

REVIEW ARTICLE

Stay wet or else: three ways in which plants can adjust hydraulically to their environment

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Abstract

The literature on whole-plant acclimation to drought is reviewed and it is proposed that leaf-level homeostasis in water status is attained during ontogeny largely thanks to whole-plant changes in physical resistance to liquid water flow caused by morphological and anatomical adjustments. It is shown that, in response to water deficits, plant resistance changes at different levels (tissue, organ, individual), levels that are correlated with the time scale of the response. It was found that such adjustments apparently tend to increase resistance to flow in the short term and to reduce it in the long term. A critical view of those findings is provided based on the principle that drought-induced changes cannot be analysed separately from the allometric changes that take place through ontogeny, as for example proposed by the widely cited hydraulic limitation hypothesis. A graphic synthetic model is presented according to which developmental responses to water deficits operate largely through reductions in whole-plant water transport capacity, combined with more or less strong reductions in leaf area (different ‘hydraulic allometries’), depending on the intrinsic tolerance of leaf tissues to partial desiccation. The model is used to show that, as the result of such adjustments, the water transport capacity per unit leaf area can decrease, remain constant, or increase, and it is argued that the expected leaf-level response would be different in each case, respectively involving a decreased, constant, or increased potential for transpiration. The article ends with a plea to collect the evidence needed to evaluate the occurrence of these three different response types across taxa and their association with different environments, including the reanalysis of existing data.

Key words: Allometry, drought, hydraulic architecture, hydraulic resistance, ontogeny.

‘Maximizing gas exchange while avoiding hydraulic failure means operating on the edge of dysfunction’

John S. Sperry (2004)

Introduction

The cohesion–tension theory of sap ascent for vascular, homeohydric plants states that: (i) evaporation of water from leaf tissues makes the microfibril cellulose matrix of cell walls develop capillary tensions (negative hydrostatic pressures; Lambers *et al.*, 1998); and (ii) thanks to the cohesion of water molecules, such tensions are transmitted downwards, all the way to root hairs, through continuous xylem tissue, literally pulling water upwards. The continuity of water columns from soil pores throughout the plant to leaf cells, linked to evaporative flux, is known as the soil–plant–atmosphere continuum (SPAC). Maintenance of this ‘hydraulic rope’ is needed to ensure a continuous water supply to leaves. The higher the capacity to provide such supply, the faster the leaf expansion (Nardini and Salleo, 2002), and the higher the potential for carbon gain (Sperry, 2000; Tyree, 2003), as has been observed between life forms (Brodribb *et al.*, 2005), species (Brodribb and Field, 2000; Sack *et al.*, 2003), and genotypes (Sangsing *et al.*, 2004). Accordingly, C₄ plants, highly efficient in water use, seem to have a reduced transport capacity in relation to C₃ plants (Kocacinar and Sage, 2004; see also Hacke and Sperry, 2001).

The association between water transport capacity and carbon gain is unrelated to the role of the water molecule as

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Abbreviations: HLH, hydraulic limitation hypothesis; SPAC; soil–plant–atmosphere continuum.

a substrate in photosynthesis (involving only about a molecule of water per molecule of carbon), or to water storage in newly formed tissues (about 10 times larger but still small). There is a much larger requirement for water because of the need to display a large surface of fully hydrated cells to obtain carbon dioxide, which happens to be in desiccating air; that is why higher plants transpire between 100 and 1000 water molecules per molecule of assimilated carbon. As this need cannot be met by water stored in the plant, it has to come from an external reservoir—the soil, causing a huge mass flow, with nearly all the water that enters the roots being lost by leaf transpiration a few hours or days later. Any shortage in water supply in relation to the requirements of leaves results in water deficit and plant stress; thus there is a strong selection for preventing such deficits without missing opportunities to acquire carbon for growth (see epigraph).

This article examines how plants cope with the challenge of supplying enough water to their leaves under the restrictions they experience at different time scales. The focus is on whole individuals and ontogeny, although at times other levels of organization from cell to species are also considered, and the article ends with a section on interspecific comparisons. As implied by the title, ‘chemical’ aspects of water stress are not covered—as the plant water literature often refers to the role of plant growth regulators and other metabolic clues; still, it is recognized that hydraulic and chemical signals can interact (e.g. Tardieu and Davies, 1993; Oren *et al.*, 1999; Freundl *et al.*, 2000). Although the article is not concerned with the mechanisms behind stomatal control of transpiration (e.g. Tardieu and Davies, 1993; Jones, 1998; Buckley, 2005), a negative association between the extent of this short-term control and longer term developmental control is predicted. The thesis is that leaf-level homeostasis in water status is maintained through ontogeny, despite varied and changing soil and atmosphere conditions, largely thanks to whole-plant changes in the physical resistance to liquid water flow. Moreover, we agree with Monteith (1986) in that, although such changes include adjustments in plant physiology and anatomy, the main control at the time scale of ontogeny is exerted by those in whole-plant morphology (see also Hsiao and Xu, 2000), without which the capacity to acquire water below-ground could not possibly match water demand from above-ground.

The aim of this article is intended to be 4-fold: (i) a depiction of the ways in which, in response to water deficits, plant resistance to liquid water flow changes at different levels (tissue, organ, individual), levels that are correlated with the time scale of the response; (ii) a compilation of published examples of changes in resistance for a range of time scales and levels of organization; (iii) the proposal that drought-induced changes cannot be analysed separately from the allometric changes that take place through ontogeny; and (iv) a graphic model showing

how water deficits can reduce total leaf area and modify whole-plant water transport capacity to different degrees, and predicting three developmental response types depending on the intrinsic tolerance of leaf tissues to partial desiccation.

Background and definitions

There is a deceptively simple equation that helps to explain the connections between liquid water flow, hydraulic resistance, and plant and soil water status (as measured by water potential; Ψ_w). In its simplest form, transport between any two points in the SPAC can be represented by:

$$F_H = -k_{H(\Psi)} \Delta\Psi_w \quad (1)$$

where F_H is volumetric flow per unit time, the proportionality factor is hydraulic conductance (k_H), and $\Delta\Psi_w$ is the difference in water potential driving the flow, which for long-distance xylem transport is more appropriately expressed as a difference in hydraulic pressure ($\Delta\Psi_p$). The negative sign indicates that the direction of flow is opposite to that of $\Delta\Psi_w$. Unlike many other properties of water, viscosity changes sharply in the range of temperatures experienced by plants (Nobel, 1999), and thus so does k_H . It should be noticed that Equation 1 emphasizes the predominance of apoplastic transport, and therefore is not appropriate for situations in which symplastic transport is important, such as low-flow conditions and short-distance transport (for reviews see Steudle, 2000; Boyer and Silk, 2004). At the shortest time scales, Equation 1 has the obvious, direct interpretation of flow being driven by $\Delta\Psi_w$. Even when it is tempting to think of k_H as the more stable part of the equation, there are counter-examples, such as sudden embolisms (which locally cause a drop in k_H), changes controlled by the ionic composition of xylem sap (Zwieniecki *et al.*, 2001), and fast-adjusting aquaporins (water channels in cell membranes; Maurel, 1997). At longer time scales, Equation 1 can be used to argue that it is conductance, as shaped during plant ontogeny and evolution, that determines the absolute drop in Ψ_w between any two points of the SPAC for a given flow need: the smaller k_H and the faster the need, the larger the drop.

