The ecological significance of long-distance water transport: short-term regulation, long-term acclimation and the hydraulic costs of stature across plant life forms

M. MENCUCCINI

Institute of Ecology and Resource Management, University of Edinburgh, The King’s Buildings, Mayfield Road, Edinburgh, EH9 3JU, Scotland, UK

ABSTRACT

Plant hydraulic conductance, namely the rate of water flow inside plants per unit time and unit pressure difference, varies largely from plant to plant and under different environmental conditions. Herein the main factors affecting: (a) the scaling between whole-plant hydraulic conductance and leaf area; (b) the relationship between gas exchange at the leaf level and leaf-specific xylem hydraulic conductance; (c) the short-term physiological regulation of plant hydraulic conductance under conditions of ample soil water, and (d) the long-term structural acclimation of xylem hydraulic conductance to changes in environmental conditions are reviewed. It is shown that plant hydraulic conductance is a highly plastic character that varies as a result of multiple processes acting at several time scales. Across species ranging from coniferous and broad-leaved trees to shrubs, crop and herbaceous species, and desert subshrubs, hydraulic conductance scaled linearly with leaf area, as expected from first principles. Despite considerable convergence in the scaling of hydraulic properties, significant differences were apparent across life forms that underlie their different abilities to conduct gas exchange at the leaf level. A simple model of carbon allocation between leaves and support tissues explained the observed patterns and correctly predicted the inverse relationships with plant height. Therefore, stature appears as a fundamental factor affecting gas exchange across plant life forms. Both short-term physiological regulation and long-term structural acclimation can change the levels of hydraulic conductance significantly. Based on a meta-analysis of the existing literature, any change in environmental parameters that increases the availability of resources (either above- or below-ground) results in the long-term acclimation of a less efficient (per unit leaf area) hydraulic system.

Key-words: hydraulic architecture; hydraulic conductance; leaf water status; stomatal regulation; structural acclimation.

INTRODUCTION

Water transport in plants has received considerable attention in the last two decades. Since the seminal paper by Jarvis (1975) and, especially, the highly influential books by Milburn (1979) and Zimmermann (1983), water transport has ceased to be a botanical curiosity and has come to be regarded as one of the ecophysiological traits that must be considered in the description of a plant response to environmental and endogenous stimuli.

In its path from the soil to the atmosphere, water moves inside xylem conduits (either vessels or tracheids) for only a fraction of the time. Accordingly, the xylary resistance to water flow represents only a fraction of the total liquid resistance from the soil to the sites of evaporation inside leaves, sometimes quite a minor fraction. However, for a number of reasons, some of which will be dealt with in this review, this fraction can play a significant role in regulating plant physiological responses at the level of individual stomata, individual leaves and whole plants.

More generally, the capacity to conduct water from soil to leaves (which includes both xylary and extra-xylary components) is an important regulatory factor of leaf-level gas exchange properties, both in the short and in the long term. Although stomatal aperture directly controls water loss to the atmosphere, it needs to do so by incorporating some kind of information about both the availability of soil water and the efficiency of the plant water transport system. If this did not happen, stomata would not balance carbon uptake against water loss very effectively. Therefore, knowledge of the main features of water transport in plants, the species-to-species variability as well as its dynamics over time are essential to understanding the ecological significance of the mechanics of guard cell function.

This review attempts to highlight some of the most important reasons why a consideration of whole-plant pro-
cesses related to water transport is required for a full understanding of leaf-level gas exchange properties and, ultimately, of the physiological ecology of plant species.

I have adopted a broad comparative approach, trying to highlight general interspecific patterns of variability. In so doing, use is made of the tools of allometric scaling, that is, morphological and physiological properties are considered as they change across several orders of magnitude (Niklas 1994; Brown & West 2000). This involves losing focus on the mechanisms and the signals involved in the coordination of leaf-level and whole-plant properties, but allows me to sketch a broader picture across the plant kingdom of the degree of convergence or divergence among species with regard to water transport.

This review is composed of four major sections. In the first, the main concepts related to the scaling between leaf physiological and whole-plant hydraulic properties across species are introduced. A simple optimality model of carbon allocation with respect to hydraulic functions is also presented. In the second section, I present the results of a meta-analysis of the published information on the scaling of hydraulic properties across plant life forms. These results are interpreted using the model previously presented. Herein, the significance of changes in hydraulic properties within the context of the plant’s carbon economy are also discussed. In the third section, the short-term temporal dynamics of hydraulic properties are considered, particularly with regard to physiological regulation. However, the implications of the vaporization of xylem water under water stress are not examined in any detail, as this aspect has already received considerable attention in other reviews (e.g. Tyree & Sperry 1989; Sperry et al. 2002). Rather, the major processes responsible for the short-term endogenous regulation of plant hydraulic conductance under conditions of ample soil water availability are highlighted. Finally in the fourth section, I focus on the long-term structural acclimation of plant hydraulic conductance to changes in environmental parameters.

General concepts related to plant hydraulic architecture (Tyree & Ewers 1991), and cavitation and embolism (Tyree & Sperry 1989) are taken for granted. A list of abbreviations used in the text is given in the Appendix.

LONG-DISTANCE WATER TRANSPORT, STOMATAL REGULATION AND OPTIMAL BIOMASS ALLOCATION

General concepts

It has been known for a long time that the supply of water through the roots and the stem must be in some form of balance with the demand for liquid water resulting from the unavoidable losses of vapour at the leaf surface (e.g. Dixon 1914). A formal representation of the relationships between flow of liquid water, water potential difference and resistance to flow was introduced only a few years later (Huber 1928). The Ohm’s law analogy provides a useful starting point to interpret the correlation between the liquid-phase and vapour-phase conductances in plants:

\[ \psi_l = \psi_s = \frac{A_l g_s D_s}{K_{pl}} - \rho_w g h \]  

(1)

where \( \psi_l, \psi_s, A_l, K_{pl}, \rho_w, g \) and \( h \) are the leaf and the soil water potentials, the total plant leaf area, the whole-plant hydraulic conductance from the soil to the leaves, the water density, the gravity acceleration and the plant height, respectively. The simplicity of Eqn 1 hides a number of complications. Some of the terms in Eqn 1 are not independent from one another. For instance stomatal conductance, \( g \), responds in the short term and acclimates in the long term to changes in \( D_s \), the vapour-pressure deficit between the inside of the leaf boundary layer and the inside of the stomatal chamber, and the same can be said of changes in \( K_{pl} \) with respect to \( \psi_l \), and possibly also with respect to changes in \( E_l \), leaf-specific transpiration rate, namely the product of \( g \) and \( D_s \). Finally, Eqn 1 is only valid under the assumption of steady-state conditions which are rarely, if ever, met.

Despite all these caveats, Eqn 1 has proved to be useful in exploring the significance of the inter-relationships among stomatal conductance, soil and leaf water potential and plant hydraulic conductance. For instance, significant positive correlations between plant hydraulic conductance and stomatal conductance or transpiration rates by individual leaves have been reported in several studies (e.g. Meinzer et al. 1995, 1997, 1999; Meinzer & Grantz 1990; Sperry & Pockman 1993; Mencuccini & Comstock 1999; Comstock 2000, etc.). This is expected based on Eqn 1 if stomata acted to maintain leaf water status within tight limits for each species (Saliendra, Sperry & Comstock 1995; Comstock & Mencuccini 1998). Meinzer (2002) has recently reviewed this topic in considerable detail.

A serious and underestimated problem with some of the evidence of a tight correlation between liquid and vapour-phase conductances is the presence of autocorrelation between estimates of hydraulic conductance and measurements of vapour phase water flux, particularly transpiration rate, as hydraulic conductance is frequently estimated by inverting Eqn 1, that is, its calculation depends on transpiration rates. Problems of autocorrelation also emerge when stomatal conductance or net assimilation rates are presented, if the same leaf area is used to scale measurements of both hydraulic and vapour-phase conductance. Even when hydraulic conductance of the whole plant is measured with an entirely independent method to that employed to measure transpiration rates, when both numbers are divided by plant leaf area, autocorrelation is introduced and the regression coefficient is inflated. A better approach to this problem is to carry out a multiple regression analysis, whereby values of transpiration rates per plant, \( E_{pl} \), are regressed against both absolute hydraulic conductance \( K_{pl} \) and plant leaf area \( A_l \), and by testing the significance of the partial correlation coefficient of \( K_{pl} \) (Mencuccini & Comstock 1999).

