

# Is a seasonally reduced growth potential a convergent strategy to survive drought and frost in plants?

Florence Volaire<sup>1,\*</sup>, Karim Barkaoui<sup>2,3</sup>, David Grémillat<sup>4,5</sup>, Guillaume Charrier<sup>6</sup>, Olivier Dangles<sup>4</sup>, Laurent J. Lamarque<sup>7</sup>, Nicolas Martin-StPaul<sup>8</sup> and Isabelle Chuine<sup>4</sup>

<sup>1</sup>CEFE, Université Montpellier, INRAE, CNRS, EPHE, IRD, F-34090 Montpellier, France, <sup>2</sup>CIRAD, UMR ABSys, F-34398 Montpellier, France, <sup>3</sup>ABSys, Université F-34060 Montpellier, CIHEAM-IAMM, CIRAD, INRAE, Institut Agro, Montpellier, France, <sup>4</sup>CEFE, Université Montpellier, CNRS, EPHE, IRD, F-34090 Montpellier, France, <sup>5</sup>Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, South Africa, <sup>6</sup>Université Clermont Auvergne, INRAE, PIAF, F-63000 Clermont Ferrand, France, <sup>7</sup>Département des Sciences de l'Environnement, Université du Québec à Trois-Rivières, Trois-Rivières, QC, G9A 5H7, Canada and <sup>8</sup>INRAE, URFM, Domaine Saint Paul, Centre de recherche PACA, 228 route de l'Aérodrome, CS 40509, Domaine Saint-Paul, Site Agroparc, France

\*For correspondence. E-mail [florence.volaire@cefe.cnrs.fr](mailto:florence.volaire@cefe.cnrs.fr)

Received: 29 April 2022 Returned for revision: 8 December 2022 Editorial decision: 12 December 2022 Accepted: 14 December 2022  
Electronically published: 26 December 2022

**2023• Background** Plants have adapted to survive seasonal life-threatening frost and drought. However, the timing and frequency of such events are impacted by climate change, jeopardizing plant survival. Understanding better the strategies of survival to dehydration stress is therefore timely and can be enhanced by the cross-fertilization of research between disciplines (ecology, physiology), models (woody, herbaceous species) and types of stress (drought, frost).

• **Scope** We build upon the 'growth–stress survival' trade-off, which underpins the identification of global plant strategies across environments along a 'fast–slow' economics spectrum. Although phenological adaptations such as dormancy are crucial to survive stress, plant global strategies along the fast–slow economic spectrum rarely integrate growth variations across seasons. We argue that the growth–stress survival trade-off can be a useful framework to identify convergent plant ecophysiological strategies to survive both frost and drought. We review evidence that reduced physiological activity, embolism resistance and dehydration tolerance of meristematic tissues are interdependent strategies that determine thresholds of mortality among plants under severe frost and drought. We show that *complete dormancy*, i.e. programmed growth cessation, before stress occurrence, minimizes water flows and maximizes dehydration tolerance during seasonal life-threatening stresses. We propose that *incomplete dormancy*, i.e. the programmed reduction of growth potential during the harshest seasons, could be an overlooked but major adaptation across plants. Quantifying stress survival in a range of non-dormant versus winter- or summer-dormant plants, should reveal to what extent *incomplete* to *complete dormancy* could represent a proxy for dehydration tolerance and stress survival.

• **Conclusions** Our review of the strategies involved in dehydration stress survival suggests that winter and summer dormancy are insufficiently acknowledged as plant ecological strategies. Incorporating a seasonal fast–slow economics spectrum into global plant strategies improves our understanding of plant resilience to seasonal stress and refines our prevision of plant adaptation to extreme climatic events.

**Key words:** Dehydration tolerance, dormancy, growth–stress survival trade-off, embolism resistance, mortality threshold, phenology, fast–slow economics spectrum, seasonality, strategy, drought survival, frost survival.

## INTRODUCTION

In their natural environments, living organisms have adapted to biotic and abiotic stresses that impact their growth, reproduction, survival and overall fitness (Grime, 2001). However, the current and predicted climate change is likely to expose organisms to more intense and less predictable heat, drought, frost and other stresses, thus jeopardizing their survival (Ummenhofer and Meehl, 2017). Consequently, many organisms already experience or will soon experience extreme environmental conditions outside their current tolerance range (Botero *et al.*, 2015). It is therefore crucial to improve our knowledge of the stress survival

strategies of plants to anticipate and manage the impacts of climate change on ecosystems. Comparative approaches can help identify convergent research avenues on processes and trade-offs underlying stress survival (Taborisky *et al.*, 2021).

Firstly, a major and convergent ecological pattern in the plant kingdom is the generally observed negative relationship between *growth* and *stress survival* (see Glossary, Box 1). This relationship has been well documented for plants facing various abiotic stresses, including drought and frost stress (Grime, 1977; Grubb, 1998). The extent to which a species can combine growth and resilience to stress remains an ongoing question that merits further investigation, especially under climate change (Doerner,

2020). We here discuss the relationship between stress survival and growth, which is usually assessed as the *maximum annual growth potential* in optimal conditions (Perez-Harguindeguy et al., 2013). We show the generality of this relationship across various model species to understand plant survival strategies. Furthermore, we propose extending the scope of these global strategies by including phenological adaptations allowing plants to tolerate seasonal stress, such as seasonal dormancy. Doing so, growth should also be assessed, but not only as the *maximum annual growth potential* and not as the *actual plant growth* (or growth reduction) during the most stressful season (Grubb, 1998). We propose to assess growth as the reduced *growth potential* (and not absolute growth) during the same most stressful season (see Box 1) since we demonstrate that the anticipated reduction in seasonal growth potential (relative to the maximum annual growth potential) may be a key strategy for survival of dehydrative stress.

Secondly, as drought and frost are abiotic stresses, both of which decrease the availability of water to plant cells (Pearce, 2001; Verslues et al., 2006), the strategies of dehydration avoidance and tolerance of plants subjected to either severe drought or freezing involve convergent physiological adaptations (Verslues et al., 2006; Lata and Prasad, 2011; Nakashima et al., 2014). Hence, solute accumulations, osmotic adjustment and modification of the properties of cell walls help plants to tolerate the dehydration induced by low water potential. These protective mechanisms for preventing or repairing cell damage are observed under various dehydrative stresses and for many species (Close, 1997; Hare et al., 1998; Krasensky and Jonak, 2012). Thus, a plant facing a primary stress (e.g. drought) can acquire the benefit of the ability to face a secondary abiotic or biotic stress (e.g. frost), i.e. have *cross-stress tolerance* (Liu et al., 2021). Cross-stress tolerance has been recently described in trees (Charrier et al., 2021), crops (Pushpavalli et al., 2020), grasses (Kong and Henry, 2016, 2019) and some resurrection plant species with double tolerance, able to recover after complete desiccation and be freezing-tolerant (Fernández-Marín et al., 2020). Consequently, in this review we highlight that the relationship between growth and stress survival can be better understood when considering the convergent physiological mechanisms ensuring plant survival, namely the strategies related to dehydration tolerance under severe summer drought and winter frost. These mechanisms should be common among vascular plant species living in climates where severe summer drought and/or winter frost are the most limiting factors and life-threatening at given seasons. We focus here on seasonal dormancy, which minimizes water flows and maximizes dehydration tolerance in many plant species, both in winter and summer.

At the crossroads of ecological and physiological approaches, this viewpoint argues that seasonal dormancy is a key strategy illustrating the relationship between growth potential and stress survival. (*Complete*) dormancy is a programmed *inability* to grow (Box 1). *Incomplete* dormancy (Box 1) can be defined as a programmed *reduction* in growth potential during the most stressful season (Volaire and Norton, 2006). We argue that this little-explored phenological adaptation could underpin a continuum of dehydration tolerance and resilience ability of plants living in bioclimatic areas with severe seasonal frost or drought. Moreover, assessing the intra- and inter-specific variability of *incomplete* dormancy could highlight whether and which plant species anticipate periodic seasonal stresses.