The literature uses a variety of alternative transport formulae. These expressions are applied to represent more aptly specific aspects of water flow, such as different levels of organization. For example, another common formulation is:

$$F_H = -K_{H(\Psi)} \Delta\Psi_w / \Delta x \quad (2)$$

The proportionality factor here is hydraulic conductivity (K_H), i.e. the ability to conduct water per unit of spatial gradient ($\Delta\Psi_w / \Delta x$). Equation 2 requires a measurement of the distance (Δx) over which the drop in Ψ_w occurs, which has the advantage over Equation 1 of making comparisons

independent of such length. For entire plants, Equation 1 is used, since either total hydraulic path length is not available or one wishes to compare hydraulic properties of individuals irrespective of differences in size. Dividing Equations 1 and 2 by total plant leaf area, the proportionality factor becomes leaf-specific conductance (k_L , also symbolized as L_W , L , or L^P) and leaf-specific conductivity (K_L), respectively, and flow becomes transpiration rate (E). While this rate is mainly driven by meteorological factors (wind speed, air humidity, and temperature), canopy factors (e.g. aerodynamic roughness) and leaf vapour-phase conductance (often, but by no means always, coupled to stomatal aperture; Jarvis and McNaughton, 1986), it is still whole-plant transport capacity (k_L , to be precise) that determines Ψ_{leaf} at any given value of E (Sperry *et al.*, 1998).

The steady-state conditions required for rigorous application of Equations 1 and 2 are not always met because tissues can store water, and thus have a certain capacitance (negatively correlated with their density; Bucci *et al.*, 2004). Besides, as will be discussed later in some depth, plant k_H is not constant but dependent on Ψ_W . These complexities apart, Equation 1 clearly highlights that keeping Ψ_{leaf} within an acceptable range requires co-ordination between liquid water flow and plant k_L (Whitehead, 1998; Hubbard *et al.*, 2001; Meinzer, 2002). Depending on how narrowly they control Ψ_{leaf} , homeohydric plants are further classified as either isohydric (tight stomatal control, resulting in a minimum, threshold Ψ_{leaf} for stomatal closure) or anisohydric (less strict control, with no discernible threshold; Tardieu and Simonneau, 1998). This distinction, however, is really a matter of degree, and most plants operate under a relatively well-buffered range of Ψ_{leaf} . Restating the thesis in terms of Equation 1, what is being proposed is that higher plants accomplish such leaf-level homeostasis largely thanks to ontogenic changes in leaf-specific hydraulic conductance (k_L).

Blueprint of hydraulic resistances

To understand how whole plants are able to adjust their liquid water transport capacity under different supply conditions, it is convenient to consider plant-level hydraulic resistance (inverse of conductance) as composed of partial resistances, most of which are arranged in series (at least upstream from a single leaf) and therefore numerically additive. These resistances are of very different types and magnitudes, and their arrangement for each particular branching pattern produces what Zimmermann (1983) called hydraulic architecture (further definitions in Cruiziat *et al.*, 2002). This section presents an overview of each type of partial resistance, specifically focusing on what is known about the ways in which they provide opportunities for adjustment, allowing plants to attain alternative architectures when faced by different degrees and types of water stress.

Soil and rhizosphere resistance

Water moves from the soil to the roots through the rhizosphere, a boundary zone that differs from bulk soil in physical–chemical conditions, and in which large Ψ_W differences can occur over a few millimetres, causing steep gradients. These develop because of the highly non-linear (texture-dependent) influence of soil water content on soil hydraulic conductivity (K_{soil} , also known as L^{soil}). The driving force behind flow in the rhizosphere is the transpiration-driven drop in Ψ_{root} , and obeys Darcy's law, a variant of Equation 2 which expresses flow per unit soil area normal to the flow direction (i.e. flux density), which is why K_{soil} has the same units as K_L . As uptake proceeds, and the explored part of the profile becomes drier and reaches a low K_{soil} , root growth into wetter parts of the profile is required (Kramer and Boyer, 1995). Still, under high transpiration rates, the soil closest to the root surface can act as a hydraulic bottleneck (Sperry *et al.*, 1998). This occurs when the increase in the spatial gradient ($\Delta\Psi/\Delta x$) is counterbalanced by a sharp drop in K_{soil} , eventually leading to hydraulic failure (flow $\rightarrow 0$; see Equation 2).

In the short term, plant control on this resistance can be exerted via Ψ_{root} —but just to a certain degree. Maintaining a relatively high Ψ_{root} lowers the risk of rhizosphere failure but at the same time reduces uptake. Early theoretical work showed that, in contrast, a much larger influence can be attained in the mid and long term via root system geometry (Gardner, 1960; Cowan, 1965), including two effects beyond the obvious ones of root area and depth. The first one is that root length per unit volume of soil (root density) determines the average distance water molecules are required to move in the soil towards the plant (Newman, 1969), which modifies the spatial gradient for a fixed Ψ_W difference between the bulk soil and the roots (Williams, 1974). The second one is that the restriction to water movement within the soil shell around each root is intensified by a sort of funnel effect caused by uptake: as water molecules converge in this cylindrical volume towards the root surface, the exchange area becomes smaller, requiring (according to the principle of continuity; Vogel, 1994) a faster movement, precisely in the driest, high resistance part of the rhizosphere. Therefore, if the same total leaf area is fed by a larger and denser root system, then not only is a smaller reduction in Ψ_{root} required to maintain the same gradient (which enhances K_{soil} in the inner rhizosphere layers), but also a lower flux density will occur for a given transpiration rate, thus lowering the risk of hydraulic failure. The opposite is true at a low root-to-leaf area ratio, because then the most important resistance of the SPAC will lie in the soil (Williams *et al.*, 2001). The extremely plastic response of the root-to-shoot ratio to water supply and soil texture shows the high degree of control plants keep on this resistance (Table 1, row 6).

Table 1. Examples of changes caused by drought on different structures that influence hydraulic conductivity (K_H)

The effect on K_H was usually not stated in the original reference and here is inferred.

