect of drought on vulnerability to frost

After a drought episode, an increase in solute concentration (i.e., lower osmotic potential) will decrease the freezing point (-1.86 °C mol^{-1} kg^{-1}; Hansen and Beck 1988) in both living cells (Charrier et al. 2013b) and the apoplasm (Lintunen et al. 2018). Soil water deficit can indeed initiate the early stages of frost hardiness in Douglas fir (Timmis and Tanaka 1976). This effect is likely to be canceled during the transition from drought-exposed to frost-exposed period in case of a wet autumn period, as often observed in temperate and montane area. 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 are more sensitive to water stress than photosynthesis (Fig. 2a), and mild water stress is expected to promote transient increase in non-structural carbohydrates for moderate level of stress (McDowell 2011;

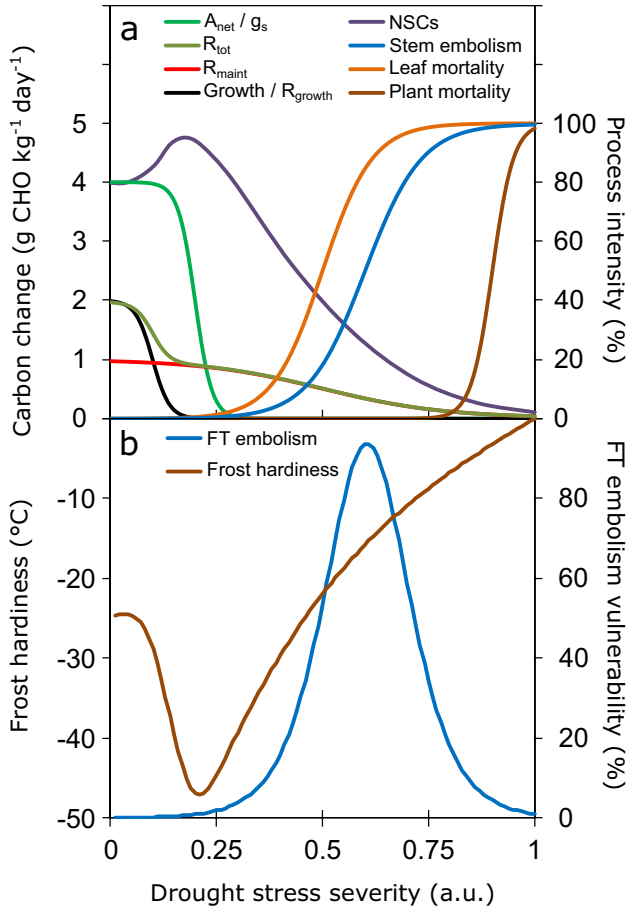

Fig. 2 A Processes and pools affected by drought stress intensity: photosynthesis A_{net}, stomatal conductance gs, respiration (growth R_{growth}, maintenance R_{maint}, and total R_{tot}), non-structural carbohydrates (NSCs), stem embolism, leaf and plant mortality. As growth is more sensitive to water stress than photosynthesis, and respiration, the NSC 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 (FT)-induced embolism