## THE GROWTH–STRESS SURVIVAL TRADE-OFF UNDERPINS THE FAST–SLOW CONTINUUM OF PLANT STRATEGIES

*A generalized fast–slow continuum should include seasonality*

The trade-off between growth, or more generally any physiological activity related to fitness (growth, development, reproduction) and stress survival, usually and hereafter called the ‘growth–survival trade-off’, is a central tenet in ecology across all types of organisms (Grime, 1974; Sibly and Calow, 1989; Turbill et al., 2011). This trade-off underpins the identification of global plant ecological strategies along a plant economics spectrum, reflecting a gradient of resource use (Reich, 2014). This gradient ranges from slow growth strategies associated with a high survival capacity and energy/carbon conservation in plants of species usually living in low-resource environments, to fast growth strategies associated with a high resource acquisition capacity but at the expense of poor stress survival, in plants of species usually living in richer environments (Grime, 2001; Wright et al., 2010). Accordingly, the survival probability of any species/population should be predictable by its position along the fast–slow plant economics spectrum in a given environment (Reich, 2014).

Here we illustrate that this fast–slow continuum is underpinned by the growth–survival trade-off. At the fast end of the continuum, highly productive and resource-acquisitive species (Fig. 1A), such as annual crop species (Claeys and Inze, 2013), are usually dehydration-sensitive and poorly adapted to severe drought and frost stresses. By contrast, species with lower growth rates are more dehydration-tolerant and survive notably better in response to severe stress. The slowest end of the spectrum (Fig. 1A) can be exemplified by resurrection plants, which are among the most resource-conservative and slow-growing herbaceous species, with long life spans (Tebele et al., 2021). They can survive months or even years of desiccation, i.e. <30% water content while maintaining tissue moisture levels in equilibrium with ambient atmospheric humidity (Zhang and Bartels, 2018), illustrating the negative relationship between desiccation tolerance and growth (Alpert, 2006).

Ecological strategies of the fast–slow plant economics spectrum have been described based on integrative plant functional traits (Wright et al., 2004) that are usually measured under the expected least limiting conditions. Doing so, traits reflect the strategies underlying the *maximum annual growth potential* (e.g. usually measured during the peak of vegetation growth), a key component of plant fitness, and allow reliable comparisons between species/populations living in environments with contrasting conditions and stress intensities. However, these conditions may poorly describe the temporal variations and adjustments in plant responses to seasonally fluctuating conditions (Volaire et al., 2020). Yet most species show seasonal activity and alternate periods of active growth (resource acquisition) and periods of restricted growth (resource conservation) whenever the environmental conditions are limiting. For example, some resurrection plants are desiccation-sensitive at certain times while desiccation-tolerant at others (Farrant et al., 2009). Likewise, some plant species can reduce their metabolic rates, becoming quiescent under unpredictable stress while recovering

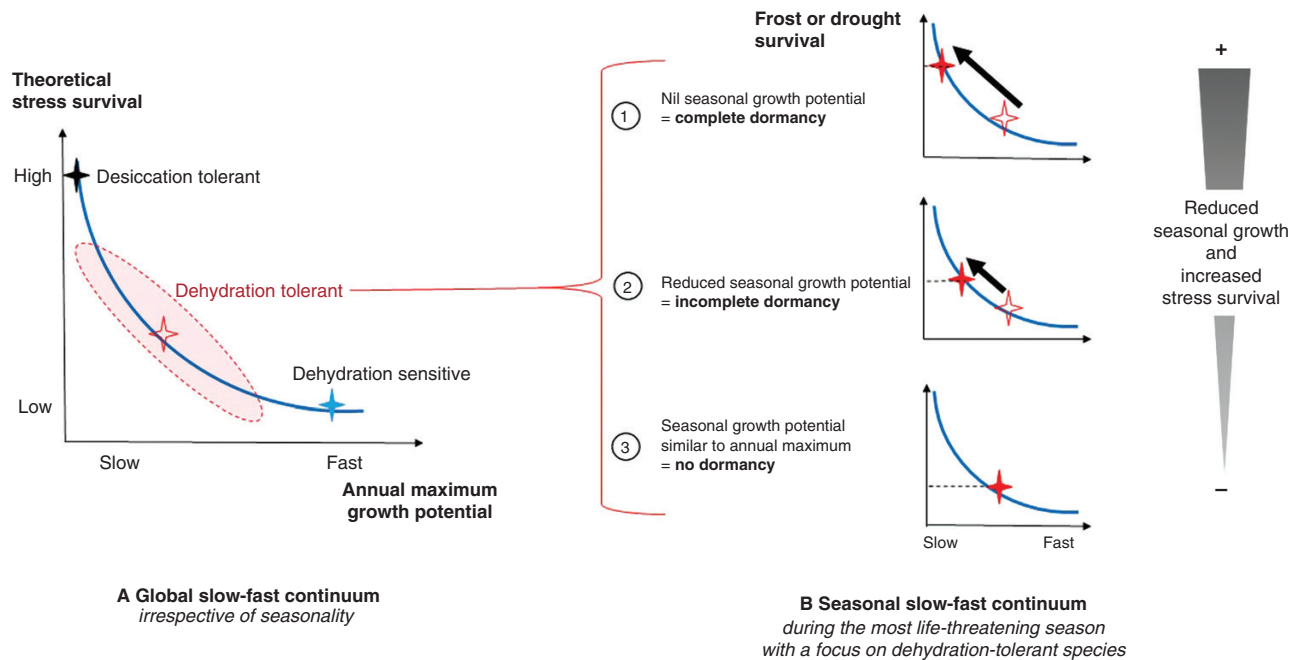


FIG. 1. The growth–stress survival trade-off (blue lines) and the fast–slow continuum of strategies in plant species—adapted from (Sibly and Calow, 1989): (A) exemplified by dehydration-sensitive, dehydration-tolerant and desiccation-tolerant species/populations along a global fast–slow continuum irrespective of seasonality but usually measured during the most favourable season; and (B) for three types (1–3) of dehydration-tolerant species or populations, along a seasonal fast–slow continuum shown to illustrate the suggested relationship between levels of *incomplete* seasonal dormancy (reduction of seasonal growth potentials) and frost or drought survival. The open red star symbols show the theoretical position of a given dehydration-tolerant plant along the global fast–slow continuum. The closed red star symbols show the actual position of the same plant along the seasonal fast–slow continuum when considering the real seasonal growth potential. In case of no dormancy (3), open and closed red star symbols align.

when the conditions become favourable again (Velappan *et al.*, 2017). Moreover, species with a seasonal dormancy periodically anticipate the incoming stress and ‘know when not to grow’ (Bielenberg, 2011), although at given seasons only (Fig. 1B). This raises the following question: is the reduction of *seasonal* growth potential during the most life-threatening seasons (Box 1, Fig. 1B) as, or even more, meaningful than the *maximum annual* growth potential to describe plant strategy and overall adaptation to seasonal stress? In this paper we propose that seasonal dormancy, whether complete or incomplete, be considered a key strategy to refine the fast–slow continuum economics spectrum by adding a temporal dimension to it (Grubb, 1998), and we suggest a methodology to do so.

#### *Seasonal dormancy is a key strategy to refine the fast–slow continuum*

Dormancy is an adaptive response, enabling survival during seasons when environmental conditions are most life-threatening (Vegis, 1964), such as winter in extratropical regions and summer in the Mediterranean and semi-arid regions. Regardless of the season, *complete* dormancy is associated with a loss of access to growth-promoting signals, generally induced by photoperiodic and thermal cues, resulting in decreased metabolic and cellular activities in anticipation of forthcoming stresses such as frost or drought (Horvath *et al.*, 2003; Gillespie and Volaire, 2017). Dormancy can be regarded as a prolonged ‘gearing down’ strategy (Grubb, 1998) without possible rapid regrowth when conditions become

briefly favourable to physiological activity. Thus, dormancy release requires a prolonged exposure to particular environmental conditions.

Notwithstanding the diversity of adaptive mechanisms to cope with frost and drought, which both generate tissue dehydration (Verslues *et al.*, 2006; Kong and Henry, 2018), we propose a unique framework to describe them (Fig. 2). Among the strategies of dehydration avoidance and tolerance shared by most vascular plant species, *complete* dormancy facilitates survival of the highest dehydration risk, either during winter or summer due to a programmed inability of meristems to grow, despite possible suitable transitional environmental conditions (Lang, 1996).

If winter dormancy is a widespread strategy in extratropical woody and herbaceous species, summer dormancy is a common strategy among herbaceous perennials in Mediterranean and semi-arid areas (Gillespie and Volaire, 2017). In tropical tree species, slow-growing habits (Oliveira *et al.*, 2021) and drought deciduousness (Vargas *et al.*, 2021) confer a high resilience to drought, suggesting there may be some level of *incomplete* dormancy during the stress period. Interestingly, summer dormancy has rarely been identified in woody species (Lei, 2005), contrary to winter dormancy. Both summer and winter dormancy are yet also common in many animal species (Wilsterman *et al.*, 2021), suggesting that dormancy may be a strategy shared by most living organisms to survive stress.