© 2003 Blackwell Publishing Ltd, Plant, Cell and Environment, 26, 163–182
A theoretical framework for optimal biomass allocation between leaves and support tissues

Herein I present a model of optimal biomass allocation with respect to hydraulic functions, which accounts for the costs of production of new support tissues and for the benefits deriving from a greater allocation to photosynthetic leaf biomass. The model develops earlier treatments of this topic (Givnish 1986; Magnani, Mencuccini & Grace 2000), but it is more specific with regard to the trade-offs between costs of hydraulic support and benefits of increased leaf area across plant life forms.

I assume that total plant mass, $M_{pl}$, is divided into two major compartments, the photosynthetic leaf mass $M_L$ and the mass of the supporting tissues, $M_S$:

$$M_L = F M_{pl}$$
$$M_S = (1-F)M_{pl}$$  \hspace{1cm} (2a, 2b)

where $F$ is the fractional leaf mass ($0 < F < 1$).

I also assume that total photosynthetic uptake, $G_{pl}$, is proportional to both leaf area, $A_L$, and net photosynthetic rate per unit leaf area, $A_N$:

$$G_{pl} = SLA M_{pl} F A_N$$  \hspace{1cm} (3)

where $SLA$ is specific leaf area.

I then express net photosynthetic rates using leaf conductance and the carbon dioxide gradient between outside air and intercellular leaf spaces:

$$A_N = (g_s - c_i)/1.6$$  \hspace{1cm} (4)

where the coefficient 1.6 is an average ratio of the diffusion coefficients for water and carbon dioxide. Although the term $(c_s - c_i)$ is not independent of $g_s$, several data-sets have shown that, across species, a unique linear relationship holds between $g_s$ and $A_N$.

For each life form, stomatal conductance scales as a function of plant leaf-specific hydraulic conductance $K_{L,pl}$ as:

$$g_s = a K_{L,pl}^{-b} \quad 0 \leq b \leq 1$$  \hspace{1cm} (5)

where $b$ indicates the responsiveness of leaf conductance to changes in the efficiency of the plant hydraulic system within each life form. Later I will show that one can also obtain a generalized interspecific scaling between $g_s$ and $K_{L,pl}$. However, it is also likely that $b$ varies within each life form (see later).

Plant hydraulic conductance is assumed to scale proportionally with the area of the conducting tissue and independently of height across species and life forms (Brown & West 2000; Mencuccini 2002). We can then calculate the biomass investment necessary to obtain the mass of the hydraulic tissues (cf. Magnani et al. 2000):

$$K_{L,pl} = k_C A_S = k_C M_L H \rho_s$$  \hspace{1cm} (6)

where $k_C$, $A_S$, $H$ and $\rho_s$ are the sapwood-specific conductivity, conducting cross-sectional area, total height and tissue density, respectively.

Substituting Eqn 6 in 5, using the notation of Eqn.2a and 2b and finally substituting in Eqn 3:

$$A_N = a' B (1-F)^{-b}$$

$$a' = a (c_s - c_i) / 1.6$$

$$B = \frac{k_C}{H \rho_s SLA}$$  \hspace{1cm} (7)

and

$$G_{pl} = SLA^* a'' B M_{pl} F_i^{-b_i} (1-F)^{b}$$  \hspace{1cm} (8)

Assuming a constant plant mass (and height) for the moment, Eqn.10 can be solved to derive the optimal value of $F$, the fractional leaf mass that maximizes $G_{pl}$:

$$F = (1 - b)$$  \hspace{1cm} (9)

Therefore the optimal fractional leaf mass that maximizes $G_{pl}$ is shown to depend on the scaling between leaf conductance to vapour and leaf-specific hydraulic conductance. The expression embodies the fundamental trade-off between the photosynthetic benefits of a greater biomass allocation to leaves and the hydraulic costs of a reduced leaf-specific hydraulic conductance.

Combining Eqs 2a, 2b and 9 yields:

$$M_L = (1-b) H \rho_s G_{pl}$$

$$G_{pl} = \frac{k_C}{H \rho_s} M_{pl}$$  \hspace{1cm} (10a, 10b)

Hence, a log–log plot of whole-plant hydraulic conductance versus leaf mass (or area) or a plot of plant mass versus whole-plant hydraulic conductance for species of each life form should yield lines with slopes of 1.00. However comparing lines across different life forms should yield variable intercepts, depending on average plant height for each life form. The dependency of the intercepts of Eqs.10a and 10b on plant height arises because maintaining a certain level of hydraulic conductance requires more biomass investment in tall than in short organisms, as a consequence of the sheer volume of tissue needed. Finally, also note that this analysis does not consider the additional effect that changes in plant height will inevitably have on the gravitational component of plant water potential across life forms.

A generalized balance between supply and demand for water and the hydraulic cost of stature across life forms

In the previous section, several comparative studies were cited to provide examples of the potential significance of the correlation between vapour- and liquid-phase properties, across a range of species and growing conditions. However, a generalized picture concerning the nature of the coordinated development of liquid-phase and vapour-phase properties has failed to emerge, for three main reasons.

First, very little attention has been paid to the anatomical and structural determinants, which may underlie this coordination. For instance, although significant effort has been devoted to describing the variability in xylem anatomical features across species (e.g. conduit frequency, diameter, length distribution, etc.), comparatively very little has been done to describe the anatomical features relating to stomatal conductance, in spite of both theoretical (Sharpe, Wu & Spence 1987) and empirical studies (Franks, Cowan & Farquhar 1998) that have demonstrated the importance and the species-to-species variability in characters such as guard cell width, stomatal pore length and area of guard cell dorsal wall. Even less frequently have the two sets of anatomical features been examined concurrently, to determine whether variability in xylem anatomy was coupled with variability in leaf anatomy (e.g. Aasamaa, Sober & Rahi 2001; Feild et al. 2001). An obvious related issue is our current lack of physiological understanding of the signals involved in regulating both leaf-level gas exchange and carbon allocation during growth.

Second, it is unclear whether such co-ordinated development of liquid- and vapour-phase properties holds across a very wide range of species of largely different form as well as leaf and xylem structure. In most cases, the reported correlations between gas- and liquid-phase properties were linear, however, in other cases curvilinear asymptotic relationships have been reported (Meinzer et al. 1995; Andrade et al. 1998; Mencuccini & Comstock 1999; Tausend, Goldstein & Meinzer 2000). The curvilinearity may arise for several reasons: stomatal resistance may represent only a fraction of total leaf (or even more, canopy) resistance. Consequently, for very large values of stomatal conductance in partially or totally uncoupled canopies, one may expect the relationship to break down, as transpiration rates are controlled by stomatal aperture only to a minor extent (Jarvis & McNaughton 1986). Another reason may be that a plot of hydraulic conductance versus maximum stomatal conductance across species may not express the full extent of the co-ordination between these two properties, as at maximum stomatal conductance, \( D \) and consequently \( E \), are normally low and possibly not limiting. Hubbard et al. (2001) have also stressed that a linear relationship between vapour- and liquid-phase conductances should be expected only if the behaviour of the plants was entirely isohydric, that is, if leaf water potential was maintained constant despite changes in hydraulic resistances.

The issue of whether species with largely different leaf and xylem structures as well as life forms converge towards a similar hydraulic balance (i.e. ratios between liquid- and vapour-phase properties), that is, the nature of the co-ordinated development between gas exchange and hydraulic properties across species, is an important one.

Third, across plant life forms, stomatal conductance changes dramatically, both in terms of maximum rates and of the degree of response to changes in environmental variables (Körner 1994). In previous studies, maximum stomatal conductance appeared to be linearly related to leaf nitrogen concentration for broad categories of vegetation types with variable leaf longevities (Schulze et al. 1994), suggesting that the overall scaling of stomatal conductance across life forms was tightly associated with photosynthetic functions, rather than water relations. Furthermore, across life forms, midday leaf water potential (averaged, let’s say, over the course of the season) may also change substantially, again questioning whether the reported relationships between liquid- and vapour-phase conductances are of general significance.

