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CURRENT TOPICS IN ECOLOGY

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Xylem embolism refilling and resilience against drought-induced mortality in woody plants: processes and trade-offs

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Abstract Understanding which species are able to recover from drought, under what conditions, and the mechanistic processes involved, will facilitate predictions of plant mortality in response to global change. In response to drought, some species die because of embolism-induced hydraulic failure, whilst others are able to avoid mortality and recover, following rehydration. Several tree species have evolved strategies to avoid embolism, whereas others tolerate high embolism rates but can recover their hydraulic functioning upon drought relief. Here, we focus on structures and processes that might allow some plants to *recover* from drought stress via embolism reversal. We provide insights into how embolism repair may have evolved, anatomical and physiological features that facilitate this process, and describe possible trade-offs and related costs. Recent controversies on methods used for estimating embolism formation/repair are also discussed, providing some methodological suggestions. Although controversial, embolism repair processes are apparently based on the activity of phloem and ray/axial parenchyma. The mechanism is energetically demanding, and the costs to plants include metabolism and transport of soluble sugars, water and inorganic ions. We propose that embolism repair should be considered as a possible component of a 'hydraulic efficiency-safety' spectrum. We also advance a framework for vegetation models, describing how vulnerability curves may change in hydrodynamic model formulations for plants that recover from embolism.

Keywords Hydraulic conductivity · Plant hydraulics · Plant water relations · Recovery · Repair

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Introduction

How plants avoid mortality: resistance and recovery strategies

The frequency, duration and intensity of drought events are expected to increase in the coming decades in many regions of the globe (Kirtman et al. 2014). Why some plants die under drought stress while other co-occurring species resist or recover from stress remains an unresolved topic of recent investigation (e.g. McDowell et al. 2011; Schenk 2014). Plant hydraulic failure (catastrophic loss of hydraulic conductivity) is one of the major and widespread mechanistic causes of drought-induced mortality (Anderegg et al. 2012; Nardini et al. 2014). Much research has investigated how plants avoid hydraulic failure by preventing formation and spread of catastrophic xylem embolism (Brodribb and Cochard 2009; Pittermann et al. 2013). However, recent research suggests the existence of a spectrum of strategies ranging from 'resistance' to 'recovery', with some plants coming remarkably close to hydraulic failure, but recovering once xylem tension is partially or fully relaxed (Ogasa et al. 2013; Martorell et al. 2014). Indeed, many woody plants commonly operate at xylem pressures close to critical thresholds for runaway embolism (i.e. with narrow safety margins) (Choat et al. 2012). This suggests that many species routinely suffer the risk of reaching high levels of xylem embolism, with angiosperms tending to have smaller safety margins than gymnosperms. A high loss of conductivity has been reported also in drought-surviving individuals (> 50%) of different species, hinting at a possible survival strategy based on post-drought hydraulic recovery, rather than a strategy relying on complete hydraulic safety (Klein et al. 2011; Trifilò et al. 2015).

Woody plants can refill embolised xylem conduits via spontaneous bubble dissolution once xylem pressure nears atmospheric values, or under positive root/stem pressure (Nardini et al. 2018). Trees can also repair the total conducting area following seasonal replacement through regrowth of new xylem (Brodersen and McElrone 2013; Nardini et al. 2014). However, debate remains over how and when woody plants can refill embolized xylem conduits under residual negative water potential, so called ''novel refilling'' (Hacke and Sperry 2003; Brodersen and McElrone 2013) and which methods are appropriate for studying embolism formation and its reversal in plants (Rockwell et al. 2014). The 'novel refilling' phenomenon is very controversial, and some researchers have argued that embolism refilling under any residual negative pressure in still functional xylem is unlikely or impossible due to thermodynamic constraints (Zwieniecki and Holbrook 2000; Rockwell et al. 2014; but see also Gouin 2015). Some researchers have also suggested that methodological uncertainties call for a thorough re-evaluation of current evidence for embolism reversal (Cochard and Delzon 2013; Torres-Ruiz et al. 2015; Charrier et al. 2016). However, the available evidence around this phenomenon suggests that embolism reversal might be an important vital process essential for plant hydraulic functioning in some or even several plant species (Nardini et al. 2011a). Hence, understanding the process of hydraulic recovery, and why it occurs in some plants and not in others, would improve the robustness of predictions of plant mortality in future climates.

In this paper, we synthesise recent experimental studies on embolism reversal, focusing on currently available methods and techniques to investigate the phenomenon, and related possible pitfalls. Then, we describe structures and processes possibly facilitating embolism reversal, followed by a conceptual framework adding 'recovery' to the safety-efficiency spectrum, and finally present a modelling framework to evaluate if, when and where xylem refilling may be an important ecological process.

Defining recovery

Plants frequently experience physiological stress from disturbance events including heat waves, drought, fire, or freezing. When of extreme duration and/or intensity, such stress factors can result in significant damage eventually leading to death. However, following disturbance, plants can avoid mortality by repairing damage, thus experiencing either partial or complete recovery. Post-stress recovery has been observed at the leaf, tree and landscape scale and can take from days to weeks (Brodribb et al. 2010), months to years (Zeppel et al. 2008), or even decades (Vertessy et al. 2001).

Full recovery may be defined as when 'pre-disturbance' levels in defined parameters are reached. From a structural viewpoint, complete recovery of biomass or leaf area index (LAI) after disturbance might represent convenient reference points (Kelley et al. 2014). Alternatively, hydraulic recovery may be defined as the point when plants reach pre-disturbance levels of transpiration, stomatal conductance (Brodribb et al. 2010), or hydraulic conductivity (Ogasa et al. 2013). A trade-off between embolism resistance and refilling ability, mediated by contrasting wood functional traits such as dense and embolism-resistant xylem *versus* less dense but refillable xylem has been reported (Ogasa et al. 2013; Trifilò et al. 2015). Following severe drought, different species may use different strategies and take different times to recover their pre-drought hydraulic status (Brodribb et al. 2010). Some recent studies describe how plants may use recovery from embolism as a mortality avoidance, or resilience strategy. However, the actual trade-offs between wood structural traits, xylem vulnerability and recovery ability among different tree species are not fully understood (Johnson et al. 2012). We now discuss potential trade-offs in mortality avoidance strategies.

Mortality avoidance strategies: resisting drought stress

Across time and spatial scales, short-term responses and long-term adaptations to avoid mortality

Plants can adopt different strategies for avoiding drought-induced mortality at different time-scales and organisational levels (see Nardini et al. 2014). For example, over the short-term, stomata close and plants rely on stored carbohydrates to fuel metabolism (Klein et al. 2014). Some species adjust their hydraulic efficiency both at the apoplastic level ('ionic effect'; Nardini et al. 2011b) and the symplastic level through aquaporins (Javot and Maurel 2002) to reduce resistance of water transport and buffer xylem pressure drops. Over the long-term, an increased root-to-shoot biomass ratio can also accomplish this task (Klein et al. 2011). Alternatively, water-use can be decreased in some species by shedding leaves (Tyree et al. 1993) or branches (Rood et al. 2000). Some species shift activity to periods when sufficient water is available (Nardini et al. 1998). Finally, disrupting the hydraulic path between the leaf and stem (Zufferey et al. 2011) or root and soil interface in some species avoids water loss and very low water potentials (Carminati et al. 2013). Over medium time scales (months–years), adjustments in the xylem anatomy are central to many drought avoidance strategies. For example, a reduction in conduit diameter is commonly observed during periods of acute water stress (von Arx et al. 2012), although opposite trends have also been reported (Bouche et al. 2014). Adjustments in pit characteristics may allow increased resistance to drought-induced embolism (Lens et al. 2011). The thickness of conduit cell walls also apparently adjusts in response to drought stress, with thicker walls providing increased mechanical strength to withstand lower water potential and prevent cell implosion (Hacke et al. 2001).

