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Review

Xylem hydraulic physiology: The functional backbone of terrestrial plant productivity

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ABSTRACT

Land plants are completely dependent on a passive system of water transport for their survival. The great bulk of the xylem tissue is non-living and consequently has no short term capacity to acclimate or adjust to changes in hydraulic demand. Yet there exists an extraordinary degree of coordination between the hydraulic and photosynthetic systems of plants that defies developmental explanation. The connection between hydraulic capacity and photosynthetic assimilation arises as a product of the shared stomatal pathway for water and CO₂ exchange in the leaf. A combination of optimization in both water use and structural xylem investment has led to a situation in vascular plants where the form and function of all individuals is moulded by the link between hydraulic and photosynthetic systems. Unlike competing models of hormonal control of gas exchange, hydraulic limitation of productivity under optimal and drought conditions accounts for much of the observed variation in plant gas exchange in natural systems. The plant water transport system places a hard physical limit to plant productivity and survival. Identifying the developmental control of key xylem traits will yield the potential for achieving new performance capabilities in plants.

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1. Introduction

Photosynthesis evolved as an aquatic process and only came to transform the land after terrestrial plants were able to produce leaves that could house photosynthetic cells in an aquatic medium. Only vascular plants evolved the extensive engineering required to bring high productivity onto dry land, and these structures dominate the form of today's crops and forests. Early plant

innovations, such as impermeable cuticles and stomata allowed photosynthetic cells to survive on land [1,2], but the evolution of internal water transport systems at the end of the Devonian laid the foundation for high primary productivity to enter the terrestrial realm [3,4].

The structure and function of water transport systems today govern the productivity and survival of land plants because the vascular architecture places a physical limit to plant function that cannot be exceeded [5]. Amidst the whirlwind of molecular biological discovery it often seems overlooked that important metabolic processes are ultimately constrained not by biochemical pathways, but rather by the physics of plant structure. Water

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transport in plants provides an outstanding example of this. Governed by the laws of fluid dynamics, the non-living xylem forms a nexus between the physics of water flow and photosynthetic metabolism. Here I discuss how the hydraulic physiology of vascular plants exercises control over photosynthesis both under optimal conditions and in response to drought.

2. Transpiration theoretically links hydraulics and photosynthesis

Water transport and photosynthetic productivity are highly distinct processes that become tightly linked the moment photosynthetic structures emerge into the atmospheric air. Photosynthesis in air has the unavoidable consequence that in exchange for CO_2 , leaves lose vast quantities of water as transpiration. Failure to replace this transpired vapour with water transported from the soil would lead to desiccation and destruction of the photosynthetic apparatus. As with any fluid system, water travelling through the vascular system of a plant encounters a resistance to flow. To overcome this resistance leaves exert a tension on the water column sustained by capillary forces in the apoplast of leaf cells and the cohesive properties of water [6]. The resultant tension is measured as a decrease in leaf water potential (Ψ_{leaf}) below zero [7]. Water flows passively along this water potential gradient from the soil to the leaves. Water potentials are analogous to electrical potentials [8] in the sense that Ψ gradients determine water flow through the resistive hydraulic system in the same way that electrical resistors affect current flow produced by electrical potential gradients (Eq. (1)):

$$E = (\Psi_{\text{soil}} - \Psi_{\text{leaf}})K_{\text{plant}} \quad (1)$$

where E is the leaf evapotranspiration rate ($\Psi_{\text{soil}} - \Psi_{\text{leaf}}$) is the water potential gradient from the soil to leaf (MPa) and K_{plant} is the hydraulic conductance of the plant.