For this purpose, I reviewed the existing literature on the subject, where measurements of both vapour-phase and liquid-phase conductances had been reported.

I adopted the following criteria to select studies for inclusion in this meta-analysis:

1. Measurements of leaf gas exchange should have included stomatal conductance \( (g_s) \) and/or transpiration rates, \( E_i \). As long as the other conditions were met, I included studies in which either one or both variables had been measured, and formed two independent data-sets. For stomatal conductance, these measurements should have been carried out on samples of leaves representative of the entire canopy. Environmental parameters should also have been measured and reported. I excluded all data points collected in periods of clearly high soil water stress and/or limited light availability. For each available data-set, I averaged the maximum values of reported stomatal conductances for a range of measured conditions and sampling times. This criterion is roughly equivalent to the one employed by Körner (1994). For transpiration rates, measurements should have been carried out on samples of leaves representative of the canopy or being carried out directly at the canopy scale (e.g. transpiration rate estimated using sap flow sensors installed on branches or central stems).

2. Measurements of whole-plant hydraulic conductance \( K_{i,pl} \) (the entire pathway from soil to leaves) and/or leaf-specific hydraulic conductance \( K_{i,pl} \) (i.e. \( K_{i,pl} \) relative to the total leaf area present in the plant) should also have been carried out, independently of measurements described in point 1. This last criterion was quite a demanding one, as it proved difficult to find even a few publications where \( K_i \) and \( E_i \) had been estimated independently. Therefore, for the purpose of the meta-analysis, I limited myself to comparisons of \( K_{i,pl} \) against \( g_s \), for those cases where \( g_s \) had been estimated independently using porometry or a gas-exchange system. All measures of hydraulic conductance were corrected for the gravitational component of water potential using the known values of plant height.

3. Measurements of plant size (leaf area, diameter at the base, total height, total mass, etc.) should also have been given. When leaf area was related to measures of whole-plant hydraulic conductance \( K_{i,pl} \), the two estimates should have been independently calculated. For a number of studies, the authors were directly contacted to obtain the additional information required.

4. When multiple reports were found for the same species, only the one that referred to the largest individu-
I have attempted to demonstrate the link between hydraulic and gas exchange properties using two different approaches. First, I related \( K_{L,pl} \) with leaf-level gas exchange properties and then I looked at the relationship between whole-plant conductance and whole-plant leaf area.

Across 50 species, spanning eight orders of magnitude of size (expressed in terms of plant dry mass) and including representatives of temperate coniferous and broad-leaved trees, tropical trees, temperate fruit trees, shrubs, desert subshrubs, ferns, lianas, succulents and herbaceous crop plants, there was a highly skewed distribution of \( K_{L,pl} \) (Fig. 1a). A large fraction of the sampled species had values of \( K_{L,pl} \) between 0 and 5 mmol m\(^{-2}\) s\(^{-1}\) MPa\(^{-1}\), but examples up to about 25 mmol m\(^{-2}\) s\(^{-1}\) MPa\(^{-1}\) have been reported. The reciprocal plot of leaf-specific hydraulic resistance, \( R_{L,pl} \), also showed significant skewness, although to a lesser degree (data not shown). Both plots became not significantly different from a Gaussian distribution, upon log-transformation of the values (Figs 1b; \( P > 0.05 \), for both skewness and kurtosis).

Under conditions of ample soil water, \( K_{L,pl} \) controls the levels of water potentials obtained within the plant at each level of transpiration rate. The majority of the highest reported values of \( K_{L,pl} \) were for desert subshrub species (\( E.\) farinosa, \( H.\) rigida, \( Hymenoclea\) salsola and \( A.\) dumosa). These very high values were obtained in three different studies using plants under ample soil water supply (Nobel & Jordan 1983; Comstock & Mencuccini 1998; Comstock 2000). These values are probably within the same order of magnitude as values of soil hydraulic conductance, even under almost complete saturation (e.g. Blizzard & Boyer 1980; Landsberg & Jones 1981). For these species therefore, which maintain very high rates of transpiration, even under ample soil water supply, a large fraction of the water potential drop may occur outside the plant, not inside. Sperry et al. (1998) proposed a theoretical model of xylem and soil pore cavitation in relation to xylem water transport and leaf gas exchange. The model predicted that plants should tend to optimize their leaf area : root area ratio to achieve optimal regulation of gas exchange. The optimal leaf area : root area ratio (equivalent to the ratio of plant to soil hydraulic conductance) was dependent on soil type and cavitation resistance but, overall, the model predicted that a plant should grow in such a way that its hydraulic path would always tend to be xylem-, rather than soil-limited; that is, such that the location of the most vulnerable site (the hydraulic bottleneck) would be inside the plant xylem. This is achievable, as soil hydraulic conductance is largely a function of fine root density. It is therefore interesting to note that the root xylem of those desert subshrub species was reported to be extremely sensitive to cavitation in comparison with the respective above-ground organs (Mencuccini & Comstock 1997). More work on the relationships between soil and xylem characteristics (e.g. Hacke et al. 2000; Ewers, Oren & Sperry 2000) under a range of plant hydraulic conductances will certainly produce interesting results.

There was a very tight relationship between \( K_{L,pl} \) and leaf-specific transpiration rate \( E \) (Fig. 2a; \( \ln E = 0.008 + 0.969 \ln K_{L,pl} \), \( R^2 = 0.87, P < 0.0001 \)). As mentioned before, this was expected, as most studies are affected by self-correlation as \( E \) is employed to calculate \( K_{L,pl} \). Figure 2b shows the same data-set with values now grouped by plant life form and plotted on a linear scale (\( \ln E = 0.004 + 1.007 \ln K_{L,pl} \), \( R^2 = 0.87, P < 0.0001 \)). Figure 2b highlights the tendency of the desert subshrub species, shrubs and herbaceous crop plants to display higher values of both \( E \) and \( K_{L,pl} \), in comparison with trees (particularly conifers) and to ferns. The calculated regression coefficients across the entire data-set (\( b = 0.969 \) and \( b = 1.007 \)) suggested a perfect isometric scaling (i.e. a linear relationship in the linear scale, or \( b = 1.00 \)) between vapour-phase fluxes and liquid-phase conductances across life.
Figure 2. Plots of leaf-specific transpiration rates against leaf-specific hydraulic conductance. (a) Data plotted in log–log form for individual species within six broad classes of life form; (b) averages for each of nine life forms plotted in the linear scale. Neither line differed from isometry \((P > 0.05)\). Data from: Bongarten & Teskey 1986; Borghetti & Vendramin 1987; Borghetti et al. 1989; Calkin et al. 1985; Cochard et al. 1996; Comstock 2000; Gibson et al. 1984; Grantly & Yang 1996; Helguist et al. 1974; Huxman et al. 1999; Kuppers 1984; Landsberg et al. 1976; Lloyd & Howie 1989; Lloyd et al. 1991; Lu et al. 1996; Meinzer et al. 1999; Nobel & Jordan 1983; Ren & Sucoff 1995; Roberts 1977; Running 1980; Salindra & Meinzer 1989; Sperry 2000; Sperry & Pockman 1993; Tognetti et al. 1998, 1999; Waring & Running 1978.

forms \((t\text{-test}, P > 0.05)\). Based on an Ohm’s law analogy, the intercept of the log–log plot can be interpreted as the average water potential gradient from soil to leaves for all the species in the regression. Both values obtained equate to an average \(\Delta W = 1\) MPa.