The occurrence and significance of embolism recovery

Is recovery from xylem embolism unique to a small set of tree species, from specific biomes, or is it rather ubiquitous? In the past few years research on xylem refilling has been rapidly increasing: the number of scientific papers containing "xylem refilling" has increased from 26 published in 2011 to 80 published in 2016. Since the last review by Brodersen and McElrone (2013) several additional species have been investigated (Table 1; Fig. 1). Overall, xylem refilling emerges as a cross-species, cross-biome phenomenon. In 33 of 43 species surveyed here, the level of native embolism decreased significantly with time following peak drought, suggesting the occurrence of refilling mechanisms. Three additional species showed visually rapid refilling, which was not directly quantified (Table 1). Most of the studied species showing evidence of embolism reversal were angiosperm trees, but observations included key gymnosperms such as *Picea abies*, *Picea glauca*, and *Pinus halepensis*, as well as shrubs, lianas, and cushion plants (Table 1). Almost two-thirds of the observations were in mature woody plants, and 78% were done on field-grown plants. Remarkably, 54% of the case studies did not include rewatering of the plants (Table 1), indicating that embolism formation and reversal might be part of a routine physiological process in some species, rather than a post-drought occurrence. In all studied species, the refilling process was accompanied by partial relaxation of xylem tension, observed by concomitant increase in shoot water potential, typically to levels above − 1.0 MPa, but still moderately negative (Fig. 1). The literature survey compiled here is still too small to draw conclusions on the partitioning of refilling among species and biomes. Yet, it is intriguing that species from temperate ecosystems had relatively high levels of embolism (37–94%), and typically showed the most efficient recovery (PLC, percent loss of conductivity, decreasing overnight by about 40%). Conversely, many species from Mediterranean ecosystems did not recover or showed relatively mild recovery (PLC decreased overnight by about 20%). This observation might relate to eco-physiological processes described below. More importantly, the 10 cases where no refilling was observed were mostly those where a decrease in PLC was mild or simply not statistically significant. For example, PLC in *Carpinus tschonoskii* stems decreased from 67% at − 3.9 MPa to 48% at − 0.2 MPa in one experiment (Ogasa et al. 2013), and from 70% at − 3.3 MPa to 35% at − 0.2 MPa in another experiment (Umebayashi et al. 2016); only the latter observation was significant. Therefore, we cannot exclude the possibility that almost all woody plants are capable of xylem refilling to some extent.

How do we measure embolism recovery or refilling?

Measurements of xylem embolism and subsequent recovery are often restricted by our limited ability to directly observe in vivo the functional status of xylem conduits. Hence, much evidence comes from indirect observations, using destructive and non-destructive methods. Here, we describe their strengths and weaknesses.

Destructive measurements

Destructive measurements of xylem hydraulics can potentially introduce a change to the native status of conduits, thus altering the object of study (Rockwell et al. 2014). However, higher replication possibilities and lower equipment costs make these methods among the most accessible and used in different laboratories. During the past recent decades, measurements of hydraulic conductivity on branch sections became the state-of-the-art methodology for embolism detection and calculation

Table 1 Study cases on xylem refilling published since 2013, divided by biome and woody plant species. Source references are: (1) Leng et al. (2013); (2) Zwieniecki et al. (2013); (3) Ooeda et al. (2016); (4) Ogasa et al. (2013); (5) Umebayashi et al. (2016); (6) Martorell et al. (2014); (7) Christman et al. (2012); (8) Choat et al. (2015); (9) Laur and Hacke (2014); (10) Mayr et al. (2014); (11) Christensen-Dalsgaard et al. (2014); (12) Rolland et al. (2015); (13) Ganthaler and Mayr (2015); (14) Trifilo et al. (2015); (15) Savi et al. (2016); (16) Klein et al. 2016; (17) Li et al. (2016); (18) Chen et al. (2017)

Species	Setting	Plants	PLC50	Method	Rewatering?	Refilling?
Temperate						
Populus alba × *P. glandulosa* (1)	G	Seedlings	NA	HHF	Y	Y
Acer rubrum (2)	G	2, 20 years	– 2.70	MRI	N	Y$^{(*)}$
Morus australis (3)	G	Potted plants	NA	HHF	Y	Y
Salix integra (4)	EF	1 year	– 1.08	HHF	Y	Y
Salix Babylonica (4)	EF	1 year	– 1.04	HHF	Y	Y
Salix Cheilophila (4)	EF	1 year	– 1.70	HHF	Y	Y
Salix Psammophila (4)	EF	1 year	– 1.18	HHF	Y	Y
Betula platyphylla (4)	EF	2–3 years	– 1.96	HHF	Y	Y
Cerasus jamasakura (4)	EF	2–3 years	– 3.62	HHF	Y	N
Carpinus tschonoskii (4)	EF	2–3 years	– 3.88	HHF	Y	N
Carpinus tschonoskii (5)	G	2 year potted plants	NA	C-SEM, MRI	Y	Y
Eucalyptus pauciflora (6)	G	2 year potted plants	– 1.61	HHF	Y	Y
Quercus gambelii (7)	F	5–8 years	– 1.08	HHF	N	Y
Sequoia sempervirens (8)	G	Seedlings	– 1.80	uCT	Y	N$^{(**)}$
Boreal/Alpine/Frost						
Picea glauca (9)	G	3 years saplings	– 4.30	HHF	N	Y
Picea abies (10)	F	Mature trees	– 3.98	HHF	Y	Y
Malus domestica (11)	F	Mature trees	– 3.95	Cavitron	N	Y
Populus deltoides x P. laurifolia x xP. Nigra (11)	F	Mature trees	– 1.70	Cavitron	N	Y
Salix dasyclados (11)	F	Mature trees	– 1.70	Cavitron	N	Y
Azorella macquariensis (12)	F	Mature cushion plants	NA	BFM	Y	Y$^{(***)}$
Colobanthus muscoides (12)	F	Mature cushion plants	NA	BFM	Y	Y$^{(***)}$
Vaccinium myrtillus (13)	F	Mature dwarf shrubs	– 2.08	HHF	Y	Y
Vaccinium vitis-idaea (13)	F	Mature dwarf shrubs	– 1.97	HHF	Y	Y
Mediterranean						
Ceratonia siliqua (14)	F	Adult trees	– 2.60	HHF	N	Y
Laurus nobilis (14)	F	Adult trees	– 2.50	HHF	N	Y
Nerium oleander (14)	F	Adult trees	– 1.50	HHF	N	Y
Pistacia lentiscus (14)	F	Adult trees	– 4.10	HHF	N	N
Quercus ilex (14)	F	Adult trees	– 3.30	HHF	N	N
Eucalyptus camaldulensis (14)	F	Adult trees	– 4.60	HHF	N	Y
Myrtus communis (14)	F	Adult trees	– 3.10	HHF	N	N
Olea europaea (14)	F	Adult trees	– 2.10	HHF	N	Y
Olea oleaster (14)	F	Adult trees	– 4.10	HHF	N	N
Quercus pubescens (15)	G	Potted plants	NA	HHF	Y	Y
Prunus mahaleb (15)	G	Potted plants	NA	HHF	Y	N
Robinia pseudoacacia (15)	G	Potted plants	NA	HHF	Y	N
Ailanthus altissima (15)	G	Potted plants	NA	HHF	Y	Y
Semi-arid						
Pinus halepensis (16)	F	40 years	– 3.10	HHF	N	Y
Salix psammophila (17)	F	Adult shrubs	– 1.70	HHF	N	Y
Caragana korshinskii (17)	F	Adult shrubs	– 2.70	HHF	N	N
Tropical						
Celtis tetrandra (18)	EF	Mature trees	– 1.53	HHF	N	Y
Ficus concinna (18)	EF	Mature trees	– 1.43	HHF	N	Y
Harpullia cupanioides (18)	EF	Mature trees	– 2.51	HHF	N	N
Michelia hypolampra (18)	EF	Mature trees	– 2.25	HHF	N	Y
Streblus asper (18)	EF	Mature trees	– 2.93	HHF	N	Y
Celastrus paniculatus (18)	EF	Mature lianas	– 1.42	HHF	N	Y
Marsdenia sinensis (18)	EF	Mature lianas	– 1.04	HHF	N	Y
Ventilago calyculata (18)	EF	Mature lianas	– 1.57	HHF	N	Y