*Complete* dormancy is the strategy exhibited, for instance, by herbaceous plants that rely on underground perennating organs (tubers, rhizomes, bulbs, ...) to survive periods of

unfavourable conditions (Lubbe *et al.*, 2021). However, dormancy can be regarded in many cases as a cryptic strategy (Albert *et al.*, 2019) that may be difficult to detect and monitor. So far, the only method is to measure meristem growth under favourable conditions, i.e. under additional summer water supply for summer dormancy (Laude, 1953) and high temperature for winter dormancy (Campoy *et al.*, 2011). Following this method in experimental conditions, recent studies (Bristiel *et al.*, 2017; Keep *et al.*, 2021) demonstrated

a strong continuous trade-off between seasonal growth potential and stress survival in European populations of *Dactylis glomerata* and *Lolium perenne* (Fig. 3). Mediterranean populations of these two perennial grasses exhibited the highest and lowest growth potential in winter and summer, respectively. Consequently, they had a low and high survival rate to winter frost and summer drought, respectively (Fig. 3). The opposite pattern was observed for populations of these species originating from northern European areas.

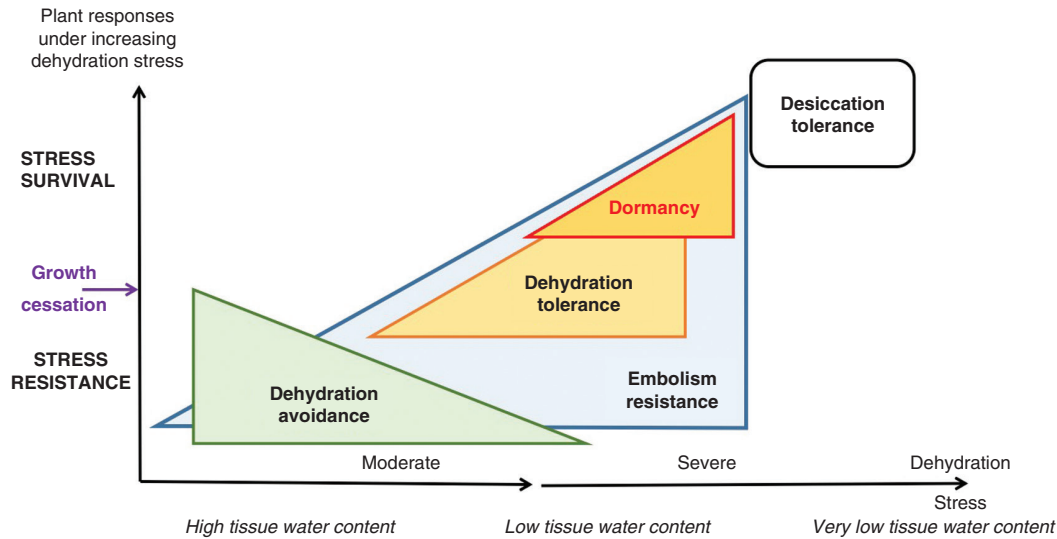


FIG. 2. Convergent plant adaptive strategies under increasing dehydration stress (due to drought or frost). The strategy of tissue dehydration avoidance (green) decreases as dehydration stress increases and underpins stress resistance (growth maintenance). As stress increases in severity, growth ceases, and stress survival is increasingly supported by dehydration tolerance (pale yellow), particularly in specific organs such as buds and meristems when plants exhibit a dormancy strategy (dark yellow). Dehydration tolerance is associated with increasing embolism resistance (blue) and decreasing tissue water content. The strategy of desiccation tolerance confers survival to the most severe stress (drought and frost) but does not imply hydraulic adaptations during the stress and therefore, no embolism resistance. Adapted from Volaire (2018).

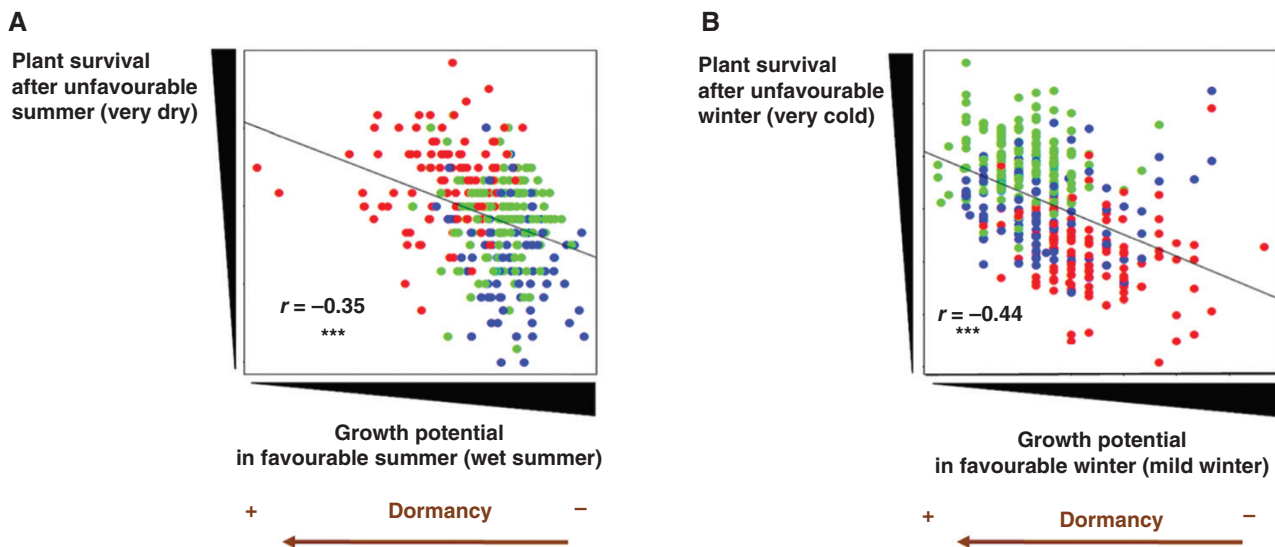


FIG. 3. Three hundred and eighty-five European populations of the perennial ryegrass *Lolium perenne* express a continuous trade-off between growth potential and stress survival, in summer and winter. Red symbols, Mediterranean populations; blue symbols, temperate populations; green symbols, northern populations. Growth potential was measured in wet summer (A) and mild winter (B) environments, showing a gradient of incomplete seasonal dormancy that differs between summer and winter conditions (brown arrows). Plant stress survival was measured in dry summer (A) and cold winter (B) environments in three common gardens along a latitudinal gradient between western France and northern Germany (Keep *et al.*, 2021). \*\*\* significant correlation ( $P < 0.001$ ).

Considering that incomplete dormancy should be mainly cryptic, it is possible that programmed seasonal reduction of growth potential could have remained largely unnoticed so far (Fig. 1B) and be considered as quiescence. We propose here that this endogenously controlled and anticipated seasonal reduction of growth potential, i.e. levels of *incomplete* dormancy (Box 1) could be included as a modality of the dormancy strategy (Fig. 2). Hence, we propose in the following that, as for species with *complete* dormancy, the relative seasonal growth potential, i.e. the reduced growth potential of incompletely dormant species measured during the usually life-threatening season (Fig. 1B) relative to the maximum annual growth potential, should be negatively correlated with dehydration stress survival.

#### PHYSIOLOGY OF THE ‘GROWTH–STRESS SURVIVAL’ TRADE-OFF

In the light of ecological strategies, it is logical that growing slowly, either permanently in a chronically harsh environment or as a response to an anticipated or accidental threatening stress, is the general cost to pay for ensuring survival. It nevertheless requires maintaining core physiological activity, albeit at a low rate, to prevent death caused by a shortage of energy (carbon starvation) and/or water supply (dehydration). The downregulation of metabolic activity contributes to adjusting the metabolism to cope with stress and reach basal metabolic rates compatible with self-maintenance while saving carbon reserves for ‘better days’ (Asami et al., 2018). Under extended periods of drought-impairing photosynthesis, plants may indeed face a carbon reserve depletion, known as carbon starvation (McDowell et al., 2008). However, the role of carbon supply, notably to minimize cellular dehydration by osmotic adjustment, strongly interacts with plant water content and flows since drought-associated mortality originates from a whole-plant water-relation backbone (McDowell et al., 2022). The understanding of plant survival to drought and frost has therefore recently focused on hydraulic adaptations, for which recent advances raise comparative questions across multiple plant growth forms and types of stress. Here we review the

physiological thresholds associated with survival versus mortality in a large range of species under severe drought and frost. We demonstrate that these adaptations may be better understood when considering seasonal growth regulations at the whole plant level, exemplified by the dormancy strategy.