Structure or process	Level of organization	Time scale	Effect on K_H	References (examples)
1 ↓Aquaporin activity, density	Subcellular, cell	Minutes, hours	↓	Tyerman <i>et al.</i> (1999); Javot and Maurel (2002)
2 ↑Wall suberization	Cell	Days	↓	Rieger and Litvin (1999); Ranathunge <i>et al.</i> (2004)
3 ↑Endodermis and exodermis thickness	Tissue	Days, weeks	↓	North and Nobel (1991); Stasovsky and Peterson (1991); Lo Gullo <i>et al.</i> (1998); Freundl <i>et al.</i> (2000)
4 ↓Vessel diameter	Tissue	Ontogeny	↓	Lovisololo and Schubert (1998); Aasamaa <i>et al.</i> (2005); Nardini and Salleo (2005)
5 ↓Vulnerability to xylem cavitation	Tissue, organ	Ontogeny	↓Under drought; ↑with no drought?	Ewers <i>et al.</i> (2000); Hacke <i>et al.</i> (2000)
6 ↑Root : leaf area ratio	Whole plant	Ontogeny	↑ $K_{\text{rhizosphere}}$; K_L	Newman, (1969); Hacke <i>et al.</i> (2001); Fernández <i>et al.</i> (2002); Serraj and Sinclair (2002)

Root radial resistance

Once within plants, water can follow two different pathways: through living cells (symplastic pathway), or through cell walls and intercellular spaces (apoplastic pathway). In terms of total path length, it is the latter which dominates (i.e. most water is destined for long-distance transport in the xylem, an apoplastic pathway), but at crucial locations the former becomes important because of its high resistance per unit path length (resistivity). In roots, thanks to their anatomical complexity, these pathways allow two modes of transport to occur simultaneously (Steudle, 2000): the hydraulic one (passive, apoplastic) and the osmotic one (metabolically active, symplastic). The hydraulic mode predominates under high transpiration rates, and the osmotic mode predominates under low or nil transpiration rates. Both modes are driven by Ψ_W gradients, but the hydraulic mode, as a mass flux, is largely controlled by pressure (Ψ_P) gradients. Resistivities under the osmotic mode are very large because water needs to cross biological membranes. Among other things, these resistances vary according to the activity and number of water channels (Table 1, row 1). Resistances in the hydraulic mode are controlled by the degree of wall suberization and the developmental state of specialized apoplastic barriers (endodermis and exodermis; Table 1, rows 2 and 3).

As for most partial resistances, the major determinants of root radial resistance for a given genotype are ontogeny (organ age) and exposure to water stress. Young unstressed roots tend to exhibit less apoplastic resistance in comparison with older and stressed roots (Steudle, 2000; see also Barrowclough *et al.*, 2000). These factors interact and, for example, bluegrama roots that survived drought had an important recovery of function, but their uptake capacity was about half of that of new roots generated after drought (Lauenroth *et al.*, 1987). In agave, young roots increased their resistance much more under drought than the already

heavily suberized old ones (North and Nobel, 1991). This perhaps occurred because older roots operate largely in the osmotic mode, more or less independently of soil water content due to their higher apoplastic resistance; thus, their absorption was less reduced under drought than that of the young roots (probably operating largely under hydraulic mode). One would expect the speed of response to be relatively slow for apoplastic resistances; however, in a study with olive, Lo Gullo *et al.* (1998) found endodermis tissue to differentiate in response to experimental drought in a matter of only a few days (Table 1, row 3).

Root and shoot axial resistance

Lumina of dead transport cells (xylem vessels and tracheids) belong to the apoplastic pathway and form the true long-distance conduits through plants. The number and diameter of these conduits tend to be negatively correlated (Preston *et al.*, 2006). According to the Hagen–Poiseuille law, the same transport capacity can be alternatively attained by a few vessels of large diameter, leading to high transport efficiency per unit of cross-section area, or by many vessels of small diameter, leading to a high transport safety by pathway redundancy. In 1806, Heinrich Cotta elegantly showed how powerful this redundancy can be (Cotta, 1806). He proved that two overlapping saw-cuts at different heights and from opposite sides of the main trunk of a tree caused no apparent short-term harm, most probably because many (and perhaps also wavy) vessels allowed sap to follow a variety of paths (Tyree and Zimmermann, 2002). The inherent safety provided by such a xylem pattern protects plants not only from mechanical damage as could be caused by storms or herbivores, but also from freezing and drought-induced embolism (see below). Most data on axial transport of water in plants come from studies, like this early one, on shoots of woody species. Now we know that shoots are not the main

resistances to water flow: about half the total plant resistance lies in roots, and most of the other half may be in leaves (Meinzer, 2002).

Main stems have to conduct water to every single leaf, and thus their hydraulic conductance (k_H) is bound to be larger than that of minor shoots. Hence, a more revealing parameter to describe hydraulic architecture is the aforementioned leaf-specific conductivity (K_L), calculated as the K_H of any plant segment per unit of leaf area that it feeds (i.e. downstream). Values of K_L encompass at least three, and probably up to six, orders of magnitude across species. Within a plant, K_L often decreases by one or two orders from the main stem towards the thinner branches, but the opposite pattern may occur in species and genotypes with strong apical dominance (e.g. López-Portillo *et al.*, 2000; Lo Gullo *et al.*, 2004). This variation along plant shoots depends on the balance of two trends: one in total sapwood cross-sectional area feeding each unit of leaf area (the Huber value, which generally increases downstream) and the other in individual vessel diameter (which tends to decrease downstream). The vessel diameter trend sometimes becomes clearer when roots are included (e.g. McElrone *et al.*, 2004). Since there is a high axial resistance when water has to cross from one vessel or tracheid to the next, conduit length distribution, although largely neglected, is an equally important component of hydraulic architecture (Comstock and Sperry, 2000). Comparisons across species, sites, and dates often report negative correlations between Huber values and branch or xylem area-specific K_H (e.g. Vander Willigen *et al.*, 2000; McClenahan *et al.*, 2004). To our knowledge, there have been no studies assessing plastic responses to water stress of vessel length and only some on Huber values (e.g. Vander Willigen and Pammenter, 1998). What seems more surprising is how few studies assessed changes in vessel diameter (Table 1, row 4).