According to Eq. (1) (which does not consider water stored inside the plant as a water source) high transpirational fluxes from leaves can only be sustained by producing a large soil–leaf Ψ gradient, or a highly conductive hydraulic system (K_{plant}). In practice it is mostly K_{plant} that constrains evaporation from leaves under well-watered soil conditions. The reason for this is that the biophysics of stomatal movement appears to be rather conservative amongst land plants, in the sense that the guard cells from a diversity of species respond similarly to turgor pressures (and hence Ψ_{leaf}) [9]. As a result, the soil–leaf Ψ gradient in unstressed plants falls in a narrow range [10,11]. With few exceptions (notably mangroves) the stomata of plants grown under natural conditions begin to limit E (and assimilation) as Ψ_{leaf} falls below -1.5 MPa with 60% closure typically occurring close to -2 MPa. An explanation for this conservative range is elusive, with suggestions ranging from osmotic control [12], to photosynthetic biochemistry [13] and xylem function [14] as potential limiters. Perhaps the unifying cause is that $>90\%$ of the extractable water has been removed at a Ψ_{soil} of -1.3 MPa [15], and hence there is little benefit to the plant of maintaining stomata open when the bulk of soil water is gone.

Conservative stomatal response to turgor ensures that the maximum sustainable plant transpiration rate (E_{max}) is proportional to K_{plant} (Eq. (1)). This is the first of two conditions that connect hydraulic and photosynthetic capacities in well-watered plants. The other key link is that leaves exchange gaseous CO_2 and H_2O through a common pore, and therefore the same diffusive limit applies to both E and A (Fig. 1). Furthermore, stomatal aperture is regulated in most species such that water loss is optimized [16] relative to photosynthetic gain. Optimal stomatal control should greatly reduce variation in the ratio $E:A$ when

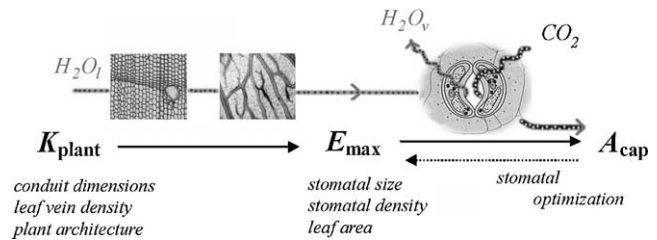


Fig. 1. Schematic showing how the hydraulic capacity (K_{plant}) of plants is linked via the stomatal pore to photosynthetic capacity (A_{cap}). The same water that leaves the stomata as vapour (H_2O_v) must be replaced by liquid water (H_2O_l) flowing through the vascular system. Under non-stressed conditions the traits that determine K_{plant} should be coordinated through plant development with photosynthetic traits. Hydraulic/photosynthetic coordination has been demonstrated at the whole-plant level as well as within branches and leaves (see text).

species are compared under similar conditions of temperature and humidity [17,18]. Carbon isotope discrimination confirms that a rather narrow operational range of $E:A$ exists in non-water stressed plants in the field [19]. Combined, the effects of uniform stomatal control and gas exchange optimization lead to a close theoretical relationship between K_{plant} and photosynthetic capacity (A_{cap}) that is mediated by hydraulic limitation of E_{max} (Fig. 1). Of course variable humidity can disrupt this relationship by modifying the ratio of $E:A$ thereby potentially allowing the same K_{plant} to achieve higher A_{cap} in humid environments than in drier air. However, the stomatal response to humidity should reduce this variation as well [18].

The preceding discussion relies heavily on stomata behaving as pressure sensitive valves that respond rapidly and continuously to Ψ_{leaf} . Under most circumstances this assumption is well supported by experimental evidence [20] leading to the conclusion that guard cells respond to changes in Ψ_{leaf} either directly or via a signal generated very close to the guard cells. “Hydraulic signalling” of this type contrasts with the type of signalling associated with stomatal closure in response to the hormone, abscisic acid (ABA). ABA signalling is not predictably associated with Ψ_{leaf} and has the potential to disrupt equilibration between water supply (xylem) capacity and water loss (through stomata). Disequilibrium between hydraulic supply and demand is expected in an ABA-controlled system because ABA appears to be transported from roots to the leaves as the soil water content declines, meaning that in most trees one would expect a considerable lag time in the response of stomata to changing soil or atmospheric water deficit.