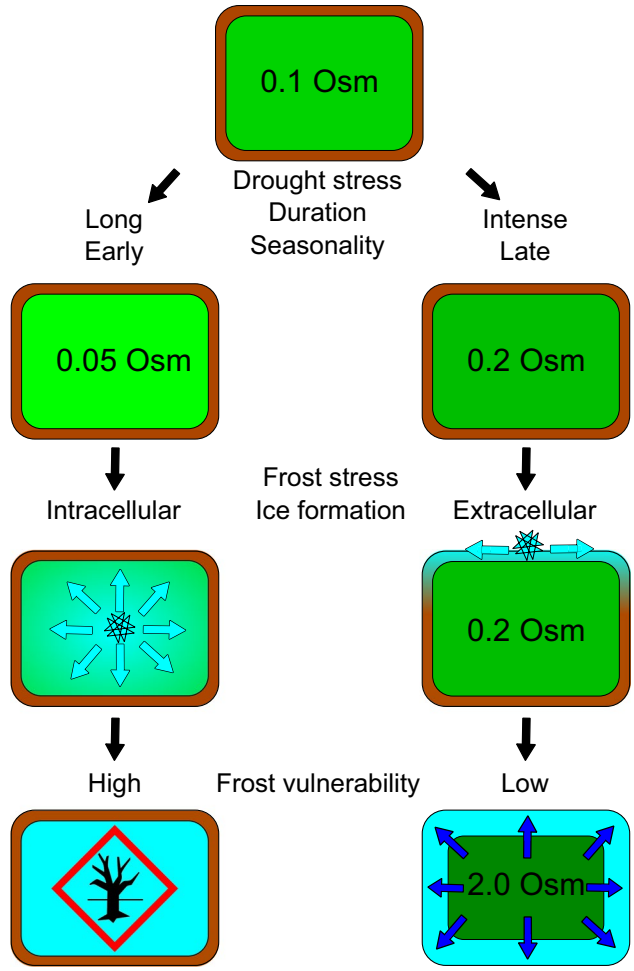

Fig. 3 Alternative pathways that would explain why contrasted frost vulnerabilities are observed after previous drought exposure. Osmolarity of intracellular sap, controlled notably by the ratio between soluble carbohydrates and water content, could be considered the main driver. On the right path, intense and/or late drought is expected to concentrate cell sap, increasing the probability of extracellular 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 is expected to happen more often and at higher freezing temperature, inducing cellular damages

Granda and 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 may be observed since higher drought stress level will result in lower carbon reserves and consequently reduced solutes (Fig. 3 right Wong et al. 2009; Galvez et al. 2013; Fig. 3).

From the xylem/hydraulic point of view, the resulting vulnerability to 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 vessel to vessel in dehydrated trees (Fig. 2b; Tyree and Sperry 1989; Mayr et al. 2007; Kasuga et al. 2015). Drought episodes during the growing season may lead to the reduction in vessel diameter (Lovisolo and Schubert 1998; Beikircher and Mayr 2009) that would result in higher resistance to freeze–thaw-induced embolism. However, a reduced level of non-structural carbohydrates after severe drought stress will limit the ability of the tree to refill embolized vessels during the winter via active mechanisms (e.g., stem pressure; Améglio et al. 2001). The main positive effect (i.e., decreasing the vulnerability to frost-induced embolism) therefore may 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).

4 Effect of frost on vulnerability to drought

Major gaps of knowledge remain with respect to frost exposure onto drought vulnerability, although assumptions can be made. Overall, frost damages before drought exposure may 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, we are not aware of 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 the walnut *Juglans regia* L.

Low, but not necessarily below 0 °C, 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-induced 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 are 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 and Malcolm 1997; Zhu et al. 2000). This syndrome has been identified as pre-disposing dieback for the yellow birch *Betula alleghaniensis* (Cox and Zhu 2003).

Lower hydraulic conductivity from winter embolism and limited spring refilling will limit hydraulic conductance of the whole plant. Under relatively high evaporative demand (high VPD), it would 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 would 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 (Bréda et al. 1995).

One important aspect to consider regarding frost damages is the temporality, since higher damages have been observed during the elongation period of new growth units in the spring (Chaar and Colin 1999). By destroying the developing organs, late frost damage (leaf, flowers, and new shoots) will immediately reduce the transpiration (water output) and the photosynthesis (carbon input). In addition, 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 positive net carbon assimilation (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 at the time when drought stress will be higher (Charrier et al. 2018b).

5 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 could 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, models predicting tree seasonality developed so far mostly consider non-stressing conditions (see Lang et al. 1987; Delpierre et al. 2016). Notably, do key variables of phenological simulations, such as critical sums of temperature for chilling and/or forcing stages, vary with stress intensity?