Numbers in parentheses indicate the reference number of the respective study in the reference list. The observed changes in embolism level for each species are in Fig. 1, except where not quantified: (*) refilling visually significant after 30 min; (**) no refilling observed; and (***) bubbles removed in 50 s

Setting: *EF* experimental field, *F* field, *G* greenhouse. PLC50: The shoot water potential (MPa) at 50% percent loss of xylem conductivity. Method: *BFM* bright-field microscopy, *HHF* hydraulic head and flushing, *MRI* magnetic resonance imaging, *C-SEM* cryo-scanning electron microscopy, *uCT* micro computed tomography

of PLC, i.e. the relative change in xylem conductivity between native and water-saturated states, usually taken as a proxy for the embolism level. Although still implicit and invasive to a certain degree, hydraulic conductivity measures directly the consequence of embolism, and the technique has been the basis for early descriptions of the

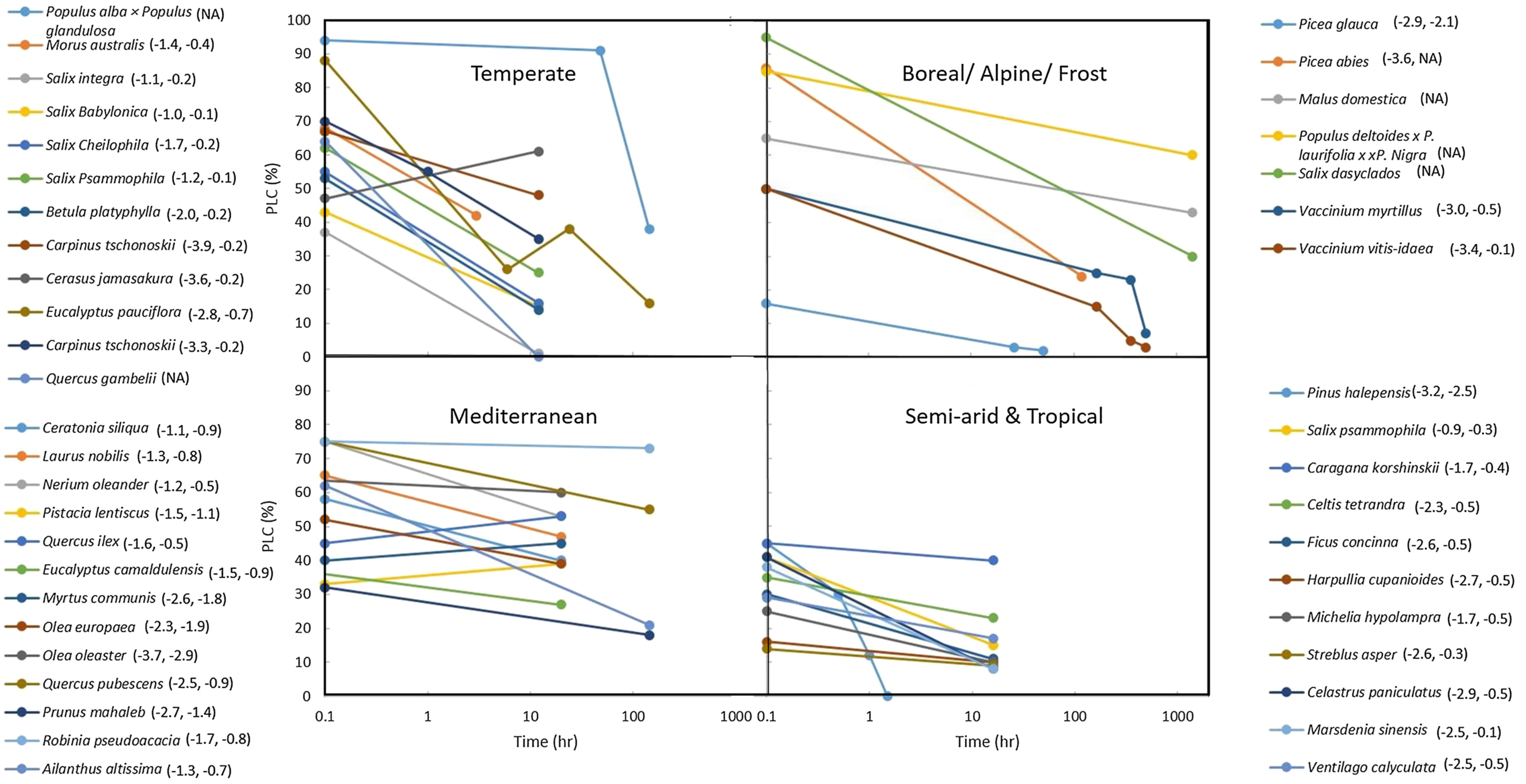


Fig. 1 Embolism dynamics in woody plant species reported in the scientific literature between 2013 and 2017 (for more details see Table 1). Note the logarithmic scale in the x axes. Numbers in parentheses indicate the shoot water potentials (MPa) measured at the start and the end of the observation period, respectively. Embolism dynamics exclude changes related to new xylem growth, even in the longer observation periods (top right panel). Significant refiling (decrease in PLC, percent loss of conductivity) is evident in 33 of the 43 species (Colour figure online)

embolism reversal phenomenon (Salleo et al. 1996). Measurements of PLC can be made on (1) samples collected in the field at different daytime/season, (2) samples from branches air-dehydrated in the lab, (3) stem segments where embolism is induced through air-injection, or (4) by inducing tension in the xylem by centrifugal forces.

Methodological precautions

When using hydraulic methods to quantify PLC, there are some restrictions set by inherent xylem properties (e.g. resin excretion in some conifers), and by sampling procedures. Three possible pitfalls have been proposed:

(1) When long-vesselled branches are measured using air-injection or cavitron methods, it is suggested that the ratio of open vessels in the sample must be quantified and removed from the PLC calculation (Cochard and Tyree 1990), as some authors have reported a long-vessel artefact in olives (Torres-Ruiz et al. 2014) and grapevines (Choat et al. 2010). However, we note that the long-vessel artefact has been rebutted by other studies (Sperry et al. 2012; Hacke et al. 2014), and this issue remains unresolved.

(2) To avoid artefactual embolism induction caused by the cutting of a branch, while the xylem is under tension, rehydration/relaxation of samples has been suggested, followed by re-cutting under degassed water (Wheeler et al. 2013), although this artefact has not been found by others (Venturas et al. 2015). Alternatively, the relaxation procedure has been shown to introduce other potential errors related to rehydration-induced embolism refilling (Trifilò et al. 2014b). Recommendations for standardizing measurements of vulnerability curves have recently been described (Torres-Ruiz et al. 2014). Future research should carefully evaluate the occurrence and magnitude of cutting or relaxation artefact in species investigated for their refilling capability. Trifilò et al. (2014b) suggested the use of refilling inhibitors (e.g. orthovanadate) to investigate the impact of cutting and relaxation on PLC values. A careful re-evaluation of PLC recovery in species already tested in previous studies would also help to assess the eventual impact of experimental artefacts in trends reported in Fig. 2.

(3) In conifer branches where torus margo sealing occurs in the pits when subjected to high pressure, embolism removal to quantify maximum hydraulic conductivity should be achieved by long (e.g. overnight) vacuum-infiltration (Delzon et al. 2010), and not by high pressure that might lead to pit membrane sealing and prevent embolism displacement. Finally, it is critical that studies report not only the PLC, but also either the sapwood area-specific conductivity or leaf-specific conductivity and ideally the area under the vulnerability curve, which will enable readers to compare absolute values of branch conductivity across studies and temporal scales.