The effect of the auto-correlation is removed by examining only those studies that report independent estimates of both stomatal conductance \(g_s\) and \(K_{L,pl}\) \((\text{Fig. 3a}; \ln g_s = 4.776 + 0.611 \ln K_{L,pl}; R^2 = 0.46, P < 0.001)\). The relationship was highly significant, suggesting that across 50 species of several different life forms, a large fraction of variability in stomatal aperture could be accounted for by the species-specific hydraulic properties. Figure 3b reports the same data-set again by averaging within broad categories of life forms and plotting them on a linear scale \((\ln g_s = 4.797 + 0.633 \ln K_{L,pl}; R^2 = 0.65, P < 0.001)\). The proportion of variance explained by the regression increased significantly when the means of each life form were examined, probably because the noise associated with the different environmental conditions when the measurements were taken \(\text{(i.e. light intensity, } D, \text{ air temperature, level of soil water stress, etc.)} \) disappeared upon averaging across sampled species. The average scaling coefficient of stomatal conductance against \(K_{L,pl}\) was \(= 0.65\), which is significantly less than expected from isometry \((P < 0.01)\, \text{and suggesting instead a saturating behaviour at large } K_{L,pl} \text{ across life forms.}

Whole-plant leaf area was highly significantly related to the subtending hydraulic conductance \(K_{pl}\) \((\text{mmol s}^{-1}\text{MPa}^{-1})\) across species of several life forms (Fig. 4a; \(\ln (A_L)\)
The ecological significance of xylem water transport

area than coniferous and broad-leaved trees ($P < 0.01$), whereas shrubs appeared not to differ significantly from either category. Therefore, herbaceous and subshrub species appeared to have a significant hydraulic advantage in comparison with woodier and taller species, such as trees. This is reflected in the tendency of these species to display higher rates of water loss per unit leaf area (Figs 2 & 3, cf. Körner 1994).

Overall, a picture of high convergence across species in the functional balance between leaf-level properties and hydraulic properties emerges (cf. Mencuccini 2002; for a discussion of interspecific versus intraspecific developmental scaling). When these properties are examined using the broad perspective of across-species scaling, the minuitae of interspecific physiological differences disappear and the essential need to maintain equilibrium between demand...
and supply emerges clearly. It is also apparent that, within this generalized picture of functional convergence, there are fundamental differences across life forms in the actual ratios of leaf area supported and underpinning hydraulic systems. Some life forms, particularly those characterized by a long life span (cf. Ehleringer 1994), greater stature and woody structure maintain higher levels of leaf area than predicted, based on a generalized functional balance scaling.

As predicted by Eqn. 12a, when whole-plant leaf-specific hydraulic conductance was plotted against plant height a significant negative relationship was found (insert of Fig. 4a). However, the slope of the relationship was -0.47, that is, significantly less than -1.00 (at least P < 0.05, for both least square and reduced major axis regression), which is the value predicted by Eqn. 12a. Therefore substantial compensation for increases in height occurred across life forms. Equation 12a assumed a constant optimal F, independent of life form. In reality, F may vary across life forms, possibly as a result of variations in b, the sensitivity of stomatal conductance to changes in plant hydraulic conductance. For instance, if trees were characterized by higher values of b, this would result in a slope that is less negative than -1.00, when leaf-specific hydraulic conductance was plotted against plant height. In Fig. 3b, trees are located near the bottom left of the graph, where the relationship between g₀ and Kₛ₀ is in its linear portion, whereas shrubs and herbaceous species are located in the region where the curvature is more accentuated. This may result in species-specific relationships with varying levels of b (cf. Frank & Farquhar 1999; for a similar discussion on the effects of life forms on stomatal sensitivity to vapour-pressure deficits).

**BIOMASS ALLOCATION AND THE CARBON ECONOMY OF THE HYDRAULIC SYSTEM: THE BIOMASS COSTS OF STATURE**

Long-term acclimation in the water transport system in response to changing environmental variables may involve several types of costs to the plants and may interact with other functions carried out by the plant. Increased carbon allocation to transport tissues may come to the detriment of other functions carried out by the plant. Increased carbon allocation to transport tissues may involve the relative transfer of resources from the growth of one organ to that of another, such that a new ‘functional balance’ is achieved that optimizes the use of resources. Some of the reported changes occurring as a consequence of experimental alterations in resource availability are of a very significant magnitude, some well in excess of 100% (cf. section on Long-term Acclimation). It is doubtful that all plants can achieve those levels of relative change in the efficiency of their organs in a time span suitable for acclimating to changes in the availability of external resources. Particularly in the case of large trees, where large masses of tissues accumulate and maintain their hydraulic functions for several decades, it could be argued that the possibilities of acclimating to changing environmental conditions are fairly minimal and, in any case, lower than for rapidly growing annual plants that can turn around their leaf or xylem relative growth rates in a matter of days.

To investigate whether the relationship between plant size and hydraulic transport capacity was influenced by plant life forms, I conducted a further literature search, based on the relationship between plant mass and whole-plant hydraulic conductance.

The criteria used for the selection of studies to be included for this analysis were similar to those applied for the analysis of the scaling of hydraulic conductance with plant leaf area (see details above). For studies carried out on herbaceous plants, lianas and shrubs, I only included those that presented measurements of total plant dry biomass (above- and below-ground biomass) as well as of hydraulic conductance. For the studies carried out on trees, I only included those for which species-specific and site-specific allometric equations were available from the literature, so that reliable estimates of tree dry (above- plus below-ground) biomass could be obtained. In addition, for those studies carried out in trees, information should have been available on the proportion of the stem occupied by sapwood area, so that only the biomass invested in tissues actively involved in water transport was taken into account. No studies that reported joint data-sets on hydraulic conductance and plant biomass could be found for ferns. For trees, biomass of fine roots was never measured in these studies, but its contribution to total tree biomass was probably very small. A discussion of the other potential errors involved in this analysis will be carried out below.

Twenty-three studies were retrieved which satisfied the selection criteria outlined above. They were grouped according to life form as trees (single-stem species), shrubs (multi-stemmed species of limited height) and herbaceous species (including both crop plants, wild annuals and perennials).

The log–log plot of whole-plant Kₛ against the estimated biomass active in water transport (Fig. 5a) showed highly significant relationships. Lines for different life forms appeared to be almost parallel to one another, but again significant intercept shifts (P < 0.01) appeared to discriminate one life form from another. Taller organisms required significantly more biomass to achieve similar levels of water transport capacity in comparison with shorter plants. When
I combined the data from different life forms, I found a common scaling coefficient of \( n = 0.50 \) \( (y = 0.0728x^{0.5777}, R^2 = 0.8628) \).

A similar scaling is also apparent when one considers the averages for each life form (Figs 5b; \( y = 0.1776x^{0.528}, R^2 = 0.92 \)). However, the individual slopes for shrubs \( (y = 0.0008x^{3.189}, R^2 = 0.99) \) and trees \( (y = 0.0019x^{0.8605}, R^2 = 0.94) \) appeared significantly higher than 0.5 and not significantly different from isometry, as predicted by Eqn 10b. Data for herbaceous crop plants were intermediate but also with a slope not different from isometry \( (y = 0.1161x^{0.7298}, R^2 = 0.84) \). From Fig 5 a clear gradient appears from life forms characterized by an herbaceous life form and lower stature to species with a woody habit and greater stature. This gradient appears to be determined by what we might call mass-specific hydraulic conductance (a measure of hydraulic transport efficiency; that is, the biomass required to obtain a certain level of hydraulic conductance), with values ranging, in increasing order, from herbaceous plants, to shrubs and to trees.

As predicted by Eqn 10b, when mass-specific hydraulic conductance was plotted against plant height a significant negative relationship was found (least square regression slope of \(-1.35\), insert in Fig. 5a). This was not significantly different \( (t\text{-test}, P > 0.05) \) from \(-1.00\), as predicted by Eqn 10b. However, the reduced major axis slope had a value of \(-1.70\), which was significantly lower than \(-1.00\) \( (P < 0.05) \). Therefore, according to least square regression, no apparent compensation occurred across life forms in terms of the mass required to obtain a certain level of hydraulic conductance, and increases in height were not compensated for. Instead, according to reduced major axis regression, the slope was more negative than \(-1.00\) and some additional effect linked to height must be...
EMPIRICAL EVIDENCE OF SHORT-TERM ENDOGENOUS REGULATION OF PLANT HYDRAULIC SYSTEMS

There is increasing evidence that hydraulic conductance may be subject to short-term changes under otherwise constant environmental conditions as a result of subtle changes in xylem sap composition, expression of aquaporins, or other endogenous processes. Several recent reviews have examined these aspects in depth (e.g. Clarkson et al. 2000; Meinzer 2002).