Because of the low absolute hydrostatic pressure (Ψ_P) caused by transpiration (Pockman *et al.*, 1995), xylem water is in a metastable liquid state which may suddenly change to a stable vapour state, leading to embolism (for a dissenting view, see Zimmermann *et al.*, 2004). This change is known as cavitation and, as far as is known, is triggered by air seeding through the vessel walls. If so, for a given Ψ_P , cavitation would be more likely (xylem would be more vulnerable) if vessels have relatively wide pit membrane pores, but not necessarily a wider diameter themselves (Sperry *et al.*, 1994; Lambers *et al.*, 1998). The finding, under some circumstances, of a positive correlation between vessel diameter and vulnerability (Grace, 1993; Linton *et al.*, 1998; Hacke and Sperry, 2001), however, does not invalidate the reasoning, even if correlations turn out to be stronger than those found up until now. Cavitation events are frequent in some species and relatively rare in others (McCully, 1999; McClenahan *et al.*, 2004). This occurs either because of a different degree of stomatal

control (such as in iso- versus anisohydric species, or a different safety margin; Lambers *et al.*, 1998; Drake and Franks, 2003), different hydraulic architecture, or different intrinsic vulnerability to cavitation (Bond and Kavanagh, 1999)—which may sometimes depend on individual short-term history (e.g. Stiller and Sperry, 2002) and details of xylem microstructure (Choat *et al.*, 2004). Plants with a tendency to experience embolism because of a more vulnerable xylem may or may not have a relatively large K_H under non-drought conditions (Maherali *et al.*, 2004), but certainly do have a reduced K_H under stress conditions (e.g. Linton and Nobel, 1999). Regardless of their cause or frequency, embolisms always increase resistance to flow, and therefore a reduced vulnerability would improve K_H under drought conditions (Table 1, row 5).

As Ψ_W values decrease monotonically along the SPAC, it is in principle downstream where plants are more likely to experience failure. Zimmermann (1983) proposed the (hydraulic) segmentation hypothesis: that it is not only likely but also advantageous for embolism events to occur in peripheral organs, which can act as hydraulic 'fuses'. At the leaf or branch level, cavitation reduces water supply and can make things worse, ending in runaway failure ($K_H \rightarrow 0$; exactly as for the rhizosphere, as first noted by Milburn, 1979). However, at the whole-plant level, cavitation does not necessarily mean a catastrophe that needs to be avoided at all costs; it could have the beneficial effect of reducing leaf area ('branch sacrifice'; Rood *et al.*, 2000; Davis *et al.*, 2002). It has also been proposed that the release of water from cavitating conduits could contribute to capacitance, and thus help mitigate short-term imbalances (Tyree and Yang, 1990; Holbrook, 1995; Nardini and Salleo, 2000; Meinzer *et al.*, 2001) and even contribute to gas exchange regulation (Sperry, 1995; Salleo *et al.*, 2000; Cochard, 2002). Embolized vessels might restore their function (e.g. Holbrook *et al.*, 2001), but the mechanism remains unclear (e.g. Bucci *et al.*, 2003; Salleo *et al.*, 2004) and may differ between species (Hacke and Sperry, 2003). Besides, different organs tend to have different vulnerability to cavitation (e.g. Alder *et al.*, 1997; Salleo *et al.*, 2000; McElrone *et al.*, 2004; but see Linton *et al.*, 1998), and thus segmentation has not only a hydraulic component but also a vulnerability component (Tyree and Zimmermann, 2002). On this basis, small root xylem has also been proposed as a possible weak, replaceable segment of the SPAC (Linton and Nobel, 1999; Hacke *et al.*, 2000; Domec *et al.*, 2004). Xylem vulnerability is a plastic trait (Table 1, row 5), and so is hydraulic architecture, but the appealing link between both predicted by the segmentation hypothesis, to be properly assessed, needs more experimental work.

The hydraulic architecture of leaves includes a high resistance, symplastic component associated with the leaf mesophyll (which, in rigour, does not belong to the 'axial' category of this section) and a generally low resistance, apoplastic component associated with leaf venation

(Cochard *et al.*, 2004; Gascó *et al.*, 2004). A peculiar situation takes place in developing grass blades (including those of cereal crops), which because of their basal meristems present a high resistance caused by the interrupted mature functional xylem (Martre *et al.*, 2000). More generally, the sum of both leaf resistances, symplastic and apoplastic, represents about a quarter of total plant resistance in the liquid phase, and is correlated with maximum rates of gas exchange across species (Sack *et al.*, 2003). From a comparison of two grape cultivars, Schultz (2003) went as far as to suggest that leaf hydraulic properties may determine whether a genotype or population is relatively more isohydric or anisohydric.

Drought versus size effects on resistance

Our previous overview of the SPAC referred mainly to the cell, tissue, and organ levels of organization, and now the perspective is widened to include higher levels of organization. Plants respond to drought, as to any other environmental factor, by a variety of mechanisms that operate at different spatial levels and span a wide range of time scales, from nearly instantaneous to evolutionary (Lambers *et al.*, 1998). These spatial and time scales are not independent, but positively associated in a nested hierarchy (Table 1). Processes at one level (e.g. leaf transpiration) are in part the consequence of faster rate processes that occur at lower levels in the hierarchy (e.g. stomatal responses to a sunfleck) but are also constrained by slower rate processes that occur at higher levels (e.g. hydraulic architecture and transpiration of neighbouring branches). According to this framework, knowledge about the effects of drought at a given level cannot be expected to be used plainly to predict what may occur at higher levels.

Drought effects

A priori, it would make as much sense to find that under water shortage plants tend to facilitate water flow, making it easier to acquire the resource in shortest supply, as to find

that they hinder water flow, allowing soil water conservation. However, nearly all the studies reviewed at the cell to tissue level showed the second pattern: increased resistance under drought ($\downarrow K_H$; Table 1, rows 1–4). The same was shown by many studies at the whole-plant level, especially short-term ones involving pot-grown plants or seedlings (Table 2). It was only when entire plants were analysed in truly long-term observations, such as encompassing a significant fraction of the life span of perennial individuals, that examples could be found of decreased resistance [$\uparrow K_H$; the studies of Maherali and DeLucia (2000) and Cinnirella *et al.* (2002) in Table 2]. It seems that it is only under long-term water restriction that hydraulic conductance can be maintained or even increased. A similar conclusion was attained in a meta-analysis by Mencuccini (2003).

The apparently frequent situations in which tissues, organs, and entire plants plastically reduce their ability to transport water when it is in short supply calls for an explanation. It is suggested that such a response is adaptive, not only because it results in a slower soil water use, which might lead to water saving under certain conditions (e.g. Cohen, 1970; Richards and Passioura, 1989), but also because it would reduce the amount of water lost to the soil if $\Psi_{W\text{soil}}$ falls below $\Psi_{W\text{root}}$ (cf. Trillo and Fernández, 2005). Cell walls and aquaporins can both have bidirectional water flow (Cheng *et al.*, 1997), and there is no underground control structure akin to the leaf cuticle/stomata system. Thus, plants are exposed to a high risk of water loss by root-to-soil flow. A proof of this is the apparently widespread phenomenon of hydraulic redistribution, in which water moves passively from relatively wet to drier soil layers through roots (Burgess *et al.*, 1998; Caldwell *et al.*, 1998). The only situation in which the rhizosphere can act as a one-way valve is when dehydration causes root shrinking, because then root–soil air gaps virtually block water loss (Nobel and North, 1993). As pointed out above, sustained root elongation in wet layers is crucial to maintain uptake; in our view, such exploration with young, low resistance roots makes sense because