Early non-destructive methods

A variety of non-destructive, indirect methods have been used to quantify changes in hydraulic conductivity upon drought stress and recovery. We define them here as non-destructive in the sense that they permit focused analysis of undisturbed part of the xylem. Patterns of sap flow coupled to measurements of water potential gradients, acoustic emissions, and sapwood water content have been used to infer changes in the relative level of embolism (see Brodersen and McElrone 2013 and references below). A caveat to some of the non-destructive methods is that observed changes can be interpreted in relation to a number of environmental factors, including changes in light intensity or temperature, which might result in hydraulic properties that do not necessarily represent the result of embolism formation or refilling.

An exception to the aforementioned methods is the measurement of acoustic emissions, developed to detect embolism. Despite early successes (Pena and Grace 1986), acoustic emissions were not fully consistent with other methods, and were advised to be used as a qualitative, complementary method (Jackson and Grace 1996). Recent advances have solved some of the issues associated with interpretation of signals with promising results (Nolf et al. 2015).

Recent non-destructive methods

The increasing interest in the physiology of embolism and plant water transport has led to the use of advanced technologies, including Magnetic Resonance Imaging MRI (Holbrook et al. 2001; Nolf et al. 2015), X-ray microtomography (Cochard et al. 2015), and cold neutron radiography (Tötzke et al. 2013). Validation and results from some of these newer techniques remain under debate (Rockwell et al. 2014). High resolution imaging of xylem embolism has been enabled by cryogenic scanning electron microscopy for over a decade (cryo-SEM; Utsumi et al. 1998), but this procedure laborious and not free of artefacts (Cochard et al. 2000). Nuclear MRI has been used to monitor water flow at high spatial and temporal resolutions in vivo (Fukuda et al. 2015). X-ray microcomputed tomography (microCT), likely the most promising technique in terms of resolution and with new desktop devices on the market, has been used to assess embolism dynamics in near real-time using 3D time-lapse imaging (Brodersen 2013). The microCT technique has provided evidence for embolism refilling in the xylem of grapevine (Brodersen and McElrone 2013) but also revealed no novel refilling oc-

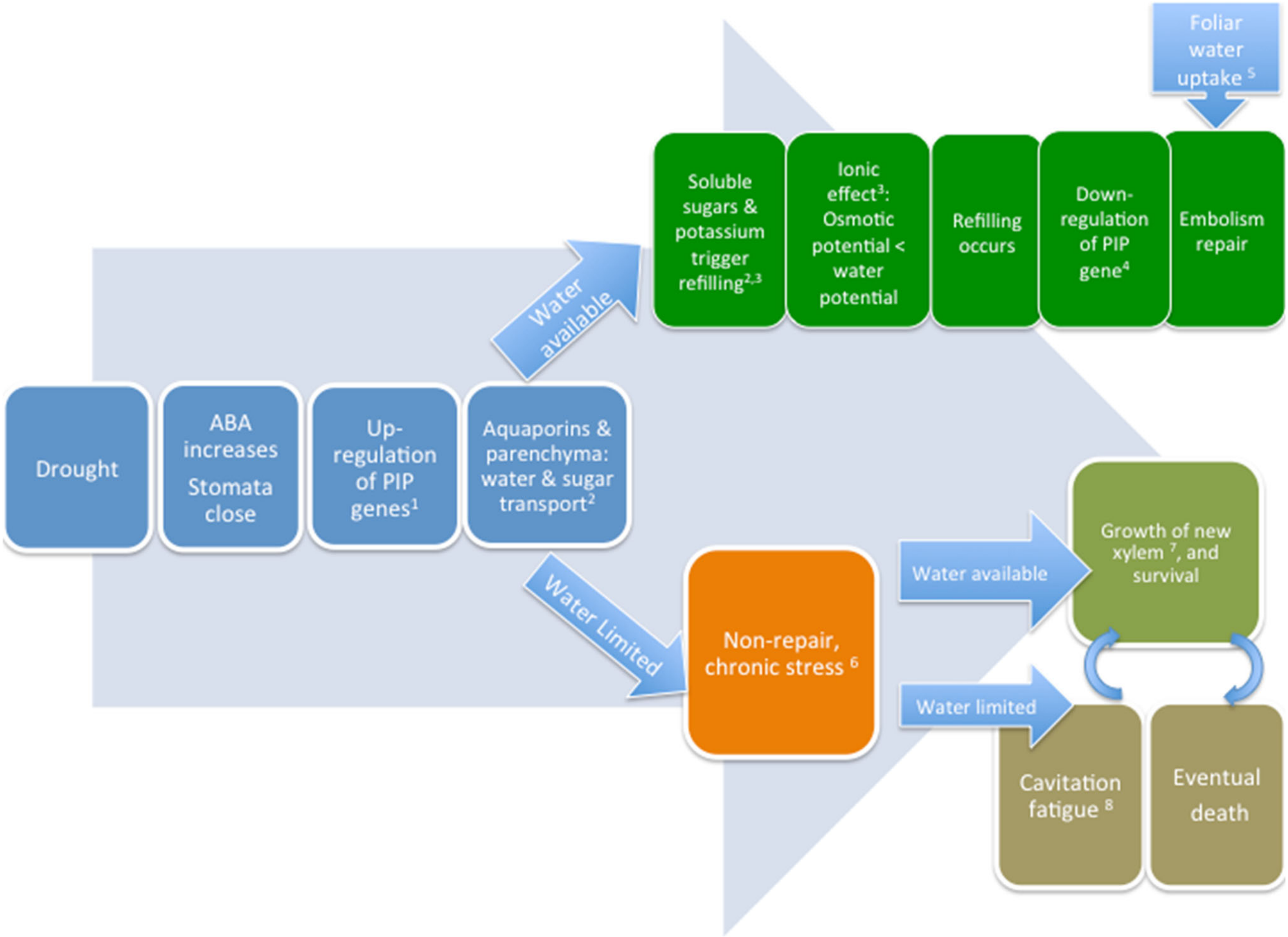


Fig. 2 A schematic diagram of processes involved in the recovery from embolism, for species which have the ability to refill (see "Hydraulic and embolism recovery"). If water is present and the osmotic potential is more negative than the water potential, due to the ionic effect, then water may be drawn into embolised conduits and refill them. Chronic stress and cavitation fatigue may result if water remains limiting. Source references include (but are not limited to) (1) Secchi and Zwieniecki (2010); (2) Laur and Hacke (2014) Chitarra et al. (2014); (3) Jansen et al. (2011), Nardini, Salleo and Jansen (2011), Trifilo et al. (2014); (4) Secchi and Zwieniecki (2010); (5) Grotsch et al. (2013), Laur and Hacke (2014) and Mayr et al. (2014); (6) Sperry and Love (2015); (7) Brodersen and McElrone (2013); (8) Anderegg (2015) and Hacke et al. (2001) (Colour figure online)

curred in coastal redwoods, the *Sequoia* (Choat et al. 2015). Interestingly, *Sequoia* is a resprouter (Zeppel et al. 2015), which may be an alternative or complementary recovery strategy to embolism refilling. Indeed, much of our knowledge of embolism refilling has been conducted on only a few woody species, including grapevines (Choat et al. 2010; Zufferey et al. 2011; Chitarra et al. 2014), Bay laurel (Trifilò et al. 2014a) and poplar (Bloemen et al. 2016). Clearly, additional studies on different species and plant functional types are urgently required to understand forest vulnerability and resilience to extreme droughts, probably beyond the capacity of direct imaging techniques. In fact, these methods require considerable time and budget investment and should hence focus on in-depth questions of embolism dynamics in selected woody species. Moreover, many of the non-invasive studies have low replication, measuring one tree in one or two species, and generally on very young trees whose xylem properties may not reflect mature individuals (McDowell et al. 2013). Still, it is very important that simple and affordable techniques, like the hydraulic ones, are validated with in vivo imaging, to be confident about the output of large-scale hydraulic surveys of embolism formation/reversal.