#### Defining physiological thresholds for plant survival to frost and drought

With the exception of resurrection plants, which can survive desiccation (Fig. 2), maintaining water supply is essential for most plant species. Under highly negative water potential, water flow may be interrupted by the embolization of the xylem, i.e. gas formation and spreading within and across xylem conducting elements. Various types of stress, including drought and frost, can induce the breakage of the water column by embolism, interrupting water transport and potentially affecting the viability of above-ground distal organs during severe stress (Charrier et al., 2021). Hence, embolism resistance, and therefore water transport capacity, has long been viewed as a key trait for stress survival (Fig. 4), although the relative importance of this strategy depends on plant growth forms. The high levels of embolism (>50 or 90 % according to studies) that can be reached during extreme drought and heat events can result in a lack of recovery of plant functioning and/or meristem reactivation once the stress is released (Urli et al., 2013; Hammond and Adams, 2019). Embolism resistance is often estimated by water potential leading to 50 or 90 % embolism ( $P_{50}$  or  $P_{90}$ ). Plants present a large variation in  $P_{50}$ , from  $-1$  MPa for hygrophilous species such as *Populus* to almost  $-19$  MPa for *Callitris tuberculata*, which is adapted to extreme droughts and reaches the physical limit of water transport (Larter et al., 2017). The range of variation of  $P_{50}$  within temperate grasses ( $-0.7$  to  $-7.5$  MPa) is similar to that found in woody angiosperm species from the same biogeographical areas (Lens et al., 2016).

The resistance to embolism is enhanced by many strategies allowing the control of water potential decline (Choat et al., 2018), such as the maintenance of sufficient water uptake

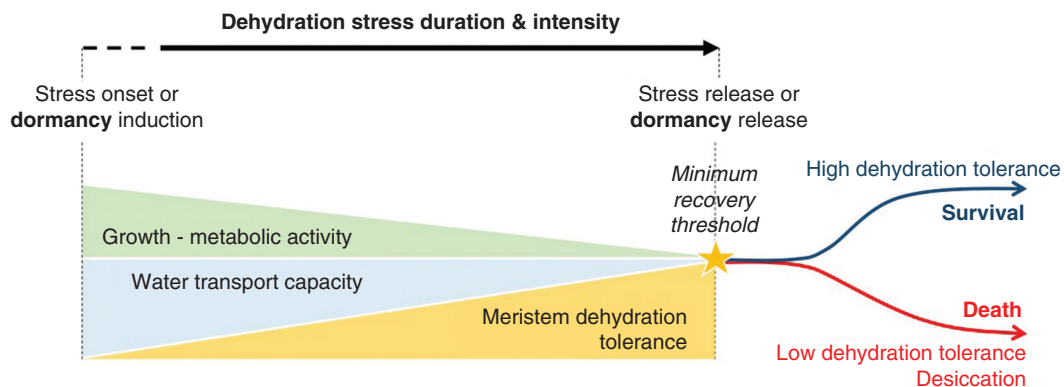


FIG. 4. Main processes determining plant survival or death from the onset to the cessation of a drought or cold period. Seasonal dormancy triggers the adaptive processes before the onset of the stress (or even with no subsequent stress occurring), therefore inducing the dehydration of some key plant tissues and reinforcing their dehydration tolerance. The reduction of growth and metabolic activity is the first process associated with the induction of dormancy and/or dehydration stress. As dehydration stress increases, the minimum recovery threshold or no-return point (yellow star) depends on plant maintenance of water transport capacity and dehydration tolerance in the surviving organs, which are often meristematic tissues. This figure is relevant for major plant species with some level of dehydration tolerance but does not apply to desiccation-tolerant plant species.

through deep rooting (Chitra-Tarak *et al.*, 2021), the control of transpiration (Martin-StPaul *et al.*, 2017; Duursma *et al.*, 2019) or hydraulic vulnerability segmentation (Charrier *et al.*, 2016). These adaptations align with the growth–stress survival trade-off since the reduction of metabolic activity and leaf shedding (Martin-StPaul *et al.*, 2013; Charrier *et al.*, 2016) contribute to minimizing growth and water flows and hence reduce the risk of embolism (Oliveira *et al.*, 2021; Vargas *et al.*, 2021).

Water transport is also affected by frost stress due to freeze–thaw cycles. In this case, embolism is generated by propagating air bubbles entrapped in an ice lattice during sap thawing. Air–water contact surfaces are likely to be displaced by the extremely low water potential at the liquid–solid interface,  $\sim -1$  MPa below the freezing point (Hansen and Beck, 1988). Vulnerability to freeze–thaw embolism is generally correlated with the mean diameter of the xylem conduits, with wider vessels containing more dissolved gas that would form larger bubbles on freezing being the most vulnerable to embolism on thawing (Charrier *et al.*, 2014). Trade-offs between freezing tolerance and growth rate have been reported (Koehler *et al.*, 2012; Yin *et al.*, 2022) and are notably illustrated in the case of dormant overwintering plants with low metabolic activity and therefore minimal embolism (see next section).

Although embolism occurs under various stresses (drought, heat, cold), empirical data do not support a universal relationship between the loss of water supply capacity and stress survival, e.g. a high embolism can be observed without entailing mortality both in plants under extreme stress (Hammond and Adams, 2019) and in overwintering plants (Mayr *et al.*, 2003). Interestingly, water pools in plant tissues are a more relevant indicator of drought-induced mortality than water transport capacity (Sapes *et al.*, 2019; Lamacque *et al.*, 2020; Mantova *et al.*, 2021). It is increasingly recognized that the dehydration tolerance of surviving organs under drought, i.e. the meristematic tissues such as shoot apical meristem buds, underground buds of perennating organs or vascular cambium in trees (Hammond *et al.*, 2021; Mantova *et al.*, 2021), could represent a common and crucial factor to ensure survival across plants subjected to severe drought or frost. In particular, the requirements for water transport and the level of water storage is thus expected to be minimal for dormant perennial species, whether herbaceous (Gillespie and Volaire, 2017) or woody (Wolfe *et al.*, 2016), in which most leaves are shed before the stress. Overall, water transport capacity and cellular dehydration tolerance may therefore interact to define the ‘no return’ point (Fig. 4). Across organisms and types of dehydration stress, state variables in surviving organs (e.g. water and solute contents) and flow variables (e.g. hydraulic conductivity) should be complementary to define minimal physiological thresholds according to species, population and dormancy.

#### *Dormancy minimizes water flows and maximizes dehydration tolerance*

Dehydration can be triggered by a lack of water and any factor disrupting water transport, such as vessel embolism caused by frost. Dormancy plays an important role in tolerance to dehydration caused by drought or frost (Vitasse *et al.*, 2014; Gillespie and Volaire, 2017). Most dormant organs, i.e.

seeds (Kleinwächter *et al.*, 2014), buds in winter (Chuine and Regniere, 2017) or buds in summer (Volaire *et al.*, 2001), exhibit minimal developmental and metabolic activities involving the upregulation of many compounds that protect the cells against dehydration, such as heat-shock proteins, late embryogenesis abundant (LEA) proteins, and some soluble carbohydrates.

Dormancy can also be regarded as a prerequisite to avoid embolism (Savage and Chuine, 2021). If living cells of meristems, phloem and xylem parenchyma are prone to frost damage, xylem conduits are prone to embolism triggered by drought and frost (Cochard and Tyree, 1990; Sperry and Sullivan, 1992). Therefore, reduced cellular and metabolic activities during stressful seasons translate into reduced sap flows, water savings, and thus reduced tension, thereby limiting embolism risks. Both buds and the vascular system undergo major transformations during the life-threatening season, which are necessary to endure dehydration during these seasons (Savage and Chuine, 2021). Noticeably, all communication pathways undergo transformation to limit and tolerate dehydration (Wisniewski *et al.*, 2014). The symplastic pathway in all living cells, including sieve elements of the phloem, is shut down by the accumulation of a  $\beta$ -glucan called callose in the plasmodesmata. This shutdown decreases the concentrations of water and also oxygen, nutrients and other molecules (e.g. hormones, transcription factors), and is responsible for the decreased metabolic and physiological activity (Rinne and Schoot, 2003). Water transport in the apoplast is limited by small intracellular spaces (Quamme *et al.*, 1995). Expression of aquaporins is downregulated, minimizing water movement between the symplast and the apoplast (Yooyongwech *et al.*, 2008). Finally, and most importantly, water transport in the xylem is disrupted at the junction between the bud and the twig, which minimizes any exchange through the vascular tissue and/or embolism spread into the bud (Savage and Chuine, 2021).