Table 2. Studies measuring conductance (*k*) or its component conductivity (*K*) whole-plant level under controlled (or, at least, carefully assessed) drought conditions

Species	Field (F) or pot (P) study	Drought duration	Effect on <i>k</i> or <i>K</i>	Reference
<i>Picea mariana</i> and <i>Pinus banksiana</i>	P	5 d	$\downarrow K_S$	Blake and Lil (2003)
Rice	P	6 d	$\downarrow k_L$	Stiller <i>et al.</i> (2003)
<i>Populus tremula</i> and <i>Tilia cordata</i>	F	3 weeks	$\downarrow k_L$	Aasamaa <i>et al.</i> (2004)
Apricot trees	F	3 weeks	$\downarrow k_H$	Nicolás <i>et al.</i> (2005)
Ponderosa pine	P	54 d	$\downarrow k_L$	Maherali <i>et al.</i> (2002)
Wheat	P	10 weeks	$\downarrow k_L$	Trillo and Fernández (2005)
Ponderosa pine	F	One summer	$\downarrow k_{\text{rhizosph}}$	Williams <i>et al.</i> (2001)
<i>Pinus laricio</i>	F	3 years	$\uparrow k_L$	Cinnirella <i>et al.</i> (2002)
<i>Eucalyptus globulus</i> and <i>E. nitens</i>	F	6 years	$\downarrow K_H$	White <i>et al.</i> (1998)
<i>Pinus pinea</i>	F	Chronic: salinity	$\downarrow k_H$	Teobaldelli <i>et al.</i> (2004)
Ponderosa pine	F	Chronic: site vapour pressure deficit	$\uparrow K_S$	Maherali and DeLucia (2000)

reversed radial flow is unlikely there. Regarding reversed axial flow, Hsiao and Xu (2000) also suggested that undeveloped vascular tissues cause a relative hydraulic isolation of root tips that protects them somewhat from desiccation.

Size effects

It has been proposed that, independently of the environment in which they grow, plants become increasingly water stressed as they age, until reaching a point from which further growth is not possible. This is the hydraulic limitation hypothesis (HLH) of tree maximum height (or, more generally, plant maximum size), which has been used to explain declining forest-stand productivity with age (Ryan and Yoder, 1997). The hypothesis is based on the reasonable assumption that axial hydraulic resistance increases with the length of the pathway, but its general applicability is still under debate (Bond and Ryan, 2000; Mencuccini and Magnani, 2000; Midgley, 2003; Meinzer *et al.*, 2005). There seems to be consensus, at least, in that hydraulic limitation is an important factor on tall (and probably also on deep-rooted) plant evolution (Becker *et al.*, 2000; Mencuccini, 2003; Midgley, 2003), i.e. paraphrasing Connell (1980), something like 'a ghost of hydraulic-limitation past'. Comparison of actual patterns of vessel branching of plants with models of vasculature proposed for both plants (Da Vinci's and pipe models) and animals (Murray's and aorta models) shows conflicting evolutionary pressures not only for water transport efficiency versus safety but also for mechanical strength (Niklas, 1992; Hacke *et al.*, 2001; McCulloh and Sperry, 2005).

If, as suggested by the HLH, plant conductance per unit of leaf area (k_L) consistently decreases with increasing size (as clearly shown at least for eucalypt and gymnosperm trees: Hubbard *et al.*, 1999; Williams *et al.*, 2001; McDowell *et al.*, 2002; Barnard and Ryan, 2003; Phillips *et al.*, 2003; Delzon *et al.*, 2004; Koch *et al.*, 2004; Gyenge, 2005), then the size effect on k_L should be first discounted from any apparent response to drought in order to discern the actual, direct drought effect. Otherwise, there is the risk of misinterpreting as a direct consequence of drought what in reality is a consequence of size (see Maherali *et al.*, 2002; Preston and Ackerly, 2003). The usual experimental procedure is to compare plants of the same age (using a single harvest approach). However, to discount size effects, an ideal experimental protocol should compare droughted and control plants of the same size (Lo Gullo *et al.*, 2004). Since sustained stress reduces plant size (height, biomass, leaf area), comparing stressed and control plants of the same age can lead to three possible errors depending on the direction and magnitude of the actual drought effect on k_L for a given plant size (Fig. 1): (i) if the drought effect is absent, then there would be an apparent positive drought effect on k_L (pure size effect; Fig. 1a); (ii) if the drought effect on k_L is

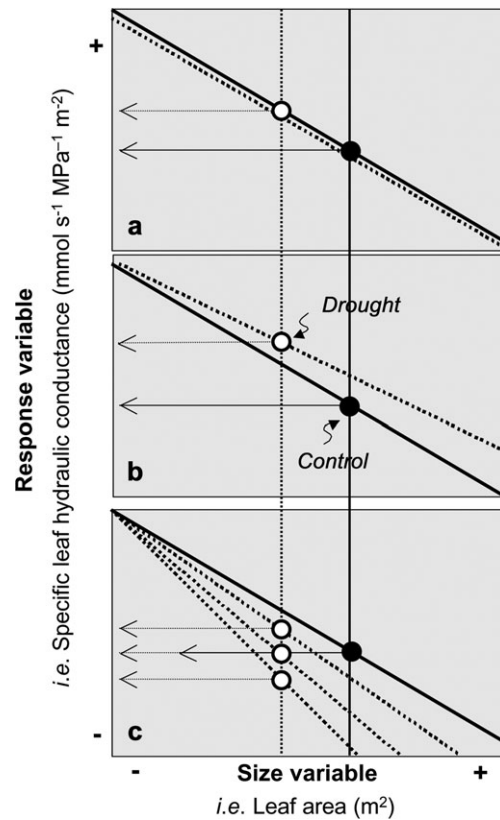


Fig. 1. Possible errors in the interpretation of drought-induced changes in k_L based on single-date harvests (applicable to any response variable affected by allometric effects). Vertical lines indicate plant size for control (full lines and filled circles) and drought treatment (dotted lines and open circles) at harvest date. The true drought effect for all cases is the distance between the control and drought diagonal lines on the same vertical line (same size). (a) Pure size effect; k_L appears to have increased even when there was no drought effect. (b, c) Combined size and drought effects; (b) k_L was increased by drought but to a smaller degree than the apparent effect; (c) k_L was decreased by drought, but, depending on how much, this can be perceived as an increase (upper point), not detected (central point), or detected but underestimated (lower point). Cases (a) and (b) always result in an overestimation of the drought effect as long as the variable of interest decreases with size.

indeed positive, it would then be artificially magnified (Fig. 1b); (iii) if the actual effect is negative, depending on its magnitude it could appear as positive, absent or negative (Fig. 1c).