Three recent studies have cross-validated hydraulic measurements of PLC versus estimates of loss of conductivity based on direct microCT observation of the functional status of xylem conduits in *Laurus nobilis* (Nardini et al. 2017), *Helianthus annuus* (Savi et al. 2017), and *Eucalyptus camaldulensis* (Nolf et al. 2017), reporting substantial agreement between the two techniques. Moreover, Fukuda et al. (2015) have validated hydraulic measurements of PLC in *Cercidiphyllum japonicum* and *Betula platyphylla* var. *japonica* via direct MRI observations of embolism rate in intact seedlings. Further comparisons of different methods, within the same laboratory, using the same plant material, would be a step towards methodological consensus. However, it is not clear to what extent microCT techniques can be considered as reliable instruments to detect vital processes, like embolism reversal, apparently based on the activity of living parenchyma cells (see below). In fact, the X-ray dose supplied during the microCT scans might be high enough to damage cells (Charrier et al. 2016, Savi et al. 2017) and possibly impede embolism reversal.

Hydraulic and embolism recovery: which structures and processes facilitate conduits refilling?

We categorize hydraulic recovery as occurring under three different circumstances: (1) growth of new xylem (Christensen-Dalsgaard and Tyree 2014); (2) refilling from spontaneous bubble dissolution when xylem pressure nears atmospheric values (Brodersen and McElrone 2013) or becomes positive under root pressure regulation (see Brodersen and McElrone 2013); (3) embolism repair while the bulk of xylem is still under tension (Nardini et al. 2014). While much agreement exists around the first two possibilities, debate remains about the occurrence and mechanisms of the third phenomenon, and around methods used to detect and quantify the refilling process. Here, we discuss structures and processes which are thought to enable embolism reversal (see Fig. 2). We then discuss evidence for and against so-called embolism reversal under tension, here referred to as 'novel refilling' (Brodersen and McElrone 2013). Two defining features of novel refilling are that it occurs on short time scales (hours to over-night) and while still functional xylem is under negative pressure. Whether embolism reversal occurs will depend on (1) species-specific ability to refill embolized conduits, (2) the degree of soil rewetting after rain (and the resulting post-drought residual xylem tension), and (3) the severity of drought stress the plant has experienced. It is currently unclear how much xylem tension must relax in each refilling-species before novel refilling commences, and whether there are maximum PLC levels that cannot be reversed at all. However, most studies to date have reported embolism reversal only when xylem tension rises above -0.5 MPa.

Various structures, including roots, phloem, xylem, parenchyma, aquaporins, and xylary chloroplasts have been mechanistically linked with embolism refilling. Current research suggests that embolism refilling is based on osmotic gradients generated by sugars and ions released in refilling conduits, and driving water inflow via intact xylem, phloem and parenchyma (Fig. 2). In this scenario, starch degradation appears to play a key role in providing the osmotica (Salleo et al. 2004; Secchi and Zwieniecki 2012), while aquaporins are required to reduce hydraulic resistance along the symplastic pathway (Mayr et al. 2014). Phloem transport has also been demonstrated to be involved in embolism reversal, as different studies showed that phloem girdling inhibits the process (Salleo et al. 2004; Nardini et al. 2014).

Xylem refilling may vary with stem age and position. Vessels close to the bark have been reported to refill faster than inner ones in grapevine segments (Wang et al. 2013), and current year xylem showed refilling over 12 h in *Betula platyphylla* whereas older xylem remained embolised (Ogasa et al. 2010). Similarly, while rapid refilling was observed in young wood of *Acer rubrum*, older wood showed no signs of recovery (Zwieniecki et al. 2013).

Axial and ray parenchyma have been suggested to influence embolism reversal (see Plavcova and Jansen 2015, for a review of xylem anatomy). Evidence for a role of parenchyma in providing water and carbohydrates have been reported in many studies. In particular, the role of living cells as sources of sugars transported into the embolised vessels has been supported by some studies (Salleo et al. 2004; Trifilò et al. 2014a). While axial parenchyma is more abundant in angiosperm species, ray parenchyma is present in most species and shows a high integration with the xylem conduits that may ensure that each conduit is connected to living cells (Fonti et al. 2015). A review of the amount of ray parenchyma in 38 gymnosperms and 54 angiosperms, found a mean of 7% of sapwood in gymnosperms and 17% in angiosperms (Myer 1922).

Aquaporin channels, which facilitate the transport of water through membranes, are also reported to influence embolism-refilling rates (Chitarra et al. 2014; Laur and Hacke 2014). Specifically, plasma membrane intrinsic proteins (PIP) are often up-regulated before or during refilling. Secchi and Zwieniecki (2010) reported that *Populus trichocarpa* showed considerable up-regulation of the PIP1 subfamily of aquaporin water channels, and down-regulation of the same isoform was detrimental to recovery (Secchi and Zwieniecki 2014). In grapevines, two aquaporin genes were activated on stress or refilling, suggesting a specific role in xylem embolism refilling (Chitarra et al. 2014). Finally, xylary chloroplasts have been observed in close proximity to xylem vessels and were suggested to play a role in refilling of embolism, in Australian mangrove species (Schmitz et al. 2012) and in poplar (Bloemen et al. 2016).

Processes

Osmotic gradients generated by the release of ions (Tyree et al. 1999) and sugars in embolized conduits are thought to be fundamental for embolism refilling (Nardini et al. 2011a). Refilling conduits have more negative osmotic potential than still functioning ones (Secchi and Zwieniecki 2012). In a hypothetical scenario that found partial experimental confirmation, drought-induced rise in abscisic acid (ABA) concentration would lead to up-regulation of several genes in vessel-associated parenchyma, including those coding for aquaporins and enzymes related to carbohydrate metabolism and starch degradation (Secchi and Zwieniecki 2010). An increased sugar concentration in conduits would create a local positive pressure, promoting phloem unloading to parenchyma cells that would become strong sinks for both carbohydrates and water (Nardini et al. 2011b). The described mechanism requires the availability of water, possibly at a sufficient free energy level, and active metabolism and phloem functioning. Related research questions which can shed light on the refilling mechanism are: (1) is there a water potential threshold below which refilling is impossible? (2) Are turgor gradients in the phloem linked to refilling capacity? (3) Is there a threshold concentration of non-structural carbohydrates (NSC) below which refilling is completely impaired? (4) How are NSC concentrations linked to an eventual 'xylem pressure threshold'? Moreover, repeated embolism events have been shown to lead to cavitation fatigue (or air-seeding fatigue, i.e. the inability to repeatedly refill vessels) and may result in death many years after drought (Anderegg 2015), according to the chronic stress hypothesis (Sperry and Love 2015). However, it is not known whether the recovery ability of plants can also undergo significant 'fatigue' over repeated drought events, as a function of tissue damage and progressive depletion of NSC reserves.

Foliar water or fog uptake may also be involved in embolism refilling (Gotsch et al. 2014; McCulloh et al. 2014). Foliar water uptake was reported when relative humidity was high, providing a potential source of water in *Picea abies* (Mayr et al. 2014), *Drimys brasiliensis* (Eller et al. 2013) and *Picea glauca* (Laur and Hacke 2014).

How does xylem refilling relate to xylem vulnerability (P50) among woody plant species?