Since the first demonstration of stomatal responses to drying soil in pressure compensated plants [21] there has been a rapidly growing interest in transportable hormones (ABA particularly) as stomatal regulators. Molecular biologists have seized upon the link between ABA and stomatal closure, seeing ABA synthesis as a golden opportunity to elucidate a biosynthetic pathway that might regulate plant production. The large subsequent investment in researching the biochemistry and genetics of ABA synthesis and guard cell ABA transduction is disproportionate to the apparent significance of ABA-mediated versus hydraulic-mediated models. Indeed hydraulic models have far better empirical support from a broad range of species growing under both stressed and non-stressed natural conditions [22]. Therefore in this review I will respect the greater evidence and proceed with the view of stomata as “hydromechanical” valves [23], restricting discussion of ABA-mediated stomatal control until the last section that examines drought.

3. Hydraulic–photosynthetic coordination

The theoretical linkage between hydraulic capacity and maximum assimilation rate has enormous implications for

understanding how plant structure limits photosynthetic performance. Furthermore it suggests that there should be some kind of developmental coordination between photosynthetic and hydraulic traits.

Considering the economics of structural investment versus carbon gain it is clear that evolution should favour the developmental coordination of hydraulic and photosynthetic traits. The hydraulic system of vascular plants constitutes a large proportion of the total dry mass of an individual [24], and increasing K_{plant} requires substantial investment in xylem plumbing of the roots stems and leaves [25]. Plants only benefit from this investment up until the point where photosynthesis is limited by factors unrelated to water supply, e.g. light, cold or nutrients. As such it would be expected that developmental control of photosynthetic and hydraulic systems would ensure that resource allocation is balanced between these linked processes.

Observations of plants growing under natural and experimental conditions provide strong evidence of such a linkage indicating that coordination between hydraulics and photosynthesis is a universal feature amongst vascular plants (Fig. 2). Anatomical studies have demonstrated positive correlations between hydraulic, stomatal and photosynthetic traits [26–29] in a range of woody plants. Also at the functional level the rate of photosynthesis has been tied to whole plant [30–33], branch [34–36] and leaf [37–39] hydraulic conductances (K_{plant} , K_{stem} , K_{leaf} , respectively) both within and between species. These data come from a range of techniques including whole-plant sap flow, and different measures using excised plant tissues including the traditional pressure–flow method [40] as well as transient pressure [41,42] and steady state evaporative methods [43]. All methods demonstrate a similar relationship between assimilation and hydraulic conductance (in C_3 plants) as either a linear [41] or saturating curve [44]. Only the very high values of K_{stem} and K_{leaf} measured in tropical plants appear to exceed the optimal linear relationship expected to exist between K and A [45]. Studies of C_4 plants [46] further strengthen the general hydraulic–photosynthetic rule by demonstrating a lower hydraulic transport capacity relative to assimilation rate that corresponds closely with the intrinsically higher water use efficiency of C_4 compared with C_3 photosynthesis. Together these

studies unanimously support the concept that evolutionary pressure has forced the coordinated development of photosynthetic and hydraulic tissues [24]. Not only is coordination apparently general amongst vascular plants, but the ratio of K and A seems to be conservative in C_3 plants, suggesting convergence upon an optimal strategy [24,47,48].

4. Economic and developmental coordination in leaves

Given that the development of hydraulic and photosynthetic systems must be interlinked in vascular plants it is important to consider how these developmentally highly distinct tissues are coordinated in a growing tree. At the whole-plant scale, allometry appears to be closely regulated such that the demand and supply of water are matched [49]. However at a smaller scale leaves provide an excellent subject to study coordinated development because they can be considered as somewhat self-contained units. Furthermore leaf hydraulic and photosynthetic capacities are genetically correlated [50] suggesting that in leaves, the same developmental genes might be involved in the expression of hydraulic and photosynthetic traits.