These protective mechanisms are likely to play a role in all dormant plants, and should be particularly investigated in summer-dormant herbaceous species, which rely on meristems protected by layers of senescent sheath bases, usually at the ground surface or below, with minimal water flows to facilitate survival of severe heat and drought (Gillespie and Volaire, 2017). Indeed, we propose that research conducted on winter dormancy and frost survival could guide that on summer dormancy and drought survival, notably in the case of *incomplete* dormancy.

#### ASSESSING RELATIVE SEASONAL GROWTH POTENTIAL TO BETTER UNDERSTAND STRESS SURVIVAL

In the context of increasingly frequent extreme climatic events, including drought and frost, we urge more integrative research between ecological and physiological approaches to better understand major commonalities among plants that allow them to face a range of dehydration stresses. In particular, we argue that research on ecological strategies should account for not only *spatial* adaptations *across* environments but also seasonal adaptations *within* environments over seasons. We propose to test the scope of a generalized fast–slow continuum at the seasonal level. To do so, the main challenge is to evaluate/test the

generality of the correlation between reduced seasonal growth potential and dehydration tolerance of plants under severe seasonal stress.

Assessing the occurrence of seasonal dormancy is a methodological challenge that requires measuring the decrease in potential metabolic activity during the expected period of dormancy compared with a stage when the plants are not dormant. We propose comparing the seasonal growth potential measured during the most life-threatening season and the maximum annual growth potential measured during the most favourable season in order to calculate an index of relative seasonal reduction of growth potential (Box 1, Fig. 5). Doing so implies relaxing the stress (by water supply or during a wet summer, by experimental warming or during mild winters) to enable measurement of plant growth potential when the conditions are usually highly stressful and limiting for growth (Fig. 5). The growth potential can be measured at the whole-plant or organ level (production of above-ground biomass, leaf extension, increase in plant size, biovolume, or total leaf area, etc.), depending on the species and the context (experimental garden, field, controlled conditions) and during the relevant period of the growing season. Moreover, stress survival (plant mortality, loss of plant cover) should be measured under harsh environmental conditions. Species or populations originating from climates with life-threatening seasons, having the lowest growth potential (in summer or winter depending on the least favourable season), relative to

their maximum annual growth potential during the most favourable season (usually spring), should exhibit the greatest dehydration tolerance under severe seasonal dehydration stress (Fig. 5). Measuring seasonal levels of *complete* and *incomplete* dormancy requires growing plants in environments suitable for dormancy induction, notably regarding temperature and daylength (Cooke et al., 2012; Maurya and Bhalerao, 2017). For instance, complete summer dormancy of the perennial grass *Dactylis glomerata* could only be induced (and thus revealed) when winter and spring temperatures reached a defined threshold (Shihan et al., 2022) while daylength was not limiting throughout most of Europe for summer dormancy expression. Ideally, growth patterns should be assessed at the provenance sites of the species/population and measured on plants artificially heated (winter) or irrigated (summer). Common gardens comparing a range of species or populations of various origins could be useful to analyse the variation of seasonal growth potential and dormancy expression along environmental gradients representative of the ecological niche of the species (Keep et al., 2021).

CONCLUSIONS

Surviving stress implies a drastic reduction of physiological activity. Seasonal dormancy represents one of the most efficient strategies to survive stress, especially dehydration stress occurring at the same period every year. By comparing

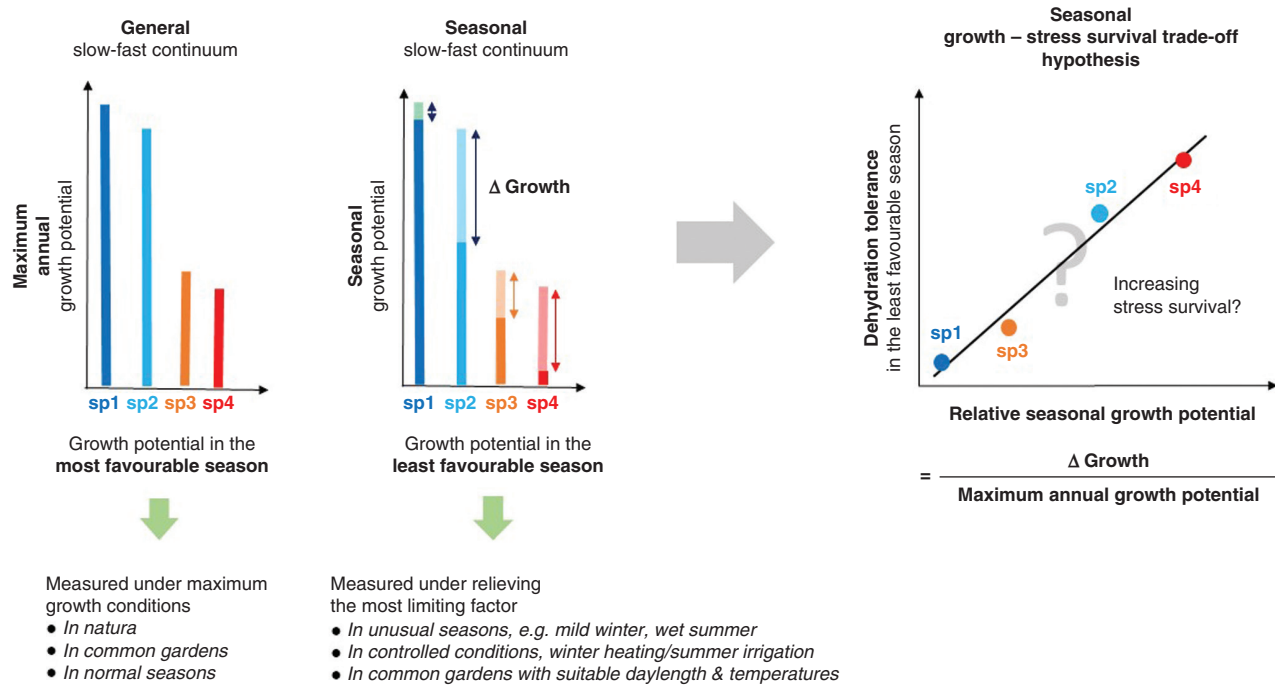


FIG. 5. Testing the correlation between seasonal growth potential and dehydration tolerance. This figure provides a methodology illustrated by the documented phenological patterns of a range of herbaceous species: sp1, e.g. temperate populations with no summer dormancy of *Dactylis glomerata*, *Lolium perenne* or *Medicago sativa*; sp2, e.g. Mediterranean populations with some level of summer dormancy of *Festuca arundinacea* or *D. glomerata*; sp3, e.g. *Festuca rubra*, with low annual growth potential and no summer dormancy; sp4, e.g. semi-arid summer dormant populations of *D. glomerata* (Voltaire, 2008; Bristiel et al., 2017; Keep et al., 2021). Species or populations originating from climates with life-threatening seasons, having the lowest growth potential (in summer or winter depending on the least favourable season), relative to their maximum annual growth potential during the most favourable season (usually spring), should exhibit the greatest dehydration tolerance under severe seasonal dehydration stress. Dehydration tolerance should be determined by the minimum water content thresholds in meristematic tissues and water transport capacity (embolism resistance), allowing plant survival and growth recovery after stress release.

ecological and physiological approaches, this viewpoint underlines a unique framework of common strategies for herbaceous and woody species under winter frost or/and summer drought, and thus raises three major points.

Firstly, we suggest that the seasonally reduced growth potential represents an overlooked adaptation to stress during the harshest seasons. It is worth testing to what extent seasonal growth reduction represents a relevant proxy of the level of plant survival to dehydration stress. The following research questions are still open: Which species/populations show a clear and anticipated reduction or cessation of growth potential? Which level of growth potential reduction and survival can they reach under extreme stresses? Is the duration of programmed dormancy across species positively correlated with greater environmental seasonality, as found within the animal kingdom (Wilsterman *et al.*, 2021)? Do the thresholds of embolism and dehydration of meristematic tissues triggering plant mortality vary with the depth of dormancy? These questions have rarely been addressed, particularly for summer dormancy, which has been much less explored than winter dormancy.

