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Current Opinion in Plant Biology

Embolism resistance as a key mechanism to understand adaptive plant strategies

Frederic Lens[1], Aude Tixier[2], Hervé Cochard[2], John S Sperry[3], Steven Jansen[4] and Stephane Herbette[2]

One adaptation of plants to cope with drought or frost stress is to develop wood that is able to withstand the formation and distribution of air bubbles (emboli) in its water conducting xylem cells under negative pressure. The ultrastructure of interconduit pits strongly affects drought-induced embolism resistance, but also mechanical properties of the xylem are involved. The first experimental evidence for a lower embolism resistance in stems of herbaceous plants compared to stems of their secondarily woody descendants further supports this mechanical-functional trade-off. An integrative approach combining (ultra)structural observations of the xylem, safety-efficiency aspects of the hydraulic pipeline, and xylem–phloem interactions will shed more light on the multiple adaptive strategies of embolism resistance in plants.

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Introduction

According to the generally accepted cohesion-tension theory, capillary wicking of cell walls is the driving force in plants that creates a negative pressure, allowing transpiration to pull up water towards the leaves via a 3-D conduit network [1]. This negative pressure makes the liquid xylem sap metastable, and thus vulnerable to vaporization by cavitation [2]. Cavitated conduits may become air-filled or embolized, and can no longer transport water. Extensive embolism formation in the xylem can block most of the water flow, potentially leading to branch sacrifice or even plant death [3–4]. Therefore, the resistance to drought or frost-induced embolism is an important adaptive trait for the growth and survival of plants [5,6,7••], evolving along with other strategies including rooting depth, leaf structure, shifts in biomass allocation, CAM metabolism, water storage and/or drought and frost avoidance.

This concise review describes how embolisms originate and spread into the conduit network, and highlights which mechanical properties of the xylem are involved in drought-induced embolism resistance. On the basis of original embolism measures in *Arabidopsis*, the mechanical-functional trade-offs may provide a novel additional explanation why some herbaceous flowering plant groups 'reinvented' wood development and turned again into the woody ancestral state (i.e. secondary woodiness).

Why and how do embolisms originate and spread into the xylem?

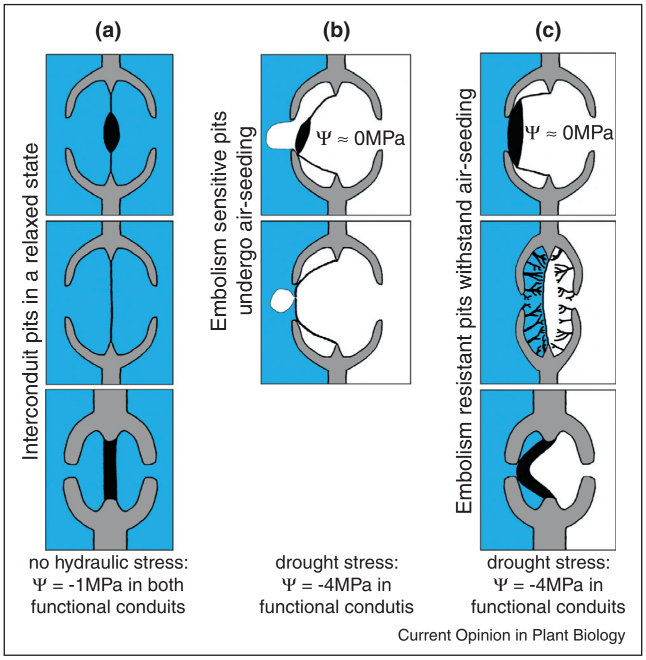
Vulnerable hydraulic pathway

When liquid water pressure drops below its saturated vapour pressure (2.3 kPa absolute at 20°C, or -99 kPa below atmospheric at sea level), it becomes metastable relative to the lower energy vapour phase [2]. As such, liquid water under negative pressure is vulnerable to cavitation: the abrupt phase change to vapour (cf. boiling). Spontaneous initiation of vapour bubbles in pure metastable water (homogenous nucleation) does not seem to be responsible for cavitation in plant xylem, because it occurs at pressures far more negative (between -30 and -140 MPa based on experimental measures [8]) than physiological xylem pressures (often between -0.1 and -10 MPa with exceptions to >-20 MPa [9–10]). Instead, xylem cavitation is likely heterogeneous, triggered by nucleating sites, which are most likely either small gas bubbles in conduits or water-conduit wall boundaries experiencing weaker adhesion forces [11].