By contrasting species-specific data on xylem refilling capacity and xylem vulnerability (Brodersen and McElrone 2013; Choat et al. 2012 respectively), we raise the hypothesis that species where xylem refilling has been identified have relatively higher (less negative) values of P50 (water potential at 50% loss of conductivity) than others. A preliminary analysis, using species where data were available to date, for both xylem refiling capacity and P50 values, showed that P50 was on average 0.8 MPa higher in refiller vs. other species ($P = 0.02$, 11 refillers and 212 others). Two experimental studies found a positive correlation between xylem recovery and P50 in eight (Ogasa et al. 2013) and nine woody species (Trifilò et al. 2015), supporting the hypothesis. We note however two important caveats: (1) there are very few data on species that do not refill, therefore more data are required to test this hypothesis, and (2) different methods have been used to measure P50 across studies (Brodersen and McElrone 2013). Although no thorough conclusions can be drawn from these data, we present this as a hypothesis to be tested once data on additional species are available. Thus, future research is needed to describe genera/species that do not refill, and compare the structure of these species with species that do refill under comparable conditions (Trifilò et al. 2015).

A new framework: safety–efficiency–recovery

The hydraulic safety–efficiency framework involves a trade-off between the ability to (1) maximise water transport, known as high 'efficiency', and (2) avoiding high levels of xylem embolism, known as 'safety' (McCulloh et al. 2014). High efficiency involves plants transporting water quickly, while high safety entails the ability to withstand very negative water potentials, which may also decrease conductivity (Brodribb and Holbrook 2004). Wood capacitance can also buffer against transient drought and increase hydraulic safety (McCulloh et al. 2014). Here we introduce recovery as an additional dimension, where plants can be both relatively efficient and resilient against hydraulic failure due to their ability to repair embolism (Fig. 3). We hypothesize that species that use high-risk hydraulic strategies would also have higher ability to refill embolism (see Fig. 3). In contrast, species that are more conservative, with less risky hydraulic strategies may not need the ability to refill embolism (Ogasa et al. 2013).

Dry biomes contain coexisting species with contrasting drought resilience strategies, and as such, are likely to represent habitats where some species use embolism refilling. One example is a mixed thermo-Mediterranean forest. *Quercus calliprinos* is a sclerophyllous oak species that maintains high gas-exchange rates throughout the 5–7 month dry season and often reaches water potentials below − 4.0 MPa (Klein et al. 2013). This species is, however, supplied with water from deep roots. The co-existing cypress *Cupressus sempervirens* has limited capacity to increase stomatal conductance, but has a high xylem resistance to embolism (P50 = − 10.4 MPa), and extends its activity range to lower water potentials. *Pinus halepensis* is another co-existing conifer, characterized by relatively low stomatal conductance and a vulnerable xylem (P50 = − 3.1 MPa). Living in this dry environment, *P. halepensis* is inevitably exposed to xylem embolism (Klein et al. 2011). Among the oak, cypress, and pine, embolism is routine only in *P. halepensis*, where both embolism formation and recovery have been observed (Klein et al. 2013). This Mediterranean study provides an example of how embolism refilling may be one of the strategies that one, but not all of the co-occurring species, use to tolerate drought. Further studies like this that examine a range of hydraulic traits will improve our understanding of which species and traits are correlated with embolism refilling.

Modelling hydraulic recovery in vulnerability curves

A consideration of hydrodynamics has a long history of development in stand-scale models (e.g. Williams et al. 1996; Bohrer et al. 2005), ecosystem models (Duursma and Medlyn 2012; Christoffersen et al. 2016), and terrestrial biosphere models (Xu et al. 2016). However, to

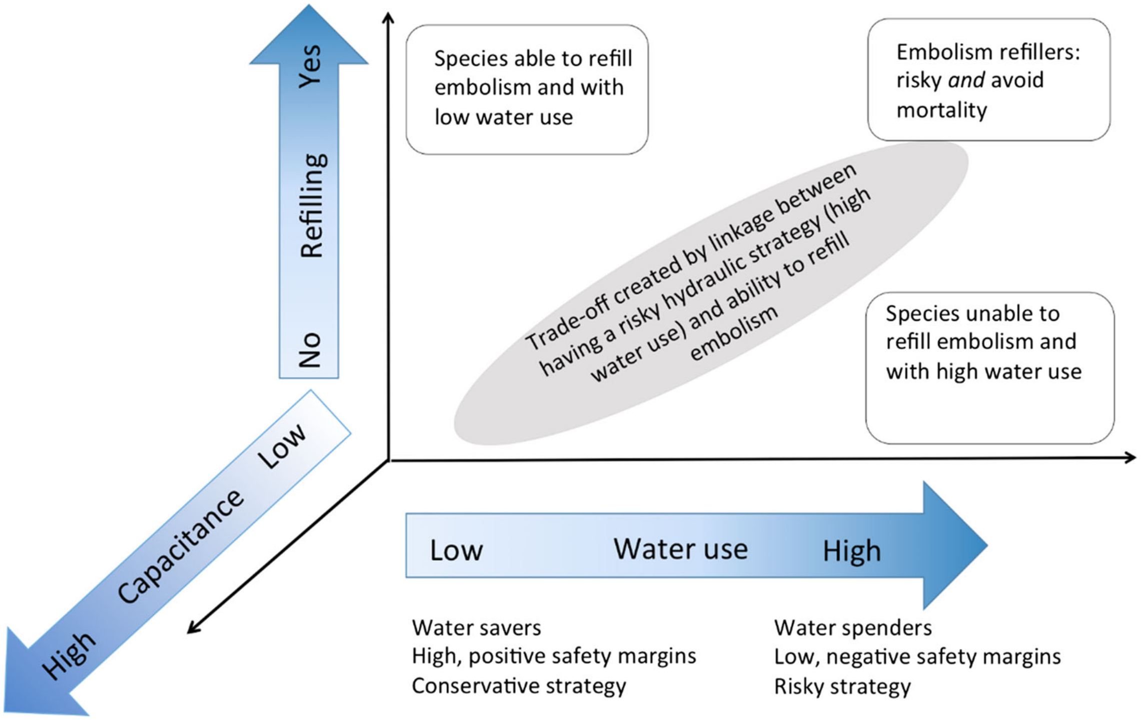


Fig. 3 A hypothesized conceptual framework proposing how embolism refilling may be an additional strategy to the continuum of hydraulic safety and hydraulic efficiency. For example, plants may have low safety, and a high ability to recover from embolism (grey ellipse). Note that capacitance, which acts as a buffer against embolism, may be regarded as one aspect of avoidance, and is presented here as an orthogonal axis, representing an additional strategy. We hypothesize that species may be able to refill embolism, particularly if they are high water users (upper right box). Species may also be high water users and unable to refill embolism (lower right box), using other drought avoidance/tolerance strategies. Alternatively, species may be able to refill embolism and have conservative hydraulic strategies (upper left box) (Colour figure online)

date, representations of alternative strategies for repairing embolisms are lacking in existing models, even though the impact may be considerable (Sperry and Love, 2015). Although the theoretical challenges outlined in "Introduction" do exist for developing a mechanistic formulation of novel refilling, individual-based dynamic vegetation models with hydrodynamics are ideally structured to explore testable hypotheses.