Secondly, we propose that investigating the relationship between the global and the seasonal fast–slow economics spectrum of plants could reveal the contribution of phenological events to ecological plant strategies. The global and seasonal fast–slow continuums are expected to align when plants originate from environments with low seasonality or constant environmental limiting factors. Conversely, the seasonal fast–slow continuum may provide a fruitful and complementary characterization of *within*-environment strategies for plants undergoing contrasting seasonal dehydration stress.

Finally, it is worth questioning whether dormancy strategies can still protect organisms from lethal stress in regions where climatic conditions move away from their climatic niche. Indeed, climate change makes the timing, frequency and intensity of stressful conditions less predictable than before and cues triggering dormancy less reliable, e.g. shifts in experienced photoperiod due to temporal and geographic species shifts (Ettinger *et al.*, 2021). The timing of dormancy is cued by air temperature and photoperiod signals that may no longer align with temperatures as climate change increases (Lubbe *et al.*, 2021). The possible modifications of dormancy expression and dormancy timing that have been already observed (Asse *et al.*, 2018; Beil *et al.*, 2021) may affect the outcome of the trade-offs between physiological activity and stress survival probability. Moreover, out-of-season severe stress, e.g. late spring freezes (Chamberlain *et al.*, 2021), also represent an increasing risk for plant survival. Climate change can also affect overwintering organs by altering snow cover depth and duration, thus modifying the exposure of plants to frost and then the duration of winter dormancy (Lubbe and Henry, 2020; Lubbe *et al.*, 2021).

Considering the more frequent occurrence and intensity of droughts in many areas, summer dormancy may become an increasingly valuable adaptive strategy (Gillespie and Volaire, 2017; Shihan *et al.*, 2022). Therefore, it is necessary to foster transdisciplinary collaboration to enhance the cross-fertilization of research questions. Investigating common strategies and processes involved in dehydration stress survival, along with genetical and evolutionary approaches, could help in understanding better plant resilience under severe seasonal abiotic

stress and hence predicting more efficiently the effects of climate change from organism to ecosystem scales.

#### BOX 1—GLOSSARY

**Stress survival:** Ability to survive after growth cessation due to an environmental factor severely restricting plant functioning (for the considered species and population), e.g. extreme and prolonged drought or frost.

**Stress resistance:** Maintenance of plant growth under an environmental factor moderately restricting plant functioning (for the considered species and population), e.g. moderate drought or cold.

**Dehydration tolerance:** Strategy allowing plants to tolerate low tissue level of dehydration (>30% water).

**Desiccation tolerance:** Strategy allowing plants to tolerate leaf water content equal to ambient atmospheric humidity and revive upon rehydration after long periods, e.g. resurrection plants.

**Complete dormancy (*sensu stricto* dormancy):** Endogenous controlled strategy that *stops* meristem activity to render it insensitive to growth-promoting signals in order to enhance plant survival during seasons when environmental conditions are most life-threatening.

**Incomplete dormancy (*sensu lato* dormancy):** Endogenous controlled strategy that *reduces* meristem activity to render it *less sensitive* to growth-promoting signals in order to enhance plant survival during seasons when environmental conditions are most life-threatening.

**Growth potential:** Growth rate, relative growth rate, or biomass production under optimum environmental conditions (without environmental stress).

**Maximum annual growth potential:** Growth potential during the most favourable season (at the ‘peak of vegetation’), usually under no environmental stress.

**Seasonal growth potential:** Growth potential during the most life-threatening seasons (winter and/or summer) when the stress is experimentally relieved to enable measurement of growth potential during a season when the conditions are usually stressful and limiting for growth.

**Relative seasonal growth potential:** The difference between maximum annual growth potential and seasonal growth potential indexed on the maximum annual growth potential. It measures the relative programmed reduction of growth potential during the harshest season (*incomplete* or *complete* dormancy). This dormancy is hypothesized in this paper to be correlated with dehydration tolerance and stress survival in summer and/or in winter, depending on the environment.

#### ACKNOWLEDGEMENTS

Thanks to Luis Miguel Chevin and Mark Norton for insights and suggestions.

#### LITERATURE CITED

Albert LP, Restrepo-Coupe N, Smith MN, *et al.* 2019. Cryptic phenology in plants: case studies, implications, and recommendations. *Global Change Biology* 25: 3591–3608. doi:10.1111/gcb.14759.