This analysis shows that, as far as the HLH applies, any increase in k_L or K_L under water stress should be looked at with suspicion, whereas, on the other hand, any decrease in k_L or K_L under water stress (e.g. Lovisolo and Schubert, 1998; Nicolás *et al.*, 2005; Trillo and Fernández, 2005) can be taken as valid (although it may be underestimated, as shown by Fig. 1c). Experiments tracking developmental trajectories under drought are not common but are feasible (at least for herbaceous plants: Fernández *et al.*, 2002; Li *et al.*, 2005). If measuring plants of different sizes is not workable, at least null hypotheses should include this 'hydraulic allometry effect'; i.e. not taking a given increase of

k_L or K_L under water stress as a direct drought effect unless it exceeds the change expected from the mere size reduction. At the moment, it is not possible to determine to what degree the results summarized in Tables 1 and 2 are influenced by such bias, which if accounted for would add to the already high prevalence of increased resistance responses. Note that this reasoning is valid as long as the parameter of interest is a function of size at least for one of the treatments, regardless of the sign of the trend (i.e. even if k_L increases with plant size and the HLH is rejected). The only case in which size would not need to be taken into account is that of isometry (proportional change in k_H and leaf area), which in Fig. 1 would be represented as horizontal lines.

A model for whole-plant acclimation

Not so long ago, Tyree and Alexander (1993) candidly admitted that, except for ‘anecdotal perceptions’, it was not really understood what confers drought resistance to plants. Now, thanks to quantitative models including the likelihood of hydraulic failure in both the soil and the plant (Sperry *et al.*, 2002), it is known that maximization of water flux in a given environment requires the harmonization of at least three parameters: stomatal sensitivity, xylem vulnerability to embolism, and root-to-leaf area ratio ($A_R:A_L$; as shown, a main determinant of k_L). The correlation between these traits is expected to be stronger under low capacitance conditions (Bond and Kavanagh, 1999) and for more isohydric species (Hubbard *et al.*, 2001). It may well be that hydraulic architecture turns out to be the most important factor explaining the degree of leaf water homeostasis (e.g. Nardini *et al.*, 2003; Schultz, 2003). However, a predictive framework for acclimation, i.e. accounting for plastic responses to drought (something that may have been better analysed for light and nutrient shortages; e.g. Grime and Mackey, 2002) still seems to be lacking. In this section, building upon the elements summarized above, a conceptual model is presented which can serve as such a framework and has the merit of suggesting a number of broad, falsifiable predictions linking leaf and whole-plant responses.

Model description

The model acknowledges that water use is controlled by different means at different time scales. In the initial drought stages (or for a short-term drought), the response is always at the leaf level but differs between species. For a fixed drought intensity, i.e. a given decrease in Ψ_{soil} or increase in vapour pressure deficit, there is a range of possible responses between two theoretical extremes: (i) a perfectly isohydric plant would close stomata, reducing transpiration exactly as needed to maintain the predrought leaf water status; (ii) a perfectly anisohydric plant would keep stomata comparatively more open, reducing Ψ_{leaf} just

enough to maintain predrought leaf transpiration (Fig. 2a). Hydraulic architecture controls both the level to which transpiration is reduced in the first case and the level to which Ψ_{leaf} is reduced in the second case. Hydraulic architecture and k_L , in turn, are controlled by plant morphology (e.g. $A_R:A_L$) and anatomy (e.g. Huber value, and conduit type, length, and diameter). For longer droughts, changes in these whole-plant properties become possible through senescence and differentiation of new tissues. It is postulated that, if the drought persists, the likely response depends largely on the type of leaf-level response. This is so because the maintenance of the same level of plant transpiration is not feasible, and it is thus likely that anisohydric plants will have to make adjustments to reduce their water demand. Isohydric species, instead, would be able to keep more of their leaf area (or keep it longer) than anisohydric ones (Fig. 2b). It could be argued here that the need to reduce leaf area by anisohydric species may be lessened if the extra carbon they gain thanks to their leaf-level response allows access to additional water resources (e.g. by root system extension); this would be a reasonable drought-avoiding behaviour which, for the sake of clarity, has been left out of the graphical model.

At even longer time scales, closer to an individual life span (e.g. several seasons for a perennial), developmental plasticity allows liquid water transport capacity to adjust to the prevailing soil and atmosphere conditions (Table 2), and so does vapour phase transport capacity (G_{max}), both adjusting together in a co-ordinated way (Meinzer, 2002; Katul *et al.*, 2003; Mencuccini, 2003). Based on this evidence, it is argued that for the ontogenic time scale, the relevant pair of axes is not leaf area and transpiration, as it is for shorter time scales, but leaf area and total plant conductance (k_H ; Fig. 2c). Here, solid arrows represent individual development trajectories starting from seedlings; k_H and leaf area increase over time, but under drought are reduced in comparison with the no-drought situation (the only exception being leaf area for *Lr*: see below). In accordance with the HLH presented in the previous section, these trajectories are not straight but convex, reflecting the decrease of k_L with increasing size. To discount size effects, and evaluate actual drought effects, here one simply has to compare k_H for a fixed leaf area.

So far two ways in which individual plants can adjust to drought have been discussed, both derived from their short-term response (Fig. 2a, b), but there is a third one at the longer ontogeny time scale. All three ways include a reduction in total conductance k_H with respect to controls, achieved by any of the mechanisms outlined in the ‘Blueprint of hydraulic resistances’ above. The main difference between the proposed trajectories resides in the shape of the k_H versus leaf area relationship. The hypothesized convexity of trajectories in Fig. 2c would be represented by an equation of the form $y=ax^b$, which in a log–log plot becomes a straight line with a slope