An important aspect of the short-term regulation of plant hydraulic conductance is the diurnal cycle observed in the root systems of several crop species. Reports of a reduced plant hydraulic conductance especially during the earlier and the later parts of the day (when transpiration rates were lower) have been known since the early 1950s (e.g. Mees & Weatherley 1953). The phenomenon has been interpreted in several ways, but the molecular bases of the inverse relationship between transpirational flow and hydraulic resistance are still unclear. The phenomenon has been replicated again recently using new techniques to measure plant hydraulic conductance in

Helianthus annuus (Tsuda & Tyree 2000). Both root and shoot resistances were found to change over the course of a day, with minimum values during the early hours of the morning, the late afternoon and at night-time. In the shoot, both stems and leaves showed variable conductance, a finding reported also by Aasamaa et al. (2001) in six deciduous tree species.

Although these results are suggestive of a mechanism by which hydraulic conductance is regulated in response to changes in transpiration rates itself, it has also been shown, for root systems of cotton, that the diurnal rhythm can continue for several daily cycles after the roots had been excised from the shoot (Parsons & Kramer 1974), suggesting the presence of a biological clock synchronized on a circadian rhythm. Recent experiments on Lotus japonicus showed that the diurnal variation in root hydraulic conductivity was coincident with a diurnal rhythm of the expression of mRNA encoding putative water channels in the root tissue, suggesting either de novo synthesis and/or degradation of water channels during the day (Henzler et al. 1999). Diurnal rhythms in root pressure could also be measured on isolated root systems for time intervals of up to 9 d (Henzler et al. 1999). Interestingly, the expression of transcripts homologous with Arabidopsis AthPIP1-type aquaporins displayed a diurnal variation that preceded the changes in root hydraulic conductivity by a few hours. These cycles may help explain the observation that the stomata of common beans opened up in response to a root pressurization treatment during the early part of the day, but were almost entirely unresponsive to manipulations of leaf water status during the later parts of the day (Mencuccini & Comstock 2000).

Aquaporins may also be involved in the response of hydraulic conductance to short- and long-term manipulations of plant nutrition. Clarkson et al. (2000) proposed a two-branched hypothesis to explain the apparent increased efficiency of root systems in scavenging nutrients under condition of nutrient stress (particularly, nitrate, phosphate and sulphate). According to this hypothesis, the perception of a stress signal would elicit a double form of response in most plants: the rates of transcription of the genes responsible for high affinity nutrient transporters will be derepressed, while at the same time, some signal will also elicit an increased carbon allocation to the root system and increased growth. Although the two branches resemble the traditional distinction between short-term physiological regulation and long-term structural acclimation to abiotic stresses, it is important to realize that these two processes can interact in complex fashions. For instance, in experiments with Arabidopsis thaliana, lines carrying antisense constructs to AthPIP1 aquaporins were found to have root systems that were five times as large as wild-type plants (Kaldenhoff et al. 1998). As a consequence, neither transpiration rates nor xylem water potentials differed between antisense lines and wild-type, bringing substantial homeostasis in plant water status (Kjellbom et al. 1999). Consequently, short-term physiological and long-term structural acclimation are inherently linked.
EMPIRICAL EVIDENCE THAT PLANT HYDRAULIC SYSTEMS ACCLIMATE OVER LONG TIME PERIODS

There is considerable evidence that hydraulic conductance can change over relatively long time periods. The process of long-term acclimation in the hydraulic system can occur as a result of both exogenous and endogenous processes. These processes may typically occur over the course of months to years, and are normally missed out during short-term experiments carried out in the laboratory or in the field.

It can be argued that for long-living organisms such as trees, structural acclimation is almost certainly the dominant process by which the hydraulic system responds to a range of external and endogenous stimuli and to changes in the intensity and direction of these stimuli over time. However, even for short-lived organisms, such as annual plants, the developmental sequence from germination to flowering stage involves changes in the absolute capacity to transport water that by far exceed any other short-term change induced by either cavitation, internal control of aquaporins, changes in sap chemical composition, etc. For instance, xylem hydraulic conductance can change over five or six orders of magnitude during development from a seedling to a mature tree. Despite the enormous potential relevance of structural acclimation in changing plant hydraulic systems, this topic has largely been neglected, both in terms of original empirical research and of theoretical analyses (but see Magnani et al. 2000). A reference search using the terms ‘acclimation’ and ‘hydraulic conductance’ returned 11 hits, whereas hundreds were retrieved when ‘acclimation’ was accompanied by either the word ‘cold’ or the word ‘photosynthetic’. I will now partially attempt to fill this gap here by reviewing the existing sparse evidence for long-term acclimation of hydraulic properties in plants.

I have limited this review to the long-term responses of hydraulic conductance to changes in one of four environmental factors, namely the impacts of long-term droughts, fertilization, air CO₂ enrichment and changes in air vapour pressure deficit. The choice to limit the analysis to these four factors is partly because of space limitations, and partly because these four factors have been analysed in a larger number of studies and therefore warrant a separate examination.

For the purpose of this meta-analysis, I used the following definitions. A truly long-term experiment of plant hydraulic acclimation is one characterized by such a length when one can expect that the entire plant hydraulic system will have responded to the changes imposed by the treatment. This period may only be as long as several weeks to a few months, in the case of crop and herbaceous species, or as long as several years or decades in the case of field experiments on mature trees, where several cohorts of leaves or needles are present. Truly long-term experiments of plant acclimation in the hydraulic structure are, by and far, lacking. They are not very easy to conduct, especially for trees, because of the inherent difficulties in designing them. For instance, one has simply to consider the fact that mature trees of several species hold up to several tens of sapwood rings, whose anatomical characteristics were fixed at the time of their formation before the treatment was imposed. Clearly, the criterion outlined above will require a long enough time to completely substitute all the old sapwood rings with new ones produced under the influence of the treatment. For practical purposes with regard to experiments with trees, I considered experiments as long-term, only if: (a) seedlings had been exposed to the treatment for the entire, or almost the entire duration of their life cycle, or (b) mature plants had been exposed to the treatment for enough years to completely substitute all the leaf cohorts with new ones produced after the start of the experiment (i.e. acclimation occurred because of changes in the amount of leaf supplied, not the amount, or quality, of sapwood present).

Beyond long-term experiments, I also included observational field studies in which, for the same four factors, the author(s) had documented differences in hydraulic conductance between sites chosen so as to represent extremes of site fertility, climatic conditions or soil water availability (i.e. an environmental gradient). I only included those observational field studies where the author(s) were able to demonstrate the significance of the site-to-site differences in environmental parameters and where it was clear from the reported description that a significant sampling effort had been made to construct the environmental gradient. Clearly, in this case, part or all of the observed differences may have been genetic in nature.

Studies differed in the type of hydraulic parameters measured, with some producing an entire suite of parameters measured for individual organs as well as for the whole plant, and others producing only one or two estimates for particular parts of the soil-plant-atmosphere pathway.

For the purpose of this analysis, I chose to focus only on parameters describing not the absolute levels of hydraulic supply (e.g. \( K_{\infty} \)), but on parameters describing the hydraulic efficiency of the vascular system in relation to leaf area, i.e. wherever studies provided estimates of leaf-specific parameters (e.g. \( K_{l,\infty} \)).

If more parameters were available from individual studies, I ranked them according to a criterion of explanatory power according to the following scheme: \( K_{l,\infty} \) (leaf-specific whole-plant hydraulic conductance) > \( K_{l,1} \) (leaf-specific segment hydraulic conductivity) > Huber value (leaf-specific conducting sapwood area for one specific cross-section, the reverse of the leaf:sapwood area ratio). Hence, for studies where all three parameters were available, I chose the first one as a better descriptor of the hydraulic features of an entire plant. However, as explained above, I also retained studies for which only the Huber value had been reported (i.e. no measure of the xylem permeability or specific conductivity, \( K_{l} \)).