Photoperiod and temperature are key signals regulating plant phenology (Maurya and Bhalearao 2017). In the 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 distinct but temporally connected processes: one photosensitive (short day) and one thermosensitive (low temperature) (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 fully characterized yet (Eilmann et al. 2011). Thus, depending on the timing of the previous stage, the onset of the following ones will be affected, leading to unpredictable behavior (Hänninen and Tanino 2011). For instance, an increase in temperature may 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 (i) drought stress (Schuldt et al. 2020) and (ii) autumn temperature (Fu et al. 2014). The carry-over effect with respect to budburst 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 and Richardson 2015).

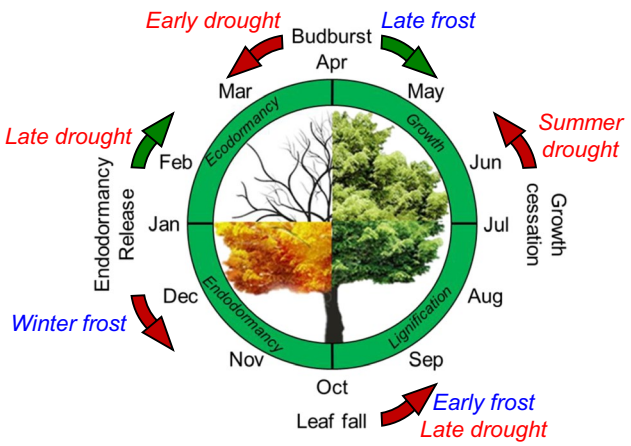

Fig. 4 Hastening (brown arrow) or delaying (green arrow) phenological stages in response to drought and frost events. At the center is presented the typical seasonal phenological stages in a deciduous tree in the Northern Hemisphere and outside the potential effects of drought and frost stress depending on their timing. It should be noted that stress factors can have a lagged effect onto phenology (e.g., late drought in the 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 effect on primary growth is relatively unexplored in trees. Drought exposure can significantly hasten the primary growth onset in *Erica multiflora*, although not in *Globularia alypum* (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 and Bhalerao 2017; Tylewicz et al. 2018). Furthermore, higher temperatures associated with drought events may induce deeper dormancy (Heide 2003; Tanino et al. 2010; Rohde et al. 2011). As this may 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 effects (Xie et al. 2015).

The impact of frost events on phenology has essentially been reported in the 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 (16–34 days; Augspurger 2013). Delayed phenology will expose the tree to higher summer drought resulting in lower carbon reserves (Menzel et al. 2015; d'Andrea et al. 2019; 2020). During the late summer, after growth cessation and dormancy induction, frost exposure may promote the dormancy release andinduces leaf fall as cold temperature do (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 damage, respectively (Fig. 4)). In addition, 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.

6 A holistic modeling 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 and water content (Charrier et al. 2013b) on one hand and water content and water potential on the other hand (Edwards and Jarvis 1982)).

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; Zweifel and Sterck 2018). 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 simulate 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 modeling 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 (phenology, carbon dynamics, and plant hydraulics). Such an integrated modeling approach should be used for the interaction between stress factors through the following steps:

(i) Quantitative description of the variable(s) of interest e.g. loss of hydraulic conductivity and 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 dynamic climate variables, 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 will easily simulate both legacy and memory effects (as a function of previous level of damages, water, and carbon contents) and / variation in state variables for the different processes based on experimental data.

7 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, potentially explaining the residual variance in current phenological predictions.

Phenological processes are likely to exhibit legacy through carbon balance e.g. trophic limitation of meristem growth (Bonhomme et al. 2010) and 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, such as promoted by the SOERE or the long-term ecological research network (Yonker et al. 2007).

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 dynamics; and (ii) develop a multi-collinearity approach aiming to evaluate the interactions between different constraints in the tree survival capacity both at short and

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 modulate 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 will improve existing mechanistic models simulating these interacting processes in order to predict accurately the effect of cumulative stress on tree physiology and survival.

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Data availability Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

Declarations

Conflict of interest The authors declare no competing interests.

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