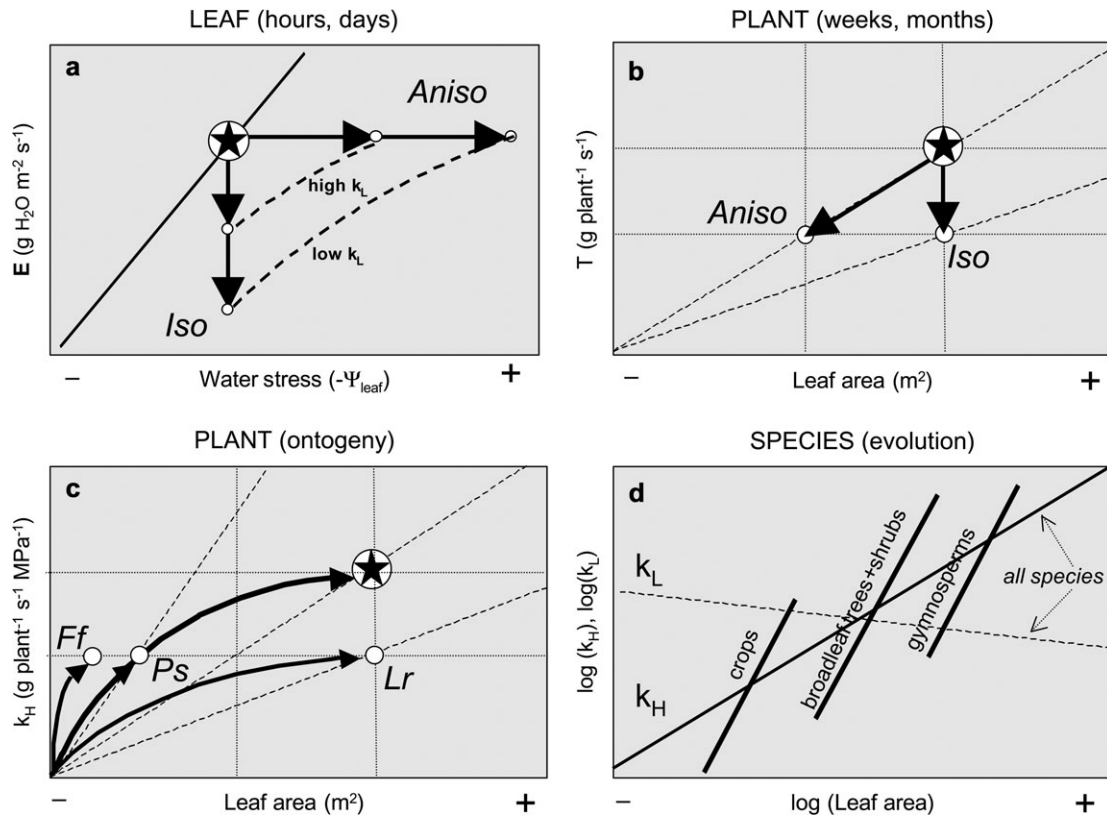


Fig. 2. Hypothetical effects of drought at four time scales. Stars represent the no-drought situation. (a) Shortest term: leaf water status is tightly linked to leaf-level transpiration (E ; diagonal solid line); responses to drought range between isohydric (Iso) and aniso-hydric (Aniso) (arrows); these responses are constrained by leaf-specific hydraulic conductance (k_L ; dashed lines). (b) Short term: plant transpiration (T) is related to total leaf area; responses to drought assuming the same reduction in T ranges between strong (Aniso) and nil (Iso) leaf area reduction (arrows); each diagonal line represents a constant E (dashed). (c) Ontogeny: plant conductance (k_H) is non-linearly related to leaf area (solid arrows); developmental trajectories under drought could mimic the no-drought one ('pure size' effect; Ps), follow a lower, 'leaf-retaining' path (Lr), or—perhaps—run above it ('fast flow' Ff, see text); all trajectories represent the same life span, and the three drought trajectories assume the same reduction in k_H with respect to the control; each diagonal line represents a constant k_L (dashed). (d) Evolution (redrawn from Mencuccini, 2003): species k_H scales similarly with leaf area within life forms [allometric coefficient $b \approx 1$ (see text); thick solid line], but not across life forms ($b = 0.8$; thin solid line); k_L decreases across species ($b = -0.2$; dashed line). Reproduced with permission. Mencuccini M. The ecological significance of long-distance water transport: Short-term regulation, long-term acclimation and hydraulic costs of stature across plant life forms. *Plant, Cell and Environment*. 26, 163–182. Published by Blackwell.

(allometric coefficient, b) smaller than 1. The three proposed types differ in the way this coefficient changes under drought. Aniso-hydric plants would tend to follow the allometric trajectory of no-drought plants (similar b). Iso-hydric plants will have a smaller b , and there would be a third type of response having a larger b than no-drought plants (Fig. 2c). This third type represents a response fundamentally different from the other two types because it allows an increased transpiration per unit leaf area (a possibility not included in the short-term leaf responses of Fig. 2a). Such a response was indeed observed by Li *et al.* (2005) and would explain the results of Maherali and DeLucia (2000); interestingly, in these two studies, drought was the consequence of a large atmospheric demand. In sum, the three drought response types result from the possible combinations between the reduction in leaf area versus that in k_H : (i) in the same proportion as a no-drought plant of an equivalent size would have (i.e. pure size

response); (ii) in a smaller proportion (leaf-retaining response); and (iii) in a larger proportion (fast-flow response). Parameter a in the allometric equation becomes important if b values are little affected by drought. In the special case of hydraulic isometry ($b = 1$), and only in such a case, a becomes k_L , and the three types above correspond to constant, reduced, and increased k_L , respectively.

Model predictions

It is argued that the three whole-plant responses just presented are co-ordinated with what happens at the leaf level. The pure size response would be the one keeping the highest degree of mid-term homeostasis in leaf-level transpiration (comparable with that of no-drought plants of equivalent size), and it was shown that such a response is in agreement with a short-term aniso-hydric behaviour of Ψ_{leaf} . The other two whole-plant responses yield opposite predictions in terms of the leaf-level response.

Leaf-retaining plants would have a reduced capacity to conduct water to each leaf, whose photosynthesis would then be strongly impaired, as expected from leaf-level isohydric behaviour. These plants would be more likely to reduce the transpiration capacity of their leaves plastically (e.g. by forming narrow xylem conduits, as observed by Aasamaa *et al.*, 2005), or developing a low stomatal density (e.g. Miyazawa *et al.*, 2006). The last possibility is that of fast flow, i.e. an increased capacity to supply water to each leaf by a strong reduction in leaf area in relation to the k_H reduction.

Consideration of these three types of responses not only yields the leaf- versus plant-level response predictions just presented, but also shows how to design suitable experiments to test them. Having only leaf area and k_H data for drought and control plants of the same age, only k_H /leaf area ratios (k_L values) could be compared, which would be misleading because these ratios are likely to include size effects (as shown in Fig. 1). This is crucial to evaluate the increased conductance pattern discussed under 'Drought effects'. On the one hand, it has already been stressed that no firm conclusion can be reached based on those data until possible size effects are considered (hydraulic allometry is accounted for). On the other hand, the existence of a fast-flow response was postulated even when, in fact, it is not known whether the no-drought trajectory constitutes an upper boundary for responses. Hence, a matter of foremost importance is to establish whether observed increases in k_L (e.g. DeLucia *et al.*, 2000; Cinnirella *et al.*, 2002) are caused by truly increased whole-plant k_H and, if so (e.g. Fig. 5c in Li *et al.*, 2005), which segments and mechanisms of the type outlined in the 'Blueprint of hydraulic resistances' above constitute the basis of such a response.