Drought-induced embolism

Experimental evidence points to 'air-seeding' as an important cause of embolism by drought stress [2,11–12]. As more negative sap pressure develops during drought, air is aspirated into the functional conduit through porous sections of the conduit wall. Once inside the conduit, these air bubbles may seed the phase change to vapour, causing the negative sap pressure to rise abruptly to near atmospheric. The gas bubble then is

Figure 1



Current Opinion in Plant Biology

Fine-scale interconduit pit adaptations regulating drought-induced embolism in gymnosperms and angiosperms. Interconduit pits showing torus-margo pit membranes in gymnosperms (top row) and homogeneous pit membranes in angiosperms (middle and bottom rows). **(a)** Pit membranes in a relaxed state between two functional conduits facing no hydraulic stress. **(b)** and **(c)** A prolonged period of drought increases the pressure difference between the water-filled and the embolized conduit, causing the porous pit membranes to deflect. At a critical pressure difference, the capillary seal can give way, allowing air-seeding among adjacent conduits that exacerbates the water flow towards the leaves. Column c illustrates adaptations in pit quality characters that can prevent air-seeding at the same pressure difference, in comparison to the embolism sensitive pits shown in column b, such as the increased size ratio of tori versus pit aperture diameters in gymnosperms (top), and the presence of highly developed vestures (middle) or thicker pit membranes with reduced pores in angiosperms (bottom).

free to expand to fill the conduit and produce an embolism as water is drained by the surrounding transpiration stream. The evidence for air-seeding is that negative embolism pressures are usually equal and opposite to the pressure required to inject air into the intact conduits [13].

Important sites for air-seeding are openings in the secondary walls of neighbouring conduits called interconduit pits (Figure 1 [12]). These pits function to restrict the spread of air throughout the conduit network in the event of conduit damage, but at the same time allow lateral water transport via pores in the pit membranes (PMs). Conduits become damaged and air-filled not only during the course of normal development in the case of ruptured protoxylem strands, but also from abscission, breakage, herbivory, or other damage, although it remains to be explored whether there are other causes for air-filled vessels. The nano-scale pores of the interconduit PMs are narrow enough to trap the meniscus against a substantial pressure difference between an embolized and a functional conduit, thus inhibiting air entry under normal conditions. But when the pressure difference becomes too large during drought, the capillary seal can give way, causing air-seeding through interconduit PMs (Figure 1b). In this way, embolism propagates from conduit to conduit. The amount of embolized cells can be measured in terms of loss of hydraulic conductivity at various negative pressures, resulting in so-called vulnerability curves (VCs, Figure 2). Since VCs measure embolism rates, and because not all cavitation events must necessarily lead to embolism formation, 'embolism resistance' is a more correct term for the commonly used 'cavitation resistance' in plant physiology.

Frost-induced embolism

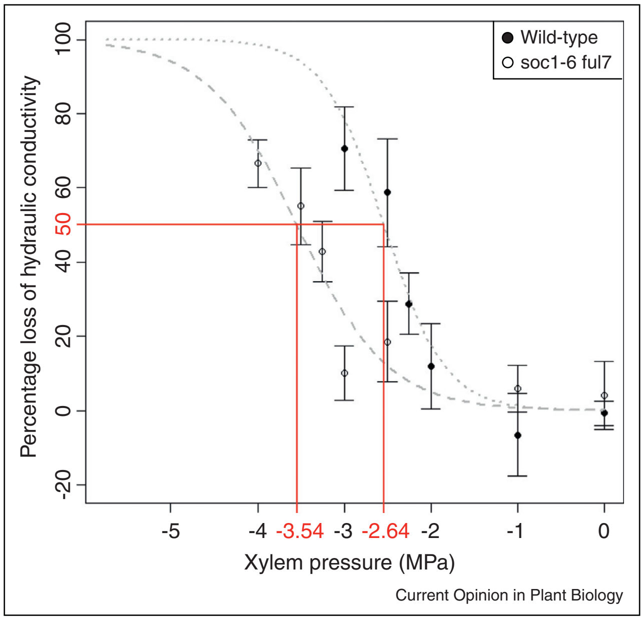
Embolism formation can also develop due to freeze–thaw cycles, and mainly depends on the diameter of the conduits [14–15]. Air is insoluble in ice, forming gas bubbles in the conduits during freezing. On thawing, these bubbles may expand when the negative pressure allows countering the bubble-collapsing force of the surface tension (thaw-expansion hypothesis). Consequently, frost-induced embolism can be amplified by drought stress [16–17].