Despite their small size, each leaf constitutes a major resistor in the total soil–atmosphere hydraulic pathway (between 30 and 80% of the whole-plant hydraulic resistance [51,52]). The significance of K_{leaf} as a potentially limiting component of the vascular system is highlighted by the strong hydraulic–photosynthetic coordination observed across a large sample of diverse species [44] (Fig. 2). Importantly, K_{leaf} is closely related to the anatomy of the leaf, specifically to the architecture of veins and their location in the lamina [27,44,53]. An empirically derived relationship based on a sample of leaves across the spectrum of terrestrial plants recently demonstrated that K_{leaf} was proportional to the proximity of vein terminals to the sites of evaporation [44]. In single-vein leaves it is the width of the leaf that determines the proximity of veins to stomata while in multi-vein leaves vein density (total length of veins per unit leaf area; mm mm^{-2}) within the leaf lamina largely determines this distance. High vein density brings xylem water delivery very close to all sites of evaporation and hence leads to a high K_{leaf} , while the converse is true for low density leaves where water must move significant distances from the veins to the stomata.

An optimal allocation of carbon to leaf veins should achieve a match between hydraulic and photosynthetic capacities thereby avoiding hydraulic limitation of photosynthesis. At the same time, high vein density is costly both in terms of structural carbon and displacement of photosynthetic tissue, and hence plants that match hydraulic and photosynthetic capacities avoid an inefficient over-expression of vein density. The best examples of this hydraulic/photosynthetic optimization come from studies of sun and shade grown leaves where large changes in photosynthetic capacity are linked to modification of the vein density within plants [54] and between species [27]. Shade leaves have lower rates of photosynthetics and stomatal conductances [55] therefore leading to lower demand for water [56] and correspondingly lower leaf vein densities [29,54]. Other leaf traits such as palisade thickness, stomatal size and density, and leaf size all vary in concert with vein density [26] again supporting a unified control of hydraulic and photosynthetic traits.

The mechanisms that drive developmental coordination of photosynthetic and hydraulic physiology in leaves are unknown. Auxins are apparently involved in both stomatal [57] and vein differentiation [58–60] providing potential for coordination, but as yet there is no genetic basis for unified control. It is possible that processes such as leaf expansion might play a part in coordination simply by regulating the distance between veins and stomata in one proportional step. Sun leaves are almost always smaller than

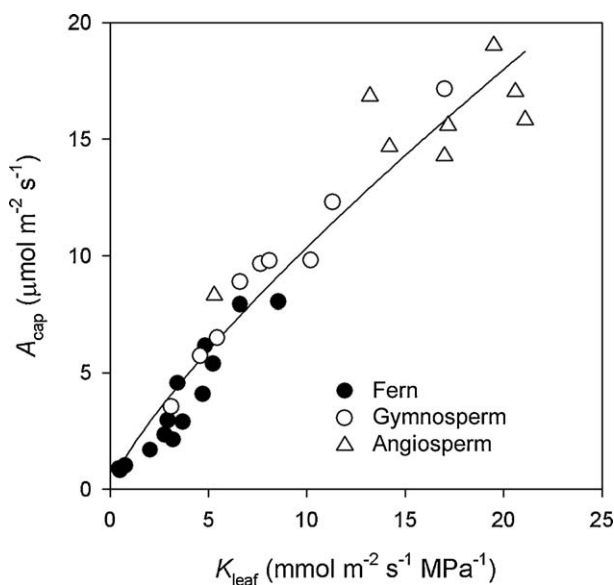


Fig. 2. A strong curvilinear correlation between leaf hydraulic (K_{leaf}) and photosynthetic performance (A_{cap}) within the leaves of a diverse sample of ferns, conifers and angiosperms. When soil water is not limiting the peak photosynthetic rate of leaves at midday is constrained by the anatomical characteristics (vein density and architecture) of the leaf.

shade leaves and the reduction of leaf expansion in the sun corresponds to an increase in the density of veins in line with the increased evaporative and photosynthetic demand for water. If reduced leaf expansion in the sun also increased stomatal density and mesophyll density in proportion it might be expected that increased hydraulic and photosynthetic demand could be met simply by regulating leaf expansion.