In hydrodynamic formulations, maximum xylem conductivity ($K_{x,max}$) is proportional to the area of the density distribution of the vessel vulnerability to decreasing xylem pressure (Ψ_x), assuming the vessel vulnerability is identical across vessels (red zone in Fig. 4a). Under non water-stressed conditions, xylem conductance (k_x) can be computed by multiplying $K_{x,max}$ by the maximum cross-sectional area of functional-xylem ($A_{x,max}$) and dividing by the path length (z). As water-stress increases in the plant, k_x drops as functional vessels become embolized under decreasing Ψ_x, thus yielding a so-called xylem vulnerability curve (VC, Fig. 4b). During periods of water-stress, the down-regulation of k_x can be approximated using a 0 – 1 scaling factor (β), which represents the fraction of maximum conductivity (or $1 - PLC/100$) as Ψ_x declines and can be formulated as:

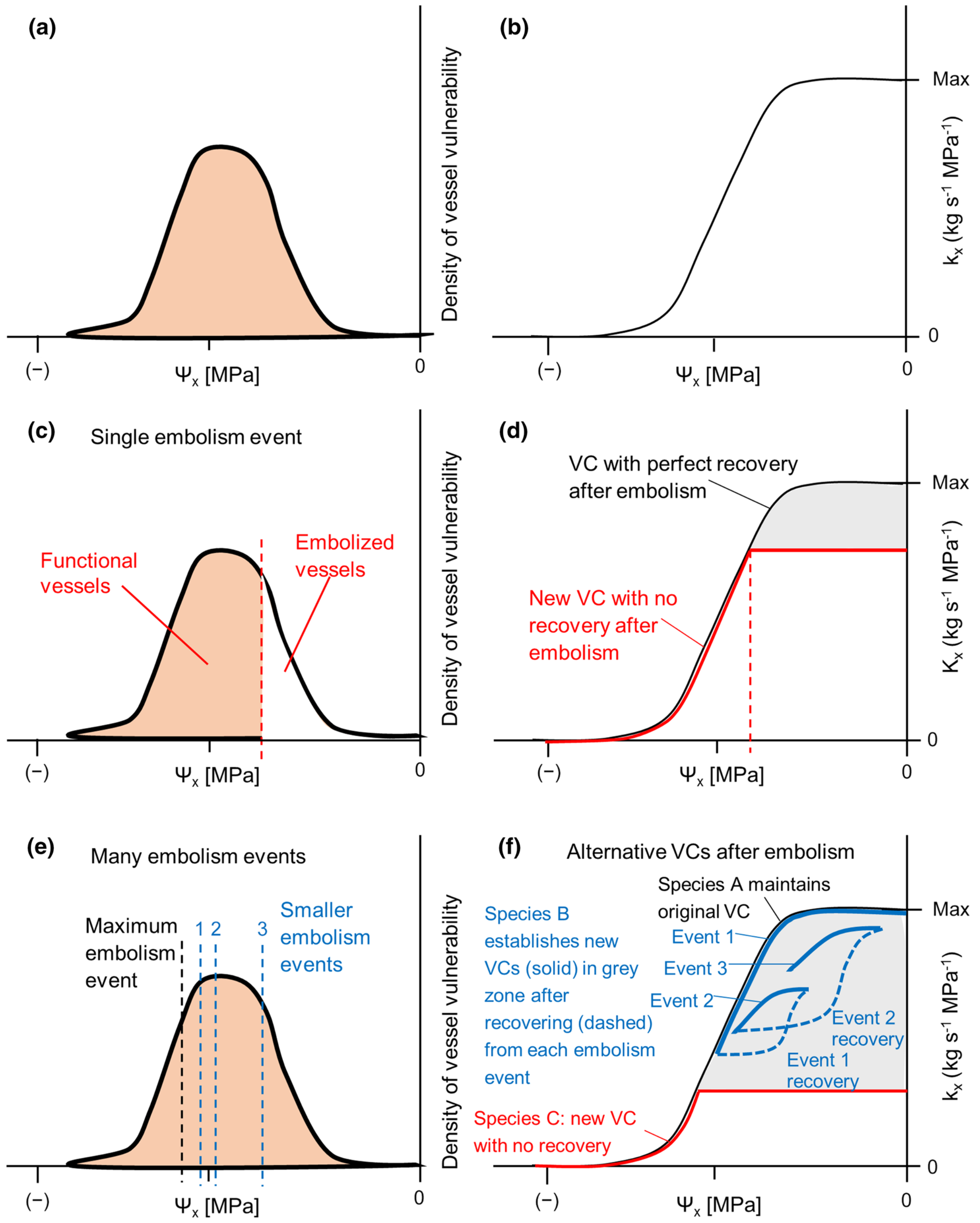
$$k_x = \frac{A_{x,\max} K_{x,\max}}{z}\beta \tag{1a}$$

$$\beta = \exp\left[-\left(\frac{-x}{c_1}\right)^{c_2}\right] \tag{1b}$$

Vulnerability curves are typically sigmoidal (Torres-Ruiz et al. 2014) and to achieve this shape, β is expressed here as a Weibull function with c_1 and c_2 as fitting parameters (Bohrer et al. 2005).

During drought events, vessels increasingly lose function as Ψ_x declines (Fig. 4c). Hydrodynamic formulations (e.g. see references above) have the term of recovery of vessel function (i.e. β returning toward 1 and hence, k_x returning toward its maximum in Fig. 4d) tightly coupled to Ψ_x. Therefore, k_x recovers completely over the same temporal scale as the increase in Ψ_x, which may occur due to the relaxation of xylem tension at night after stomata close or as Ψ_s increases following a rain event (Fig. 4d, black curve) irrespective of the degree of embolized vessels in the xylem (dashed black line, Fig. 4c). Hence, such hydrodynamic formulations fail to represent those species where xylem refilling and recovery of k_x does *not* occur as Ψ_x increases (Fig. 4d, red curve).

We propose a new framework for evaluating xylem recovery as a strategy for drought tolerance. In real



systems, plants experience highly dynamic Ψ_x from variation in transpiration demand, soil moisture supply and stem water storage, all of which results in episodic embolisms (Fig. 4e). Therefore, k_x is governed by two distinct phases for A_x determined by the sign of $d\Psi_x/dt$: (1) a growth phase for when functional xylem area is increasing through repair or growth of new xylem ($d\Psi_x/dt > 0$), and (2) a cavitation phase when functional xylem is decreasing ($d\Psi_x/dt \le 0$). Accordingly, Eqs. (1a, 1b) can be reorganized to include a time dimension that represents the recovery of xylem function at different time scales ranging from sub-daily to seasons and is decoupled from both Ψ_s and Ψ_x:

◀**Fig. 4** Framework illustrating alternative strategies for xylem repair following embolism events. We hypothesize that the range of potential strategies consists of species with xylem vulnerability curves (VCs) that fully recover, partially recover or do not recover until new xylem is grown. **a** Hypothetical density distribution of vessel vulnerability to embolism along a xylem water potential (Ψ_x) continuum. The shape of this density distribution differs between species. **b** Each species' VC is the integral of its vessel density distribution (i.e. panel **a**) and is expressed as the reduction of xylem conductance (k_x, kg s^{-1} MPa^{-1}), as Ψ_x declines. **c** A single embolism event occurring at a given Ψ_x (black dashed line), where vulnerable vessels above it embolize while vessels below it remain functional. **d** When vessels refill perfectly following an embolism event, the VC continues to operate along the original VC (solid black curve). When vessels do not refill following embolism, a new VC is established (solid red curve) and remains until new xylem grows. **e** During droughts, Ψ_x may decrease and increase multiple times leading to several embolism events of varying degrees. **f** Alternative VCs for 3 species after embolism events. Species A completely refills its vessels and k_x recovers (black curve) on the same time scale as soil moisture re-wetting. Species B recovers k_x on a time scale that is slower than soil moisture re-wetting. The initial loss of k_x tracks the original VC (black line), but recoveries are delayed (dashed blue), and subsequent VCs (solid blue) operate in the grey zone beneath the original VC. Species C does not refill; rather, a new VC is established after an embolism event (red). The new maximum k_x for Species C is established at the point on the original VC where the minimum Ψx is reached and extends horizontally back toward 0 as xylem tension relaxes with soil rewetting. For species C, growth of new xylem is required for k_x to return to its original maximum (black). In panels **c**–**f**, the dashed vertical black line represents the minimum Ψx reached and hence, the maximum embolism event during a drought period before new xylem is grown (Colour figure online)

$$\text{cavitation phase} \left(\frac{d_x}{dt} \leq 0\right): \quad A_x^t = \begin{cases} A_x^{t-1} - f\left(\frac{d_x}{dt}, \tau\right), & A_x^{t-1} < A_{\max}\beta^t - \tau \\ A_{\max}\beta^t, & A_x^{t-1} \geq A_{\max}\beta^t - \tau \end{cases} \tag{2a}$$