- Alpert P. 2006. Constraints of tolerance: why are desiccation-tolerant organisms so small or rare? *Journal of Experimental Biology* **209**: 1575–1584. doi:10.1242/jeb.02179.
- Asami P, Mundree S, Williams B. 2018. Saving for a rainy day: control of energy needs in resurrection plants. *Plant Science* **271**: 62–66. doi:10.1016/j.plantsci.2018.03.009.
- Asse D, Chuine I, Vitasse Y, et al. 2018. Warmer winters reduce the advance of tree spring phenology induced by warmer springs in the Alps. *Agricultural and Forest Meteorology* **252**: 220–230. doi:10.1016/j.agrformet.2018.01.030.
- Beil I, Kreyling J, Meyer C, Lemcke N, Malyshev AV. 2021. Late to bed, late to rise—warmer autumn temperatures delay spring phenology by delaying dormancy. *Global Change Biology* **27**: 5806–5817. doi:10.1111/gcb.15858.
- Bielenberg DG. 2011. Knowing when not to grow. *New Phytologist* **189**: 3–5.
- Botero CA, Weissing FJ, Wright J, Rubenstein DR. 2015. Evolutionary tipping points in the capacity to adapt to environmental change. *Proceedings of the National Academy of Sciences of the USA* **112**: 184–189.
- Bristiel PM, Gillespie L, Østrem L, Balachowski JA, Violle C, Volaire F. 2017. Is there a constant trade-off between stress tolerance and growth potential in the perennial grass *Dactylis glomerata*? *Functional Ecology* **32**: 1944–1958.
- Campoy JA, Ruiz D, Egea J. 2011. Dormancy in temperate fruit trees in a global warming context: a review. *Scientia Horticulturae* **130**: 357–372. doi:10.1016/j.scienta.2011.07.011.
- Chamberlain CJ, Cook BI, Morales-Castilla I, Wolkovich EM. 2021. Climate change reshapes the drivers of false spring risk across European trees. *New Phytologist* **229**: 323–334.
- Charrier G, Charra-Vaskou K, Kasuga J, Cochard H, Mayr S, Ameglio T. 2014. Freeze-thaw stress: effects of temperature on hydraulic conductivity and ultrasonic activity in ten woody angiosperms. *Plant Physiology* **164**: 992–998. doi:10.1104/pp.113.228403.
- Charrier G, Torres-Ruiz JM, Badel E, et al. 2016. Evidence for hydraulic vulnerability segmentation and lack of xylem refilling under tension. *Plant Physiology* **172**: 1657–1668. doi:10.1104/pp.16.01079.
- Charrier G, Martin-StPaul N, Damesin C, et al. 2021. Interaction of drought and frost in tree ecophysiology: rethinking the timing of risks. *Annals of Forest Science* **78**: 1–15.
- Chitra-Tarak R, Xu C, Aguilar S, et al. 2021. Hydraulically-vulnerable trees survive on deep-water access during droughts in a tropical forest. *New Phytologist* **231**: 1798–1813.
- Choat B, Brodribb TJ, Brodersen CR, Duursma RA, Lopez R, Medlyn BE. 2018. Triggers of tree mortality under drought. *Nature* **558**: 531–539. doi:10.1038/s41586-018-0240-x.
- Chuine I, Regniere J. 2017. Process-based models of phenology for plants and animals. In: Futuyama DJ, ed. *Annual review of ecology, evolution, and systematics*, Vol. 48. Palo Alto: Annual Reviews **159**: 182.
- Claeys H, Inze D. 2013. The agony of choice: How plants balance growth and survival under water-limiting conditions. *Plant Physiology*, **162**: 1768–1779.
- Close TJ. 1997. Dehydrins: a commonality in the response of plants to dehydration and low temperature. *Physiologia Plantarum* **100**: 291–296.
- Cochard H, Tyree MT. 1990. Xylem dysfunction in *Quercus* – vessel sizes, tyloses, cavitation and seasonal changes in embolism. *Tree Physiology* **6**: 393–407. doi:10.1093/treephys/6.4.393.
- Cooke JEK, Eriksson ME, Junttila O. 2012. The dynamic nature of bud dormancy in trees: environmental control and molecular mechanisms. *Plant, Cell and Environment* **35**: 1707–1728. doi:10.1111/j.1365-3040.2012.02552.x.
- Doerner P. 2020. Extreme environments: crucibles of potent abiotic stress tolerance. *Journal of Experimental Botany* **71**: 3761–3764. doi:10.1093/jxb/eraa269.
- Duursma RA, Blackman CJ, Lopez R, Martin-StPaul NK, Cochard H, Medlyn BE. 2019. On the minimum leaf conductance: its role in models of plant water use, and ecological and environmental controls. *New Phytologist* **221**: 693–705.
- Ettlinger AK, Buonaiuto DM, Chamberlain CJ, Morales-Castilla I, Wolkovich EM. 2021. Spatial and temporal shifts in photoperiod with climate change. *New Phytologist* **230**: 462–474.
- Farrant JM, Lehner A, Cooper K, Wiswedel S. 2009. Desiccation tolerance in the vegetative tissues of the fern *Mohria caffrorum* is seasonally regulated. *Plant Journal* **57**: 65–79. doi:10.1111/j.1365-313x.2008.03673.x.
- Fernández-Marín B, Nadal M, Gago J, et al. 2020. Born to revive: molecular and physiological mechanisms of double tolerance in a paleotropical and resurrection plant. *New Phytologist* **226**: 741–759.
- Gillespie L, Volaire F. 2017. Are winter and summer dormancy symmetrical seasonal adaptive strategies? The case of temperate herbaceous perennials. *Annals of Botany* **119**: 311–323.
- Grime JP. 1974. Vegetation classification by reference to strategies. *Nature* **250**: 26–31. doi:10.1038/250026a0.
- Grime JP. 1977. Evidence for existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* **111**: 1169–1194. doi:10.1086/283244.
- Grime JP. 2001. *Plant strategies, vegetation processes, and ecosystem properties*, 2nd edn. Chichester: John Wiley & Sons.
- Grubb PJ. 1998. A reassessment of the strategies of plants which cope with shortages of resources. *Perspectives in Plant Ecology, Evolution and Systematics* **1**: 3–31. doi:10.1078/1433-8319-00049.
- Hammond WM, Adams HD. 2019. Dying on time: traits influencing the dynamics of tree mortality risk from drought. *Tree Physiology* **39**: 906–909. doi:10.1093/treephys/tpz050.
- Hammond WM, Johnson DM, Meinzer FC. 2021. A thin line between life and death: radial sap flux failure signals trajectory to tree mortality. *Plant, Cell and Environment* **44**: 1211–1314.
- Hansen J, Beck E. 1988. Evidence for ideal and non-ideal equilibrium freezing of leaf water in frosthardy ivy (*Hedera helix*) and winter barley (*Hordeum vulgare*). *Botanica Acta* **101**: 76–82. doi:10.1111/j.1438-8677.1988.tb00014.x.
- Hare PD, Cress WA, Van Staden J. 1998. Dissecting the roles of osmolyte accumulation during stress. *Plant, Cell and Environment* **21**: 535–553. doi:10.1046/j.1365-3040.1998.00309.x.
- Horvath DP, Anderson JV, Chao WS, Foley ME. 2003. Knowing when to grow: signals regulating bud dormancy. *Trends in Plant Science* **8**: 534–540. doi:10.1016/j.tplants.2003.09.013.
- Keep T, Sampoux JP, Barre P, et al. 2021. To grow or survive: which are the strategies of a perennial grass to face severe seasonal stress? *Functional Ecology* **35**: 1145–1158. doi:10.1111/1365-2435.13770.
- Kleinwächter M, Radwan A, Hara M, Selmar D. 2014. Dehydrin expression in seeds: an issue of maturation drying. *Frontiers in Plant Science* **5**. doi:10.3389/fpls.2014.00402.
- Koehler K, Center A, Cavender-Bares J. 2012. Evidence for a freezing tolerance-growth rate trade-off in the live oaks (*Quercus* series *Virentes*) across the tropical-temperate divide. *New Phytologist* **193**: 730–744.
- Kong RS, Henry HAL. 2016. Prior exposure to freezing stress enhances the survival and recovery of *Poa pratensis* exposed to severe drought. *American Journal of Botany* **103**: 1890–1896. doi:10.3732/ajb.1600176.
- Kong RS, Henry HAL. 2018. Does cross-acclimation between drought and freezing stress persist over ecologically relevant time spans? A test using the grass *Poa pratensis*. *Plant Biology* **20**: 280–287.
- Kong RS, Henry HAL. 2019. Interactions of plant growth responses to spring freezing and summer drought: a multispecies comparison. *American Journal of Botany* **106**: 531–539. doi:10.1002/ajb2.1264.
- Krasensky J, Jonak C. 2012. Drought, salt, and temperature stress-induced metabolic rearrangements and regulatory networks. *Journal of Experimental Botany* **63**: 1593–1608. doi:10.1093/jxb/err460.
- Lamacque L, Charrier G, Farnese FS, Lemaire B, Ameglio T, Herbette S. 2020. Drought-induced mortality: branch diameter variation reveals a point of no recovery in lavender species. *Plant Physiology* **183**: 1638–1649. doi:10.1104/pp.20.00165.
- Lang GA. 1996. Preface. In: Lang GA, ed. *Plant dormancy: physiology, biochemistry and molecular biology*. Wallingford: CAB International.
- Larter M, Pfautsch S, Domec JC, Trueba S, Nagalingum N, Delzon S. 2017. Aridity drove the evolution of extreme embolism resistance and the radiation of conifer genus *Callitris*. *New Phytologist* **215**: 97–112. doi:10.1111/nph.14545.
- Lata C, Prasad M. 2011. Role of DREBs in regulation of abiotic stress responses in plants. *Journal of Experimental Botany* **62**: 4731–4748. doi:10.1093/jxb/err210.
- Laude HM. 1953. The nature of summer dormancy in perennial grasses. *Botanical Gazette* **114**: 284282–284292. doi:10.1086/335770.
- Lei SA. 2005. Ecotypic variation in summer dormancy of blackbrush (*Coleogyne ramosissima*) and its ecological significance. *Journal of the Arizona-Nevada Academy of Science* **38**: 1–5. doi:10.2181/1533-6085(2005)038[0001:evisdol]2.0.co;2.