5. Hydraulic evolution in stems and leaves

Most of the foundational work on plant hydraulics was undertaken on plant stems inspired by the discovery of major disjunctions between the anatomies of gymnosperm versus angiosperm wood. Hydrodynamics dictate that under a particular driving gradient, the rate of water flow through a pipe is proportional to the fourth power of its radius. Hence the unique presence of very large xylem tubes in angiosperms (termed vessels) means that angiosperms can carry considerably more water per unit xylem cross-sectional area than their vessel-less predecessors. The ability of angiosperms to produce “cheap” wood by using wide vessels instead of the narrow tracheids found in other plant groups is considered a major economic advantage that has contributed to angiosperm success [61]. Recent work has focussed on the contribution of end-wall resistance as well as lumen resistance as an important component of xylem evolution. The degradation of end-walls between vessel elements (perforation plates) appears to have undergone gradualistic evolution with single large pores between vessel elements superseding more resistive barred perforation plates [62,63]. The combination of vessel lumen sizes up to 600 μm in diameter and lengths of over 4 m confer enormous stem hydraulic conductances in some tropical vines [64], but in trees the maximum size of vessels is much smaller because large lumen vessels compromise the mechanical support in stems [65]. In fact the advantage of vessels in wood becomes very much reduced when viewed in the context of both support and hydraulic aspects of stem, and is further narrowed by the highly efficient torus-margo pitting that is utilized by conifers [66].

Leaves appear to have also undergone a major evolutionary upgrade in parallel with stem evolution in angiosperms. Augmentation of leaf hydraulic capacity in angiosperms has occurred as a massive rise in the density of veins present in the lamina. For 400 million years the leaf vein density in land plants remained rather static between 1 and 4 mm mm^{-2} , but early in the evolution of angiosperms this number rose to above 10 mm mm^{-2} (Fig. 3) [67]. The resultant rise in photosynthetic capacity (T.J. Brodribb & T.S Field submitted) must have impacted significantly on the ecology and competition of late Cretaceous forests, with angiosperms being able to out-grow competitors, particularly in warm aseasonal environments such as the tropics.

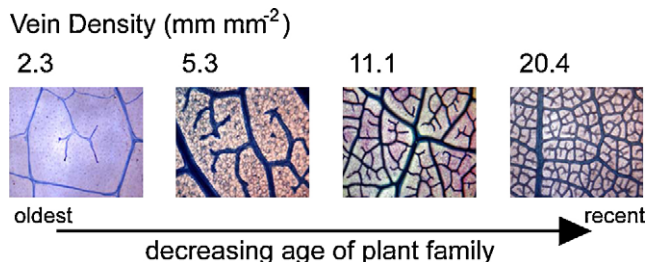


Fig. 3. A sequence of cleared leaves taken at the same magnification showing leaf vein densities of *Amborella trichopoda*, *Atherosperma moschatum*, *Rehdera trinervis* and *Bauhinia binata*, respectively. The ages of the plant families represented here extend from the basal-most angiosperm (left) to a highly derived Fabaceae, and the vein density trend shown exemplifies the trend across the angiosperms [67].

6. Hydraulics versus ABA in drought

Hydraulic control of photosynthesis and plant productivity is as important during drought as it is under well-watered conditions. Under optimal conditions K_{plant} determines maximum stomatal conductance and photosynthetic capacity but as soil dries Ψ_{soil} becomes the dominant controller of stomatal aperture (Fig. 4). At some point during drought, the pipes that constitute the xylem pathway begin to cavitate [5,68] or collapse [69], rendering them non-functional. This process limits the recovery of plants from drought [70], and determines the point at which leaves are shed (C. Blackman & T.J. Brodribb submitted) and plant death occurs [39]. Such a hydraulic-centred view of plant function contrasts with the perspective of an increasing number of physiologists who consider the combined effects of apoplastic pH and the plant hormone ABA to be the dominant regulators of stomatal aperture during water stress [71,72].