Fine-scale interconduit pit adaptations regulate drought-induced embolism resistance

Mechanical behaviour of pit quality characters

Ultrastructural modifications of interconduit pits are good predictors to explain embolism resistance via air-seeding [18–22]. Within angiosperms, the huge variation in PM thickness (70–1900 nm) and maximum PM porosity (10–225 nm) show that species with thicker PMs have smaller PM pores and are better adapted to avoid air-seeding (Figure 1c bottom [19]). Thicker PMs are also presumed to be mechanically stronger, causing more resistance to stretching and preventing PM pores to become larger [18,24]. Likewise, narrower pit chambers [22,25] and vestured pits (Figure 1c middle [23]) prevent excessive PM deflection in some groups. The mechanical behaviour of pits and their PMs remains to be investigated thoroughly, and therefore also PM chemistry [26] needs special attention with reference to the pit type and developmental stage. Noncellulosic compounds, such as pectins and hemicelluloses, occur in gymnosperm PMs [27], but the chemical composition of angiosperm PMs seems to be more diverse [18,28–29]. According to recent studies, intervessel PMs contain little or no pectic homogalacturonans and rhamnogalacturonan-I [29–30], which raises serious doubts about the swelling/shrinking hypothesis of interconduit PMs related to the ionic effect [31–34].

Figure 2



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Xylem vulnerability to embolism in *Arabidopsis thaliana* wild-type (WT) and the woody *soc1-6 ful7* mutant. Vulnerability curves of the WT (closed circles) and the mutant (open circles) show a significant difference (Student's *t*-test, $P < 0.05$). The P50, or the pressure inducing 50% loss of hydraulic conductivity due to embolism formation, corresponds to −3.54 MPa in the woody mutant stems versus −2.64 MPa in the WT stems (red lines). Plants were grown under long days (16 hours light per day). Each data point represents the mean value from two to four plants and bars represent standard errors. Dotted grey lines are sigmoidal regressions.

Within conifers, embolism resistance of torus-margo pits in unicellular tracheids seems most closely correlated to the size ratio of torus versus pit aperture diameter [20–21,25]. This suggests that the adhesion of the torus to the pit border is a major determinant of drought-induced embolism resistance (seal capillary-seeding, Figure 1c top [20]), although some conifer species show plasmodesmatal pores in their tori assuming air-seeding through these tori pores [35].

Pit quantity characters

The chance of initiating air-seeding through a single PM with large pores appears to be larger when more intervessel pits per vessel are present (rare pit hypothesis [36]). However, while the link between pit quantity per vessel and vulnerability to embolism is demonstrated in some angiosperm groups [37], it is lacking in others [22]. Opponents of the rare pit hypothesis use the quantity of intervessel pits per vessel to explain why long-vesseled species usually show vulnerable embolism rates [37–38]. The vulnerability of large vessels, however, is the subject of contradictory opinions. For instance, recent studies in grapevine based on a wide range of traditional and up-to-date *in vivo* techniques suggest that the high embolism ratios in long-vesseled species may be a typical problem of the commonly used centrifuge technique [39–41], while others finding no long-vessel artefact [42].

More evidence for the mechanical-functional trade-off in xylem

Wood density and thickness-to-span ratio

Embolism resistant species are often characterized by a high wood density and a high thickness-to-span ratio of water conducting cells [43–45], and some studies have also highlighted increased fibre wall area, Modulus of Elasticity, and Modulus of Rupture as additional trade-offs [44]. The mechanical reinforcement in drought-induced embolism resistant wood is often explained by the stronger negative pressures in the conduits. Nevertheless, conduit implosion due to negative pressures has never been observed in wood. Alternatively, conduit wall reinforcement might prevent microfractures in walls [44] that in turn might trigger heterogeneous nucleation from air particles in walls or in intercellular spaces. But again, there is no experimental evidence for these microfractures, leaving the underlying mechanisms for the mechanical-functional trade-off in the xylem tissue unresolved.