I divided all the studies into categories corresponding to one of the four environmental factors mentioned above (some belonged to more than one category, e.g. factorial

experiments of air CO₂ enrichment and fertilization). For each study and each reported variable, I calculated a measure of the effects size of the treatment as:

\[
\% \text{ change} = 100 \times \frac{(X_n - X_c)}{X_c}
\]

where \(X_n\) and \(X_c\) are the average response of the study variable in the treatment and in the control, respectively. If no significance difference was reported between treatment and control, I returned a percentage change of zero.

All together 37 studies were retrieved (Table 1a–d), with the majority \((n = 20)\) being conducted for the purpose of testing the effects of elevated CO₂. A significant number of studies had been conducted to test the effects of long-term fertilization \((n = 8)\) or the effects of \(D\) \((n = 6)\). Only three were found which tested the effects of long-term soil drought on hydraulic properties and, of these three, one tested it only indirectly, using soil texture (sandy or loamy) as the primary treatment. Table 1e also lists three studies where ecotypes of one species were compared under common garden conditions to test for the effects of genetic differences in hydraulic parameters associated to one of these four environmental gradients.

The results of this meta-analysis are given in Fig. 6, where all data are summarized based on the mean and the 10th, 25th, 75th and 90th percentiles separately for each of these four environmental factors. Several significant points emerge. Treatments of decreasing air humidity as well as of long-term soil drought tended to result in long-term increases in measures of plant hydraulic efficiency (in the sense of a greater capacity to supply water to the unit of leaf area), whereas treatments of increasing nutrient availability and elevated CO₂ tended to result in the opposite effect. Large variability was found in the magnitude of the response to the treatments across studies. This was expected, as studies differed largely in the structure, aims, design and power to detect differences.

Some long-term responses contrasted markedly with the reported patterns for short-term responses. For instance, the common response under short-term drought normally entails reductions in hydraulic conductivity of both the xylary and the extra-xylary plant pathways, via development of xylem cavitation, interruption of water flow at the soil–root interface, suberization of root epidermal cells, and, possibly, down-regulation of aquaporin expression. However, the available evidence suggests that, under long-term exposure to drought, substantial increases can occur in hydraulic transport efficiency. The same argument can be applied to treatments of high \(D\), in as much as high levels of water loss to the atmosphere would elicit xylem cavitation. Under the heading of this group, I included both studies of the effects of high \(T\) (which included both direct temperature effects as well as high levels of \(D\) as a consequence of the higher temperatures) as well as studies specifically designed to test for high air \(D\) (i.e. at constant \(T\)). Of the six studies grouped under this category, four were conducted in greenhouses and two represented field studies of environmental gradients. Of the greenhouses studies, three controlled for \(T\) and only \(D\) was changed, whereas in the fourth the temperature dependency of water viscosity was accounted for in the presentation of the hydraulic conductivity data. In the two field studies instead, changes in \(T\) and \(D\) were confounded and the only supporting evidence put forward by the authors in favour of a direct acclimation to \(D\), as opposed to \(T\), came from theoretical arguments.

Table 1e also lists the results of three studies designed to test whether genetically controlled differences existed among ecotypes that had been growing along environmental gradients but were tested under common garden conditions. All three were designed to test ecotypic differences linked with gradients of air \(D\). All three of them showed a pattern of change in hydraulic properties, from one extreme to the other of the ecotypes, consistent with the trends highlighted in Fig. 6, suggesting that long-term acclimation may reflect more faithfully the processes and forces acting through natural selection than short-term experiments.

A second aspect emerging from the analysis of Fig. 6 relates to the magnitude of the reported changes in hydraulic properties. Several studies reported changes in excess of 100% in response to various factors, showing the plasticity of the hydraulic system and the potential for acclimation. It must be remembered that the parameters employed in this analysis were all originally derived as ratios of measures of hydraulic transport to the leaf area supplied. Therefore the reported changes may have been due to two concomitant phenomena: (a) changes in the properties and

![Figure 6](image-url)
Table 1. Synthesis of available studies on the acclimation of whole-plant hydraulic conductance to various environmental factors