It is clear that ABA can induce stomatal closure [73] as well as a raft of adaptive responses to drought [74], but these responses are generally secondary to the primary influence leaf water potential over stomatal aperture as modulated by the plant hydraulic system. Some degree of integration between chemical and hydraulic signalling probably takes place in plants. For example there is evidence that ABA acts to briefly override hydraulic signals during stress thereby facilitating embolism repair by reducing the hydraulic gradient within the plant [75]. However the concept that ABA is an important contributor to the daytime regulation of water loss in the majority of plant species [76] is far from certain [77].

Given that a strong hydraulic signal drives stomatal closure during soil drying, ABA is somewhat redundant as a further motivator for stomatal closure during water stress [78]. Therefore it seems that ABA might be important in regulating the recovery of plants from drought events and directing adaptive responses to water stress [79–81]. However, recent studies of gas exchange in

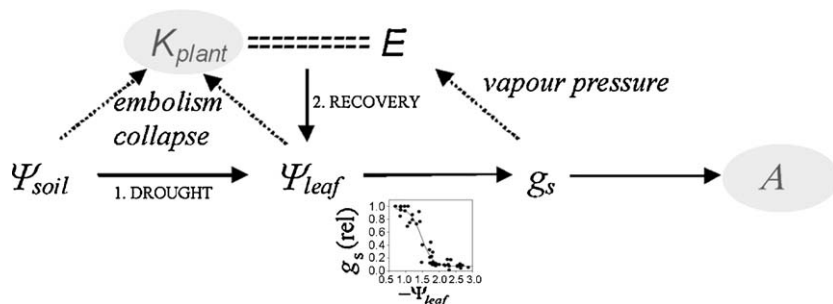


Fig. 4. Interactions between hydraulics and photosynthesis during drought and post-drought. In this hormone-free model, Ψ_{leaf} controls the photosynthetic response to drought by its influence on stomatal aperture. During soil drying (1) Ψ_{soil} dominates control of Ψ_{leaf} , but post-drought (2) the slow recovery of K_{plant} from embolism exerts control over Ψ_{leaf} and the rate of photosynthetic gas exchange. Hormones potentially influence the relationship between Ψ_{leaf} and g_s , but recent drought trials suggest that the post-drought recovery of woody plants adheres closely to this hydraulic-dominated control model.

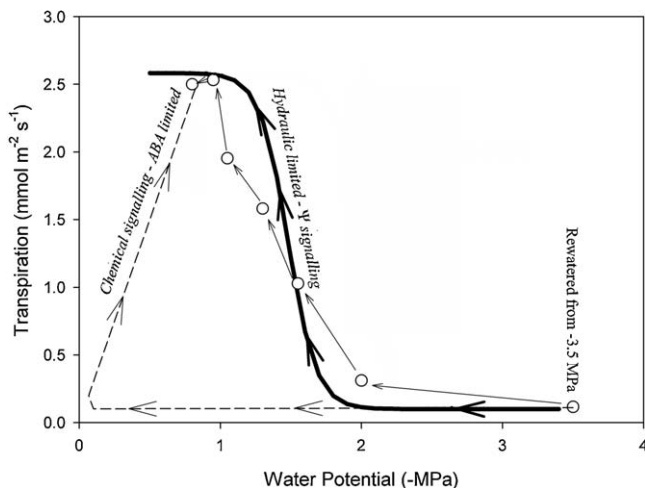


Fig. 5. Observed recovery of a droughted conifer after rewatering. Arrows connect daily measures of Ψ_{leaf} and whole-plant transpiration for 7 days. The observed recovery trajectory closely follows a hydraulically limited model (solid line), with little correspondence with an ABA limited model (broken line). Reproduced from Brodribb & Cochard [70].

naturally and artificially drought stressed trees demonstrate that the slow recovery of hydraulic conductivity after drought-induced embolism was the dominant control limiting the reopening of stomata [70] and re activation of photosynthesis [82]. Hydraulic effects in conifer species explained over 70% of the variation in transpiration during recovery from mild to severe imposed drought stresses [70]. Similarly, gas exchange in native shrubs rewatered after rain exclusion responded according to a hydraulic recovery model [82]. Interestingly, wild species of tomato were shown to recover from drought according to a hydraulic limitation of gas exchange [83] despite the fact that tomato stomata are known to be highly responsive to apoplastic pH and ABA [84]. One wonders whether an enormous over-representation of small herbs in chemical signalling research might overemphasize the importance of non-hydraulic control of stomata as it applies to woody plants.