Plant-level responses in Fig. 2c were described as the result of long-term ontogenic trajectories in more or less stable environments, and those in Fig. 2b as the result of shorter term responses to year-to-year variations. Obviously, real environments include responses at both time scales, which could be drawn in the same axes of Fig. 2c as more complicated trajectories than the ones now included. Also, the focus has been on three idealized trajectories, but those are just examples; clearly, there is room for a range of many possible intermediate ones, which would represent variation in acclimation potential among species. A potentially important aspect of acclimation that the model does not consider, though, is that of the effects of shifts in growth rate (caused by drought) on the characteristics of the tissue produced.

The three model responses of Fig. 2c share the prediction of a reduction in k_H under drought, i.e. a decreased capacity of the whole plant to absorb, transport, and lose water in comparison with control plants of the same age. Two ways in which this could benefit plants have already been discussed: saving soil water and reducing the likelihood of water loss from roots to the soil (see 'Drought effects').

A third benefit would be that low conductance tissue may reduce the risk of embolism (e.g. Pockman and Sperry, 2000; Maherali *et al.*, 2004). Hacke *et al.* (2001) have shown that low conductance, cavitation-resistant wood is also dense, and therefore expensive to construct. So, it seems unlikely that such a type of tissue would simply be produced because high conductance tissue is not needed under drought; rather, there have to be benefits that offset its higher cost. It may also be argued that the optimal decrease in k_H depends on the likelihood of having relatively rapid access to extra sources of water (because of either the existence of moisture deeper in soil, as mentioned before, or the likelihood of incoming rainfall): the lower the chance, the stronger the expected k_H reduction (e.g. Drake and Franks, 2003). Thus, depending on the environment in which they evolved, species of all three types can present a range from conservative (strong) to drought-avoiding (slight) reduction in k_H .

Intra- versus interspecific comparisons

A review of the literature reveals how incipient quantitative knowledge of what happens during ontogeny under disparate environmental conditions is. Very limited data are available to quantify relationships such as those in Fig. 2c, especially considering that to separate drought effects from size effects measurements are needed on plants of similar genotype growing under different water deficit conditions at comparable size, which requires at least two harvests (as shown by Fig. 1). Even worse, two harvests may not be enough to distinguish between pure size and the two other responses to drought, because for this the actual ontogenic trajectory under no-drought conditions needs to be described in some detail. The paucity of data might be related to the different focus of studies on trees (measuring age-related hydraulic parameters) and herbaceous species or crops (applying experimental drought).

Bibliographic searches show that much more comparative hydraulic work has been done between species than between individuals of the same species grown under different water regimes, and thus a pertinent question is whether interspecific data could be used to infer the shape of ontogenic trajectories. Chapin *et al.* (1993) hypothesized that the response to stress at the evolutionary level parallels that at the phenotypic plasticity level (see also DeLucia *et al.*, 2000; Bucci *et al.*, 2004). Mencuccini (2002), however, cautioned against uncritically interchanging interspecific regressions with ontogenetic trajectory models. Besides, interspecific comparisons should take into account the degree of relatedness between species in order to correct for the lack of independence it entails (e.g. Maherali *et al.*, 2004). It has been hypothesized that ontogenic trajectories include hydraulic allometry (convex trajectories in Fig. 2c). This contrasts with the finding of hydraulic isometry

(no evidence of size dependence, $b \approx 1$) in the relationship between leaf area and whole-plant k_H for interspecific comparisons within life forms (Figure 4a in Mencuccini, 2003). However, and perhaps thanks to the larger number of points, allometry ($b=0.8$) does become detectable in interspecific comparisons pooling species across life forms (Mencuccini, 2003, recalculated from his Figure 4b). A graphic summary of these conclusions is included in Fig. 2d.

A fair amount of work is being devoted to contrast and link these and other empirical relationships to the theoretical models of plant vasculature mentioned above and, most notably, to the fractal hypothesis of West *et al.* (1999), all of which make predictions based on assumed costs and benefits for the transport system (McCulloh and Sperry, 2005; Meinzer *et al.*, 2005). Important as such work is, it would also be worthwhile to determine whether b values found for interspecific surveys could be aptly used as null, no-drought reference within a species. Considering the scarcity of leaf area estimates for large individuals, another important empirical task would be to check how useful the relationships between branch diameter (e.g. Zotz *et al.*, 1998) or biomass (e.g. Meinzer *et al.*, 2005) and hydraulic parameters are. If predictive power is found acceptable, regressions of leaf area versus stem diameter for a given species (or taxonomic or functional group) could be extrapolated to obtain dependable scaling coefficients between leaf area and k_H . Something similar might be said of biomass as a predictor of k_H (e.g. Figure 5 of Mencuccini, 2003: $b \approx 0.5$), as long as the allometry and drought effects of the relationship between leaf area and biomass are separately taken into account (e.g. Fernández *et al.*, 2002). The answer to these questions would reveal how far we are from having the leaf-specific hydraulic parameters needed to evaluate the HLH and the model in Fig. 2c properly.

Conclusion

The aim of this was critically to examine the literature on plastic responses to drought, with a focus on whole plants and ontogeny. It was found, despite much excellent work on the subject, that there is a lack of a sufficiently explicit and predictive framework for acclimation, and an attempt was made to propose one.

After reviewing the ways in which, in response to water deficits, plant resistance to liquid water flow changes at different levels (tissue, organ, individual), it was shown: (i) that these levels are correlated with the time scale of the response; and (ii) that, through many different ways (physiological, anatomical, and morphological), adjustments seem to increase resistance to flow in the short term and to reduce it in the long term. Then: (iii) a critical view of those findings was provided, based on the principle that drought-induced changes cannot be analysed sepa-

rately from the allometric changes that take place through ontogeny (of which the hydraulic limitation hypothesis is just one example) and (iv) it was shown that a simple model just including total plant leaf area and total plant hydraulic conductance might be all that is needed to summarize what is known (and unknown) regarding architectural responses to water deficits.

The model proposes that life-long acclimation to drought can involve three contrasting changes in the water transport capacity per unit leaf area for a given plant size: decrease, constancy, or increase. The type of evidence needed to evaluate the actual occurrence of these responses is scarce, but it is suggested: (v) that those three types of response are likely to occur in plants; and (vi) that interspecific surveys, used with caution, might provide appropriate baselines for comparisons. The main reason why it is argued that the model is a useful framework for acclimation is heuristic: it makes explicit predictions about the type of leaf-level responses to be expected for different whole-plant responses. Just to exemplify with the extremes: what may be considered a conservative leaf behaviour (sensitive Ψ_{leaf} stomatal threshold) might turn out to be balanced by a risky whole-plant leaf area preservation behaviour, and what may be considered a risky leaf behaviour (low or non-existent Ψ_{leaf} stomatal threshold) might turn out to be balanced by a conservative whole-plant leaf area reduction behaviour.

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