<table>
<thead>
<tr>
<th>Species</th>
<th>Investigated factors</th>
<th>Measured parameters</th>
<th>Observed response</th>
<th>Authors</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Summary of reported changes in response to changes in soil water availability</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Pinus laricio</em></td>
<td>3-year-long drought experiment in the field on 35-year-old trees</td>
<td>(a) $K_{L,pl}$</td>
<td>(a) 117% increase</td>
<td>Cinnirella <em>et al.</em> (2002)</td>
</tr>
<tr>
<td></td>
<td>Drought (~0.6 MPa) and well watered (~0.1 MPa predawn water potential) for 6 months for five 2-year-old ecotypes in greenhouse</td>
<td>(b) Sapwood : leaf area ratio</td>
<td>(b) 40% increase in drought treatment</td>
<td></td>
</tr>
<tr>
<td><em>Fraxinus pennsylvanica</em></td>
<td></td>
<td>(a) $K_h$</td>
<td>38 and 43% increase under drought</td>
<td>Shumway <em>et al.</em> (1991)</td>
</tr>
<tr>
<td><em>Pinus taeda</em></td>
<td>Two 14-year-old populations growing on sandy or loamy soil textures</td>
<td>$K_{L,pl}$</td>
<td>65% increase in sandy soil</td>
<td>Hacke <em>et al.</em> (2000)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(b) Summary of reported changes in response to changes in atmospheric vapour-pressure deficit and temperature</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Glycine max</em></td>
<td>High (19°C) and low (10°C) dew point temperatures for 6 months from germination in greenhouse</td>
<td>$K_{L,pl}$, $K_{L,shoot}$, $K_{L,root}$</td>
<td>30, 44 and 22% increase under high $D$</td>
<td>Bunce &amp; Ziska (1998)</td>
</tr>
<tr>
<td><em>Medicago sativa</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>As above</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Pinus sylvestris</em></td>
<td>Populations growing at 12 sites along $T$ and $D$ gradient across Europe (age between 20 and 80 years)</td>
<td>Sapwood : leaf area ratio</td>
<td>103, 133 and 101% increase under high $D$</td>
<td>Mencuccini &amp; Bonosi (2001)</td>
</tr>
<tr>
<td><em>Pinus sylvestris</em></td>
<td>One seed source planted at two sites along $T$ and $D$ gradient (age of 40 years)</td>
<td>Sapwood : leaf area ratios</td>
<td>33, 87 and 191% increase from low $T$, high RH to high $T$, low RH sites/populations</td>
<td></td>
</tr>
<tr>
<td><em>Pinus ponderosa</em></td>
<td>Populations growing at two sites along $T$ and $D$ gradient (diameters between 20 and 60 cm)</td>
<td>(a) $K_{L,pl}$</td>
<td>(a) 129% (summer) and 162% (autumn) increase at warmer and drier site;</td>
<td>Callaway (1994); Maherali &amp; DeLucia (2001); Maherali &amp; DeLucia (2000b)</td>
</tr>
<tr>
<td></td>
<td>(b) Sapwood : leaf area ratio</td>
<td>(b) 78% increase at warmer and drier site;</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(c) $K_h$</td>
<td>(c) 18% increase at warmer and drier site</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Pinus ponderosa</em></td>
<td>High and low air $T$ and $D$ for 6 months from germination in greenhouse</td>
<td>(a) $K_h$</td>
<td>(a) 476% increase (b) 31% decrease, and (c) 348% increase for high $T$/low RH treatment</td>
<td>Maherali &amp; DeLucia (2000a)</td>
</tr>
<tr>
<td></td>
<td>(b) Sapwood : leaf area ratio</td>
<td>(b) $K_h$</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(c) $K_s$</td>
<td>(c) $K_s$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(c) Summary of reported changes in response to changes in air CO₂ concentration</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Glycine max</em></td>
<td>Ambient and elevated CO₂ (700 p.p.m.) for 3 weeks from germination in growth rooms</td>
<td>$K_{L,pl}$, $K_{L,shoot}$, $K_{L,root}$</td>
<td>46, 70 and 26% decrease under elevated CO₂</td>
<td>Bunce (1996)</td>
</tr>
<tr>
<td><em>Medicago sativa</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>Investigated factors</td>
<td>Measured parameters</td>
<td>Observed response</td>
<td>Authors</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>---------------------------------------------------------------------------------------</td>
<td>---------------------</td>
<td>--------------------------------------------------------</td>
<td>---------------------------</td>
</tr>
<tr>
<td>Maranthes corymbosa</td>
<td>Ambient and elevated CO₂ (700 p.p.m.) for 20 months from germination in the field</td>
<td>$K_{s,pl}$</td>
<td>78% decrease under elevated CO₂</td>
<td>Eamus et al. (1995)</td>
</tr>
<tr>
<td>Eucalyptus terodonta</td>
<td>Ambient and elevated CO₂ (700 p.p.m.) for 20 months from germination in the field</td>
<td>$K_{s,pl}$</td>
<td>72% decrease under elevated CO₂</td>
<td>Eamus et al. (1995)</td>
</tr>
<tr>
<td>Zea mays</td>
<td>Ambient and elevated CO₂ (700 p.p.m.) for 3 months from germination in greenhouse</td>
<td>$K_{s,pl}$</td>
<td>No change</td>
<td>Bunce &amp; Ziska (1998)</td>
</tr>
<tr>
<td>Amanthus hypochondriacus</td>
<td>As above</td>
<td>$K_{s,pl}$</td>
<td>No change</td>
<td>Bunce &amp; Ziska (1998)</td>
</tr>
<tr>
<td>Abutilon theophrasti</td>
<td>As above</td>
<td>$K_{s,pl}$</td>
<td>No change</td>
<td>Bunce &amp; Ziska (1998)</td>
</tr>
<tr>
<td>Pinus ponderosa</td>
<td>Ambient and three levels of elevated CO₂ for 6 months from germination in greenhouse</td>
<td>(a) $K_{s,pl}$</td>
<td>(b) Sapwood : leaf area ratio</td>
<td>Maherali &amp; DeLucia (2000a)</td>
</tr>
<tr>
<td>Pinus taeda</td>
<td>Ambient and elevated CO₂ (650 p.p.m.) for 4 years in 4-year-old saplings in greenhouse</td>
<td>$K_{s,pl}$</td>
<td>No change</td>
<td>Pataki et al. (1998)</td>
</tr>
<tr>
<td>Quercus robur</td>
<td>Ambient and elevated CO₂ (600 p.p.m.) for 3 years in 3-year-old saplings in greenhouse</td>
<td>$K_{s,pl}$</td>
<td>21% decrease at elevated CO₂</td>
<td>Heath et al. (1997)</td>
</tr>
<tr>
<td>Fagus sylvatica</td>
<td>As above</td>
<td>$K_{s,pl}$</td>
<td>No change</td>
<td>Heath et al. (1997)</td>
</tr>
<tr>
<td>Quercus robur</td>
<td>Ambient and elevated CO₂ (600 p.p.m.) for 10 months in 10-month-old seedlings in greenhouse</td>
<td>(a) $K_{s,pl}$</td>
<td>(b) Sapwood : leaf area ratio</td>
<td>Atkinson &amp; Taylor (1996)</td>
</tr>
<tr>
<td>Pinus avium × pseudocerasus</td>
<td>Ambient and elevated CO₂ (600 p.p.m.) for 2 months in less than 1-year-old seedlings in greenhouse</td>
<td>(a) $K_{s,pl}$</td>
<td>(b) Sapwood : leaf area ratio</td>
<td>Atkinson &amp; Taylor (1996)</td>
</tr>
<tr>
<td>Quercus ilex</td>
<td>Natural CO₂ spring versus control site nearby</td>
<td>$K_{s,pl}$</td>
<td>No change</td>
<td>Tognetti et al. (1998)</td>
</tr>
<tr>
<td>Quercus pubescens</td>
<td>As above</td>
<td>$K_{s,pl}$</td>
<td>14% increase at elevated CO₂</td>
<td>Tognetti et al. (1999)</td>
</tr>
<tr>
<td>Erica arborea</td>
<td>As above</td>
<td>$K_{s,pl}$</td>
<td>9% decrease at elevated CO₂</td>
<td>Tognetti et al. (2000)</td>
</tr>
<tr>
<td>Myrtus communis</td>
<td>As above</td>
<td>$K_{s,pl}$</td>
<td>19% decrease at elevated CO₂</td>
<td>Tognetti et al. (2000)</td>
</tr>
<tr>
<td>Juniperus communis</td>
<td>As above</td>
<td>$K_{s,pl}$</td>
<td>No change</td>
<td>Tognetti et al. (2000)</td>
</tr>
</tbody>
</table>
(d) Summary of reported changes in response to changes in nutrient availability

<table>
<thead>
<tr>
<th>Species</th>
<th>Investigated factors</th>
<th>Measured parameters</th>
<th>Observed response</th>
<th>Authors</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Larrea tridentata</em></td>
<td>Ambient and elevated CO₂ (600 p.p.m.) for 12 months on 1-month-old plants in greenhouse</td>
<td>$K_{L,root}$</td>
<td>No change</td>
<td>Huxman et al. (1999)</td>
</tr>
<tr>
<td><em>Helianthus annuus</em></td>
<td>Ambient and elevated CO₂ (600 p.p.m.) for 37 d from germination in greenhouse</td>
<td>$K_{L,root}$</td>
<td>38% decrease at elevated CO₂</td>
<td>Huxman et al. (1999)</td>
</tr>
<tr>
<td><em>Quercus robur</em></td>
<td>Different levels of fertilizer application for 3 years</td>
<td>$K_{L,shoot}$</td>
<td>No change</td>
<td>Heath et al. (1997)</td>
</tr>
<tr>
<td><em>Fagus sylvatica</em></td>
<td>As above</td>
<td>$K_{L,leaf}$</td>
<td>No change</td>
<td>Heath et al. (1997)</td>
</tr>
<tr>
<td><em>Pinus taeda</em></td>
<td>Control, fertilized, irrigated and irrigated/ fertilized plots of 15-year-old trees</td>
<td>(a) $K_{i,pl}$</td>
<td>(a) 55% and (b) 45% decline in fertilizer treatment, no change in the others</td>
<td>Ewers et al. (2000)</td>
</tr>
<tr>
<td><em>Pseudotsuga menziesii</em></td>
<td>6-year-long fertilized plots of 24-year-old trees plus control</td>
<td>Sapwood : leaf area ratio</td>
<td>34% decrease in fertilized plots</td>
<td>Brix &amp; Mitchell (1983)</td>
</tr>
<tr>
<td><em>Picea sitchensis</em></td>
<td>8-year-long fertilized plots of 30-year-old trees plus control</td>
<td>(a) $K_{i,h}$</td>
<td>No change</td>
<td>Whitehead et al. (1984)</td>
</tr>
<tr>
<td><em>Pinus taeda</em></td>
<td>Low and high site index stands</td>
<td>(b) Sapwood : leaf area ratio</td>
<td></td>
<td>Shelbourne et al. (1993)</td>
</tr>
<tr>
<td><em>Eucalyptus grandis</em></td>
<td>Control and three treatments of N fertilization for 1 year in the field on 1-year-old seedlings</td>
<td>(a) $K_{i,h}$</td>
<td>No change</td>
<td>Clearwater &amp; Meinzer, (2001)</td>
</tr>
<tr>
<td><em>Pinus sylvestris</em></td>
<td>Comparison of 70–80-year-old trees on two site types with different fertility</td>
<td>Sapwood : leaf area ratio</td>
<td>50% increase in fertile sites</td>
<td>Vanninen et al. (1996)</td>
</tr>
</tbody>
</table>

(e) Genetically controlled differences among ecotypes growing along environmental gradients but tested under common garden conditions

<table>
<thead>
<tr>
<th>Species</th>
<th>Investigated factors</th>
<th>Measured parameters</th>
<th>Observed response</th>
<th>Authors</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Hymenoclea alsola</em></td>
<td>Populations from northern cooler and southern hotter origins grown in greenhouse for 5–6 months</td>
<td>$K_{L,pl}$, $K_{L, shoot}$, $K_{L, root}$</td>
<td>33, 58 and 26% increase in populations from southern hotter region</td>
<td>Comstock (2000)</td>
</tr>
<tr>
<td><em>Ambrosia dumosa</em></td>
<td>Populations from northern cooler and southern hotter origins grown in greenhouse for 5–6 months</td>
<td>$K_{L,pl}$, $K_{L, shoot}$, $K_{L, root}$</td>
<td>72, 57 and 94% increase in populations from southern hotter region</td>
<td>Comstock (2000)</td>
</tr>
<tr>
<td><em>Phaseolus vulgaris</em></td>
<td>Twelve populations from gradient of hot and dry to cool and wet sites grown in greenhouse</td>
<td>$K_{L,pl}$</td>
<td>98% increase from cool and wet to hot and dry sites</td>
<td>Mencuccini &amp; Comstock (1999)</td>
</tr>
</tbody>
</table>
extent of the hydraulic system per se, and (b) changes in the amount of leaf area present. That the two are inherently linked has been already demonstrated with the theoretical analysis presented in the first section of this review.