The important questions are what limits water use, photosynthesis, growth and productivity in crops and wild plants? We know that evapotranspiration (and inferred photosynthesis) in trees and shrubs under natural conditions conforms extremely well to a hydraulic limitation model [22,85–87]. Furthermore, seedlings rewatered after drought follow a hydraulic recovery model rather than a chemically signalled recovery model [58] (Fig. 5). Crop plants must also be bound by hydraulic limits on gas exchange, but perhaps due to their small size they may be unusually sensitive to chemical signalling as well. A comprehensive answer to what limits gas exchange in the light will require a detailed study of the conditions under which chemical versus hydraulic signalling becomes an important component of stomatal control.

7. Plant death

The most difficult problem associated with pulling water from the soil is that the high tension created exposes the water transport system to large mechanical stress, and causes the transpiration stream to flow through xylem as a meta-stable liquid, highly prone to cavitation [88]. Minimizing these limitations comes with attendant costs in terms of functional performance [89] as well as increased structural investment [65]. Increased safety from dangerous xylem cavitation requires a reduction in the porosity of the pit membranes that join xylem conduits reducing the efficiency

of water flow in the xylem [90]. At the same time, reinforcement of the xylem walls is necessary to resist the higher hydraulic tensions that accompany maintaining water column integrity under large water deficits [69]. As a result, xylem resistance to water stress-induced dysfunction constitutes a fundamental axis of drought tolerance [91]. Recent studies have demonstrated that the vulnerability of the stem and leaf xylem to cavitation sets a quantitative limit to the drought tolerance of evergreen conifers [70] and angiosperms [82]. This is highly significant in terms of predicting distributional limits for native plants [92] and for predicting the conditions likely to result in plant death during drought.

Other putative measures of drought tolerance quantified in terms of leaf damage by fluorescence [93], changes in gas exchange [13], and permanent wilting [94,95] have only enjoyed limited success. The advantage of xylem physiology as a quantitative tool for assessing drought tolerance is that unlike indices based on the tolerance of living cells, xylem conduits are non-living, and therefore unable to be modified during drought acclimation. As a result, the xylem “hardware” places a definitive boundary to plant function during water stress. Furthermore the variation in xylem resistance to cavitation during drought appears to be under strong genetic control [96–98] raising the prospects for identifying and manipulating the responsible genes. The characters that determine xylem vulnerability involve the structure and area of pit membranes between xylem conduits as well as the thickness and stiffness of xylem cell walls [99–102]. Some information about industry-linked traits such as wood density and lignin chemistry [103–106] has begun to elucidate the genetic control of wood traits, but there is far to go before it is possible to target genes to modify drought resistance. Furthermore any genetic modification of cellulose chemistry that changes the elastic properties of cell walls will need to carefully consider the impact on potential collapse of xylem cells under the enormous tensions generated by the transpiration stream [107].

8. Conclusions

Our understanding of the hydraulic physiology of plants is far from complete, particularly considering that the most limiting parts of the hydraulic pathway in leaves and roots remain poorly understood. Symplasmic pathways in these organs are known to be responsive to the presence of water transporting proteins suggesting a role for genetics and biochemistry in the short term modification of hydraulic function [108,109]. Understanding the control and expression of genes involved in the regulation and development of the water transport system represents a crucial challenge for the future. Water transport physiology defines many aspects of the daily function of plants, and investigations into the developmental coordination and genetic control of hydraulic capacity and resistance to cavitation will yield great advances in our ability to manipulate plant function. Biochemical processes such as hormone regulation of stomata or cell death [110] are clearly significant in directing the way plants respond to the environment, but these processes have evolved to maintain plant function within the physical constraints of the plant body. Major transformations in the function of plants will require modification of the physical capacity of the plant body to improve the capacity and integrity of the water transport system.

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