$$\text{growth phase} \left(\frac{d_x}{dt} > 0\right): \quad A_x^t = \min\left[A_{\max}\beta^t, A_x^{t-1} + f\left(\frac{d_x}{dt}, \tau\right)\right] \tag{2b}$$

$$k_x = \frac{K_{x,\max}}{z} A_x^t \tag{2c}$$

The superscript t indicates either the current (t) or previous (t − 1) time step. The parameter τ is in units of area and determines how quickly A_x regenerates over one time step. When $f(d\Psi_x/dt, \tau) = 0$, no recovery of k_x occurs as the xylem tension relaxes; but instead a new VC is established at each minimum Ψ_x that is reached during a drought period (e.g. red,curve, Fig. 4d). In this case as presented in Fig. 4f, during the first event the initial reduction in Ψ_x also happens to be the maximum embolism event (vertical dashed line, Fig. 4d). Here k_x first tracks down the original VC to the minimum Ψ_x that is reached; and then, as xylem tension relaxes during rehydration, k_x tracks horizontally back toward the origin during rehydration (red horizontal line, Fig. 4f). When subsequent embolism events occur (vertical blue dashed lines, Fig. 4e), k_x tracks horizontally back to the left along the new VC (red) until it reaches the original VC (black) where it then resumes its decent along the original VC if the embolism event becomes even more severe (not shown in Fig. 4f). Alternatively, when $f(d\Psi_x/dt, \tau)$ is relatively high, perfect recovery of k_x occurs along the original VC as xylem tension relaxes (black curve, Fig. 4f). When $f(d\Psi_x/dt, \tau)$ is relatively low, but still > 0, imperfect recovery of k_x occurs more slowly below the original VC (i.e. blue dashed curves in Fig. 4f). This formulation allows for new VCs to establish after recovery and provides flexibility for them to establish anywhere within the grey zone of Fig. 4f. The right hand portion of Eq. (2a) establishes the conditional logic that constrains k_x to the grey zone in Fig. 4f during the cavitation phase. The position of any new VC within the grey zone (e.g. solid blue curves, Fig. 4f) is dependent on the species-specific magnitude of τ and the minimum Ψ_x attained during the cavitation phase (dashed blue curves, Fig. 4f). Finally, xylem recovery that occurs through radial growth could be represented either with this model if $f(d\Psi_x/dt, \tau)$ is parameterized to be relatively low, or through a separate stem-growth function.

Our proposed framework can be readily incorporated into individual-based dynamic vegetation models that represent direct competition for resources between species with alternative growth and survival strategies (e.g. ED2, Xu et al. 2016). We present a general form for our xylem recovery model, rather than suggesting specific functional forms for $f(d\Psi_x/dt, \tau)$ since mechanisms controlling novel refilling are under debate. This general form can accommodate multiple xylem-refilling hypotheses such that one can be agnostic about the phenomenon of refilling while using it within a dynamic vegetation model to evaluate if, when, and in what ecosystems rapid refilling emerges as ecologically important. For example, one species $f(d\Psi_x/dt, \tau)$ could be formulated within a given dynamic vegetation model with a curve with relatively steep slope that runs parallel and to the inside of the original VC curve (Fig. 4f), which implies that the larger, more conductive vessels refill first. Another species $f(d\Psi_x/dt, \tau)$ could be formulated with a curve with relatively shallow slope as Ψ_x returns toward 0, which implies the smaller and less conductive vessels are the first to refill under tension. A third species could be formulated with no refilling. Competition between these species could then be simulated with the dynamic vegetation model to determine the performance of each strategy under the given meteorological forcing.

It should be noted that the *cost* for xylem recovery must also be accounted for in models that consider plant competition; otherwise, plants that recover xylem function more quickly will eventually dominate. Costs associated xylem recovery, and drought tolerance in general, are poorly understood; yet research to date suggests that these costs likely involve potassium and carbon (Secchi and Zwieniecki 2011; Trifilò et al. 2014a). This framework is, therefore, also structured to easily accommodate new hypotheses about the economics of xylem function and recovery. Finally, Eqs. (2a, 2b) provides a testable hypothesis explaining why larger trees are more vulnerable to drought (Nepstad et al. 2007) or have an apparently lower xylem P50 compared to smaller trees of the same species (Rowland et al. 2015).

Future research directions

Plant hydraulics research has rapidly advanced in recent years, and yet many unresolved questions remain, including methodical ones. We suggest that future research focus on the following major unresolved problems:

- Which species, biomes, and plant functional types show embolism refilling, and which do not? Current research shows that the ability to refill is variable across species. Therefore, we need a comprehensive understanding of species that do not refill, as well as refillers, under comparable growth conditions, so we may understand which traits are linked with refilling.
- Do multi-year, or repeated drought events impact the ability of plants to refill previously embolised conduits?
- Is there a continuum for refilling or a threshold, defined by the amount of embolism, xylem pressure reached upon rehydration and/or the availability of stored carbohydrates (and/or partial recovery of photosynthesis)?
- Are changes in vulnerability curves related to adjustments in xylem anatomy, and to what degree do anatomical structures or genetics constrain this plasticity? Quantifying ring-to-ring variability in vulnerability curves especially with regards to drought stress and drought history would be very valuable.

Conclusions

Some species are reported to show embolism refilling, in certain circumstances, whereas others are not. However, these reports are often based on different methods, each with different strengths and weaknesses. Newly emerging non-destructive methods of measuring embolism and refilling are generally free from cutting artefacts, and should be used to validate hydraulic measurements and to reach consensus on artefact-free sampling and handling protocols. At the same time, some of them might lead to injuries to living cells, thus limiting the possibility to detect vital phenomena like embolism reversal.

Given that some studies report embolism refilling in certain species, while others report no refilling in certain species, we conclude that the synthesis of evidence presented here suggests refilling does occur in some circumstances in some species. This leads to the question—in what species and circumstances does refilling occur? Embolism refilling has been reported in roots, stems, or petioles, through positive root pressure, under negative pressure (up to a certain water potential), or a combination of these. It appears likely that there must be enough water available, although the water potential threshold remains an unknown key research question. Embolism refilling is influenced by phloem, ray and/or axial parenchyma, xylem age and location. There appears to be a trade-off to embolism refilling that involves costs associated with metabolism and transport of soluble sugars, water and potassium.

Further research is required to test which species can and cannot refill embolism, and under what conditions, which will advance our knowledge of why some plants die, while others are able to survive during drought. This information would be very valuable for future research efforts aimed at breeding and selecting cultivars and genotypes of crops and forest species able to cope with projected increase in frequency/intensity of drought and heat waves. Current research is mainly focused on selecting traits conferring resistance or tolerance to drought stress, like embolism resistance (Cochard et al. 2008; Aranda et al. 2015; Fichot et al. 2015). Evidence accumulating around the role of embolism refilling might indeed suggest shifting the focus to traits conferring resilience to drought. It is also possible that selection strategies aimed at improving plant resilience to drought based on embolism refilling might do so while maintaining or even improving plant productivity, thus avoiding the possible trade-offs between plant hydraulic safety and efficiency/productivity (Gleason et al. 2016). Anatomical (wood parenchyma fraction and spatial pattern) and functional (NSC content) traits might represent useful proxies to estimate the recovery ability of different species/genotypes in screening projects.

Further, understanding which species refill embolism will help constrain model formulations that are important for improving predictions of vegetation dynamics and carbon and water fluxes in hotter, drier climates. Including refilling in functional models of vegetation performance under recurrent drought would facilitate models to capture subtle effects of drought/rewetting cycles on ecosystem productivity, which simpler models would be unable to capture. Considering that future global change-type drought might take multiple shapes in terms of intensity and frequency, the impact of physiological strategies for short-term recovery of plant hydraulic functioning cannot be ignored, if we aim to accurately predict the impact of such droughts on ecosystem functioning.

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