A new additional evolutionary hypothesis for secondary woodiness

The existing mechanical-functional correlation in xylem can be translated into a novel hypothesis explaining why the habit shift from herbaceousness towards *secondary woodiness* (SW) occurs in some angiosperms. This habit shift was initially observed on islands by Charles Darwin and described as *insular woodiness* [46]. Today, several hypotheses are raised explaining why herbaceous lineages undergo massive convergent evolutionary shifts towards SW shrubs (summarized in [47]), but compelling evidence for this increased woodiness remains absent. Our Canary Island review shows that many of the SW species are native to the markedly dry coastal regions, suggesting for the first time a link between increased woodiness and embolism resistance [48•]. However, we want to emphasize that many SW lineages also occur in very wet environments, suggesting the involvement of multiple environmental factors. For instance, lack of frost is an important criterion influencing the occurrence of SW [49].

Embolism measures in herbaceous species are scarce because of their fragile stems. Not surprisingly, the few herbaceous species studied do have rigid stems, such as corn [50] and bamboos [51•]. Recently, Tixier *et al.* [52•] have managed to reconstruct VCs from the fragile herbaceous *Arabidopsis thaliana* stems. They demonstrate that short-day plants with slightly more wood development at the base of their stems are significantly more embolism resistant than long-day plants with less wood development, supporting the above-mentioned trade-off. We go one step further and compare the herbaceous wild-type with the shrubby *A. thaliana* mutant [53,54•]. The VCs of the woody mutant stems show significantly lower embolism rates than VCs of the herbaceous accession grown under the same growth conditions (Figure 2). This is the first experimental evidence supporting increased embolism resistance in SW shrubs compared to their herbaceous relatives.

Different strategies in embolism resistance between angiosperms and gymnosperms

High risk versus safety

Angiosperms and gymnosperms have a strikingly different strategy to cope with drought-induced embolism resistance: the majority of angiosperms show a risky behaviour and operate close to their lethal hydraulic limit (i.e. pressure resulting in 70–80% loss of conductivity), while most of the gymnosperms develop a much safer hydraulic margin that is further away from their lethal 50% boundary [3,4,7••]. The greater ability of angiosperms versus gymnosperms to repair stem embolisms may partly explain this different strategy [55•].

Refilling embolized conduits

Positive xylem pressures have been linked to vessel refilling in a variety of angiosperms, such as temperate woody trees [56], woody tropical plants [57], and many herbaceous species [51•]. Refilling has also been reported under negative pressures, for instance in bay laurel [58] and rice [59], and requires pressures that need to rise close to atmospheric levels while the bulk xylem remains under negative pressure [60]. This seems contradictory, but what we do know is that sugars and ions from living xylem and phloem cells are involved [58,60–61]. This is demonstrated by amongst others girdling experiments [38,58] and the observed transport of water and solutes between phloem and xylem [62].

Conclusion and future prospectives

Various structure–function relationships in the xylem are known to play a role in embolism resistance. Pit membrane thickness and porosity are crucial to prevent drought-induced embolism via air-seeding, and more insights into PM composition in different cell types in the xylem of angiosperms are urgently desired to understand the interaction between the dead conduits and the living cells. Emphasis is also placed on trade-offs between mechanical wood properties and embolism resistance, and is further supported by original embolism measures showing that stems of secondarily woody *Arabidopsis* mutants are more embolism resistant than the ones of the herbaceous wild-type.

The self-regulation of water flow (ionic effect) and refilling of embolized conduits suggest that water transport does not entirely rely on a passive cohesion-tension process, but also requires input from living cells. Future research should focus on these refilling mechanisms, and continue to elaborate on a broad-scale integrative approach linking xylem and phloem physiology with in-depth anatomy of the hydraulic pathway [63•]. Existing database projects, such as TRY [64] and the Xylem Functional Traits database [7••], are the necessary first steps to accomplish this effort. Once we know the crucial features characterizing embolism formation and refilling in plants, we can find and manipulate the genes underlying these characters using woody model species [65] and apply it to tree forest species. A global analysis on the vulnerability of forests to drought shows that many trees operate with narrow hydraulic safety margins, inferring that embolism-related research will become increasingly important under the current Climate Change predictions [7••].

Conflict of interests

The authors declare that they have no competing interests.

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This paper provides for the first time VCs of the herbaceous model *Arabidopsis thaliana*, showing that short-day plants producing more wood cells at the base of the stem are more embolism resistant than the long-day plants. This supports the view that *Arabidopsis* can be used as a new model for xylem hydraulics.

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