The third, and perhaps the most important, aspect emerging from this literature review is that, contrary to reports strictly related to allometry (root : shoot ratios), in this case the response to changes in the availability to any of these four factors was in the same direction, i.e. when the availability of one resource increased (no matter whether above- or below-ground), the efficiency of the plant hydraulic system tended to decrease.

As acclimation takes place in the long-distance water transport system and in the amount of leaf area supplied, presumably gas exchange properties are also subject to change and leaf structural and physiological properties also show acclimation. In as much as structural properties can regulate short-term gas exchange, acclimation in structural properties may elicit substantial changes in the level of regulation that can be achieved this way. For instance, if the efficiency of the hydraulic system (per unit of leaf area) is down-regulated under elevated CO\textsubscript{2} conditions, relief from water stress as a consequence of stomatal closure, reduced stomatal density, reductions in pore width or length, etc., will simply not occur. Similar levels of water potentials might be expected with a less efficient hydraulic system and the degree of stomatal control by leaf water status may stay unaltered. On the contrary, under increased nutrient levels, greater levels of stomatal conductance and photosynthetic rates might be expected. The down-regulation of the hydraulic system efficiency may push plants to explore deeper soil horizons to scavenge for available water and may increase the level of stomatal regulation determined by short-term episodes of drought (Ewers et al. 2000). Finally, the up-regulation of the hydraulic system efficiency in response to drought may also help to maintain homeo-stasis in leaf water status in the face of lower soil water potentials (Cinnirella et al. 2002).

In natural ecosystems, changes in environmental conditions occur continuously and the processes of short-term physiological regulation and long-term structural acclimation take place simultaneously. At any one time, plants have the possibility of making use of both tools to accommodate reductions in, for example, soil water or nutrients, and it is possible that, in so doing, an optimal balance is achieved. Obviously, further theoretical advancements are required to take both sets of processes into account and to complement, for example, the traditional theories of short-term optimization of gas exchange with respect to water loss (e.g. Cowan 1977, 1986; Givnish 1986).

CONCLUSIONS

The static picture emerging from the scaling exercise reveals a high degree of convergence of functional properties across several plant species belonging to largely different life forms. The conclusions drawn here with regard to the details of such a scaling are largely preliminary, as the analyses above were all limited by the available evidence published in the literature. No doubt, further studies will reveal more aspects of the inescapable need for a balance between demand and supply of water.

Further comparative studies across life forms, considering several aspects of plant physiological ecology and at several spatial scales (i.e. leaf, plant, stand, ecosystem) are clearly needed and will provide invaluable information on the ecology of plants. Further meta-analyses would also be valuable, as a substantial body of knowledge has already been produced in the last few decades in this field.

The complementary features and the interplay between short-term physiological regulation and structural acclimation in plant hydraulic conductance should also be explored in detail. In the meta-analyses reported here, for instance, it was assumed that the changes observed in any experiment carried out over a reasonably long time scale was the result of long-term acclimation only. Although this was certainly the case for parameters such as sapwood : leaf area ratios, the reported estimates of whole-plant hydraulic conductance may also have been influenced by short-term physiological regulation.

ACKNOWLEDGMENTS

I am entirely responsible for any misunderstanding of the published data, which formed the bases of my meta-analyses. I am directly indebted to many scientists whose work I have cited here, and to whom I have written directly to have clarifications and additional information not available from the original publications. I am also indebted to several colleagues and friends for helpful conversations, particularly Jonathan Comstock and Dirk Vanderklein. Keith McNaughton drew my attention to the potential significance of the changes in the parameter $b$ across life forms and spent several hours discussing the significance of stomatal responses (or lack thereof) to $D$.

REFERENCES


Received 12 April 2002; received in revised form 20 September 2002; accepted for publication 10 October 2002.
### APPENDIX

List of abbreviations used in the text

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>$g_s$</td>
<td>Stomatal conductance</td>
<td>mmol m$^{-2}$ s$^{-1}$</td>
</tr>
<tr>
<td>$g_l$</td>
<td>Leaf conductance</td>
<td>mmol m$^{-2}$ s$^{-1}$</td>
</tr>
<tr>
<td>$D$</td>
<td>Leaf-to-air vapour-pressure difference</td>
<td>mmol mol$^{-1}$</td>
</tr>
<tr>
<td>$D_s$</td>
<td>Leaf-to-leaf surface vapour-pressure difference</td>
<td>mmol mol$^{-1}$</td>
</tr>
<tr>
<td>$E_L$</td>
<td>Transpiration rate per unit leaf area</td>
<td>mmol m$^{-2}$ s$^{-1}$</td>
</tr>
<tr>
<td>$E_pl$</td>
<td>Transpiration rate per plant</td>
<td>mmol plant$^{-1}$ s$^{-1}$</td>
</tr>
<tr>
<td>$\Psi_c, \Psi_l$</td>
<td>Soil and leaf water potential</td>
<td>MPa</td>
</tr>
<tr>
<td>$K_pl$</td>
<td>Hydraulic conductance of the whole plant (i.e. from soil–root interface to leaves)</td>
<td>mmol s$^{-1}$ MPa$^{-1}$</td>
</tr>
<tr>
<td>$K_{shoot}$</td>
<td>Hydraulic conductance from shoot base to leaves</td>
<td>mmol s$^{-1}$ MPa$^{-1}$</td>
</tr>
<tr>
<td>$K_{root}$</td>
<td>Hydraulic conductance from soil–root interface to root base</td>
<td>mmol s$^{-1}$ MPa$^{-1}$</td>
</tr>
<tr>
<td>$K_{s,leaf}$</td>
<td>As $K_pl$, but calculated as leaf-specific rates, i.e. dividing the previous parameters by leaf area</td>
<td>mmol m$^{-2}$ s$^{-1}$ MPa$^{-1}$</td>
</tr>
<tr>
<td>$K_{s,shoot}$</td>
<td>As $K_{shoot}$, but calculated as leaf-specific rates, i.e. dividing the previous parameters by leaf area</td>
<td>mmol m$^{-2}$ s$^{-1}$ MPa$^{-1}$</td>
</tr>
<tr>
<td>$K_{s,root}$</td>
<td>As $K_{root}$, but calculated as leaf-specific rates, i.e. dividing the previous parameters by leaf area</td>
<td>mmol m$^{-2}$ s$^{-1}$ MPa$^{-1}$</td>
</tr>
<tr>
<td>$K_c$</td>
<td>Segment hydraulic conductivity</td>
<td>mmol m s$^{-1}$ MPa$^{-1}$</td>
</tr>
<tr>
<td>$K'$</td>
<td>Segment-specific conductivity, or permeability</td>
<td>mmol m$^{-2}$ s$^{-1}$ MPa$^{-1}$</td>
</tr>
<tr>
<td>$A_L$</td>
<td>Plant leaf area</td>
<td>m$^2$</td>
</tr>
<tr>
<td>$c_s, c_l$</td>
<td>Concentration of CO$_2$ at the leaf surface and in the leaf intercellular spaces</td>
<td>$\mu$mol mol$^{-1}$</td>
</tr>
</tbody>
</table>