- Lens F, Picon-Cochard C, Delmas C, *et al.* 2016. Herbaceous angiosperms are not more vulnerable to drought-induced embolism than angiosperm trees. *Plant Physiology* **172**: 661–667.
- Liu H, Able AJ, Able JA. 2021. Priming crops for the future: rewiring stress memory. *Trends in Plant Science* **27**: 699–716.
- Lubbe FC, Henry HAL. 2020. The role of perennation traits in plant community soil frost stress responses. *Annals of Botany* **126**: 873–881. doi:10.1093/aob/mcaa104.
- Lubbe FC, Klimesova J, Henry HAL. 2021. Winter belowground: changing winters and the perennating organs of herbaceous plants. *Functional Ecology* **35**: 1627–1639.
- Mantova M, Menezes-Silva PE, Badel E, Cochard H, Torres-Ruiz JM. 2021. The interplay of hydraulic failure and cell vitality explains tree capacity to recover from drought. *Physiologia Plantarum* **172**: 247–257. doi:10.1111/pp.13331.
- Martin-StPaul N, Limousin JM, Vogt-Schilb H, *et al.* 2013. The temporal response to drought in a Mediterranean evergreen tree: comparing a regional precipitation gradient and a throughfall exclusion experiment. *Global Change Biology* **19**: 2413–2426.
- Martin-StPaul N, Delzon S, Cochard H. 2017. Plant resistance to drought depends on timely stomatal closure. *Ecology Letters* **20**: 1437–1447. doi:10.1111/ele.12851.
- Maurya JP, Bhalerao RP. 2017. Photoperiod- and temperature-mediated control of growth cessation and dormancy in trees: a molecular perspective. *Annals of Botany* **120**: 351–360. doi:10.1093/aob/mcx061.
- Mayr S, Schwienbacher F, Bauer H. 2003. Winter at the alpine timberline. Why does embolism occur in Norway spruce but not in stone pine? *Plant Physiology* **131**: 780–792. doi:10.1104/pp.011452.
- McDowell N, Pockman WT, Allen CD, *et al.* 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist* **178**: 719–739. doi:10.1111/j.1469-8137.2008.02436.x.
- McDowell NG, Sapes G, Pivovarov A, *et al.* 2022. Mechanisms of woody-plant mortality under rising drought, CO<sub>2</sub> and vapour pressure deficit. *Nature Reviews Earth & Environment* **3**: 294–308.
- Nakashima K, Yamaguchi-Shinozaki K, Shinozaki K. 2014. The transcriptional regulatory network in the drought response and its crosstalk in abiotic stress responses including drought, cold, and heat. *Frontiers in Plant Science* **5**. doi:10.3389/fpls.2014.00170
- Oliveira RS, Eller CB, Barros FV, Hirota M, Brum M, Bittencourt P. 2021. Linking plant hydraulics and the fast–slow continuum to understand resilience to drought in tropical ecosystems. *New Phytologist* **230**: 904–923. doi:10.1111/nph.17266.
- Pearce RS. 2001. Plant freezing and damage. *Annals of Botany* **87**: 417–424. doi:10.1006/anbo.2000.1352.
- Perez-Harguindeguy N, Diaz S, Garnier E, *et al.* 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* **61**: 167–234.
- Pushpavalli R, Berger JD, Turner NC, Siddique KHM, Colmer TD, Vadez V. 2020. Cross-tolerance for drought, heat and salinity stresses in chickpea (*Cicer arietinum* L.). *Journal of Agronomy and Crop Science* **206**: 405–419. doi:10.1111/jac.12393.
- Quamme HA, Su WA, Veto LJ. 1995. Anatomical features facilitating supercooling of the flower within the dormant peach flower bud. *Journal of the American Society for Horticultural Science* **120**: 814–822. doi:10.21273/jashs.120.5.814.
- Reich PB. 2014. The world-wide ‘fast-slow’ plant economics spectrum: a traits manifesto. *Journal of Ecology* **102**: 275–301. doi:10.1111/1365-2745.12211.
- Rinne PLH, Schoof C. 2003. Plasmodesmata at the crossroads between development, dormancy, and defense. *Canadian Journal of Botany* **81**: 1182–1197.
- Sapes G, Roskill B, Dobrowski S, *et al.* 2019. Plant water content integrates hydraulics and carbon depletion to predict drought-induced seedling mortality. *Tree Physiology* **39**: 1300–1312. doi:10.1093/treephys/tpz062.
- Savage JA, Chuine I. 2021. Coordination of spring vascular and organ phenology in deciduous angiosperms growing in seasonally cold climates. *New Phytologist* **230**: 1700–1715. doi:10.1111/nph.17289.
- Shihan A, Barre P, Copani V, *et al.* 2022. Induction and potential role of summer dormancy to enhance persistence of perennial grasses under warmer climates. *Journal of Ecology* **110**: 1283–1295.
- Sibly RM, Calow P. 1989. A life-cycle theory of responses to stress. In: Calow P, Berry RJ, eds. *Evolution, ecology and environmental stress*. London: Academic Press, Linnean Society of London.
- Sperry JS, Sullivan JEM. 1992. Xylem embolism in response to freeze-thaw cycles and water stress in ring-porous, diffuse-porous, and conifer species. *Plant Physiology* **100**: 605–613. doi:10.1104/pp.100.2.605.
- Taborsky B, English S, Fawcett TW, *et al.* 2021. Towards an evolutionary theory of stress responses. *Trends in Ecology & Evolution* **36**: 39–48. doi:10.1016/j.tree.2020.09.003.
- Tebele SM, Marks RA, Farrant JM. 2021. Two decades of desiccation biology: a systematic review of the best studied angiosperm resurrection plants. *Plants (Basel)* **10**. doi:10.3390/plants10122784.
- Turbill C, Bieber C, Ruf T. 2011. Hibernation is associated with increased survival and the evolution of slow life histories among mammals. *Proceedings of the Royal Society B Biological Sciences* **278**: 3355–3363.
- Ummenhofer CC, Meehl GA. 2017. Extreme weather and climate events with ecological relevance: a review. *Philosophical Transactions of the Royal Society B Biological Sciences* **372**: 20160135.
- Urli M, Porte AJ, Cochard H, Guengant Y, Burlett R, Delzon S. 2013. Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees. *Tree Physiology* **33**: 672–683. doi:10.1093/treephys/tpt030.
- Vargas GG, Brodrribb TJ, Dupuy JM, *et al.* 2021. Beyond leaf habit: generalities in plant function across 97 tropical dry forest tree species. *New Phytologist* **232**: 148–161.
- Vegis A. 1964. Dormancy in higher plants. *Annual Review of Plant Physiology* **15**: 185–224. doi:10.1146/annurev.pp.15.060164.001153.
- Velappan Y, Signorelli S, Considine MJ. 2017. Cell cycle arrest in plants: what distinguishes quiescence, dormancy and differentiated G1? *Annals of Botany* **120**: 495–509. doi:10.1093/aob/mcx082.
- Verlues PE, Agarwal M, Katiyar-Agarwal S, Zhu JH, Zhu JK. 2006. Methods and concepts in quantifying resistance to drought, salt and freezing, abiotic stresses that affect plant water status. *Plant Journal* **45**: 523–539. doi:10.1111/j.1365-3113x.2005.02593.x.
- Vitasse Y, Lenz A, Korner C. 2014. The interaction between freezing tolerance and phenology in temperate deciduous trees. *Frontiers in Plant Science* **5**: 12.
- Volaire F. 2008. Plant traits and functional types to characterise drought survival of pluri-specific perennial herbaceous swards in Mediterranean areas. *European Journal of Agronomy* **29**: 116–124. doi:10.1016/j.eja.2008.04.008.
- Volaire F. 2018. A unified framework for plant drought adaptive strategies: across scales and disciplines. *Global Change Biology* **24**: 2929–2938. doi:10.1111/gcb.14062.
- Volaire F, Norton M. 2006. Summer dormancy in perennial temperate grasses. *Annals of Botany* **98**: 927–933. doi:10.1093/aob/mcl195.
- Volaire F, Conejero G, Lelievre F. 2001. Drought survival and dehydration tolerance in *Dactylis glomerata* and *Poa bulbosa*. *Australian Journal of Plant Physiology* **28**: 743–754.
- Volaire F, Gleason SM, Delzon S. 2020. What do you mean ‘functional’ in ecology? Patterns versus processes. *Ecology and Evolution* **10**: 11875–11885. doi:10.1002/ece3.6781.
- Wilsterman K, Ballinger MA, Williams CM. 2021. A unifying, eco-physiological framework for animal dormancy. *Functional Ecology* **35**: 11–31.
- Wisniewski M, Gusta L, Neuner G. 2014. Adaptive mechanisms of freeze avoidance in plants: a brief update. *Environmental and Experimental Botany* **99**: 133–140. doi:10.1016/j.envexpbot.2013.11.011.
- Wolfe BT, Sperry JS, Kursar TA. 2016. Does leaf shedding protect stems from cavitation during seasonal droughts? A test of the hydraulic fuse hypothesis. *New Phytologist* **212**: 1007–1018. doi:10.1111/nph.14087.
- Wright SJ, Kitajima K, Kraft NJB, *et al.* 2010. Functional traits and the growth–mortality trade-off in tropical trees. *Ecology* **91**: 3664–3674. doi:10.1890/09-2335.1.
- Wright IJ, Reich PB, Westoby M, *et al.* 2004. The worldwide leaf economics spectrum. *Nature* **428**: 821–827. doi:10.1038/nature02403.
- Yin X-H, Hao G-Y, Sterck F. 2022. A trade-off between growth and hydraulic resilience against freezing leads to divergent adaptations among temperate tree species. *Functional Ecology* **36**: 739–750.
- Yooyongwech S, Horigane AK, Yoshida M, *et al.* 2008. Changes in aquaporin gene expression and magnetic resonance imaging of water status in peach tree flower buds during dormancy. *Physiologia Plantarum* **134**: 522–533. doi:10.1111/j.1399-3054.2008.01143.x.
- Zhang QW, Bartels D. 2018. Molecular responses to dehydration and desiccation in desiccation-tolerant angiosperm plants. *Journal of Experimental Botany*, **69**: 3211–3222.