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Functional convergence in plant responses to the environment

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Abstract Much comparative ecophysiological research has focused on contrasting species-specific behavior or ecological strategies with regard to regulation of basic physiological processes such as transpiration, photosynthesis and growth, leading to an emphasis on divergence rather than convergence in plant functioning. This review highlights selected examples in which substantial functional convergence among taxonomically, phylogenetically and architecturally diverse species has been revealed by applying appropriate scaling factors and identifying universal constraints or trade-offs. Recent empirical and theoretical scaling models emphasize the strong role that plant size, architecture, allometry and chemistry play in constraining functional traits related to water and carbon economy and growth. Taken together, the findings summarized here strongly suggest that there are a limited number of physiological solutions to a given problem of plant adaptation to the environment. Comparative ecophysiological studies will therefore benefit from consideration of the constraints that plant anatomical, structural and chemical attributes place on physiological functioning.

Keywords Carbon balance · Plant allometry · Plant growth · Plant-water relations · Scaling models

Introduction

The botanical, ecological and forestry literature is replete with examples of what appear to be contrasting species-specific behavior or ecological strategies with regard to regulation of basic physiological processes such as transpiration, photosynthesis and growth. This emphasis on divergence rather than convergence in functioning

seems to have strong historical roots in the course of development of botanical science, which began with plant classification and a necessary emphasis on differences. In contrast, convergence in functioning among phylogenetically diverse animal species has been known for a long time. Classic examples include the dependence of metabolic rate and lifespan on body size (Calder 1984; Schmidt-Nielsen 1984). Explicit analyses of the influence of body size on fundamental processes in plants have been largely lacking until recently, however (Enquist et al. 1998, 1999; West et al. 1999; Niklas and Enquist 2001).

Widespread recognition of functional convergence in plants appears to have been obscured by ambiguities concerning the true scale at which measurements are being made, even though the importance of explicitly considering scale is often acknowledged (e.g. Levin 1992; Ehleringer and Field 1993). For example, measurements of gaseous fluxes in individual leaves expressed on a unit leaf area basis are often tacitly assumed to represent organismal properties when in reality they do not, unless the fluxes can be (1) corrected for differences in boundary layer conditions experienced by unenclosed leaves and those in the gas exchange measurement chamber, and (2) scaled to a whole-plant basis by determining total leaf area and showing that the behavior of the leaves measured is representative of the plant's entire complement of leaves. Consistent with studies of animals, the desirable scale for characterizing ecophysiological behavior and responses of plants is often the individual because it is the integration of activities and processes in the entire individual that contributes to features such as survival, growth and reproductive success. In some cases, such as rhizomatous and clonally reproducing plants, ambiguities are admittedly involved in defining the size of an individual plant.

The aims of this review are to (1) highlight selected examples in which substantial functional convergence among taxonomically, phylogenetically and architecturally diverse species has been revealed by applying appropriate scaling factors and identifying universal constraints or trade-offs, (2) emphasize the strong role that plant size,

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Table 1 List of species for which sap flow data are plotted in Fig. 1A, B. The number of individuals from which sap flow data were available and the diameter of the stem at the point of sap flow probe insertion are given. Source indicates reference for previously published data

Species	Family	Individuals	Stem diameter (cm)	Source
<i>Anacardium excelsum</i>	Anacardiaceae	1	32	Meinzer et al. (2001)
<i>Mangifera indica</i>	Anacardiaceae	1	6.1	Lu and Chacko (1998)
<i>Spondias radlkoferi</i>	Anacardiaceae	1	60	Meinzer et al. (2001)
<i>Guatteria dumetorum</i>	Annonaceae	2	46–69	Meinzer et al. (2001)
<i>Didymopanax macrocarpum</i>	Araliaceae	4	5.3–9.5	
<i>Jacaranda copaia</i>	Bignoniaceae	2	73–86	Meinzer et al. (2001)
<i>Ochroma pyramidale</i>	Bombacaceae	1	51	Meinzer et al. (2001)
<i>Pseudobombax septenatum</i>	Bombacaceae	2	98–130	Meinzer et al. (2001)
<i>Quararibea asterolepis</i>	Bombacaceae	3	28–50	Meinzer et al. (2001)
<i>Cordia alliodora</i>	Boraginaceae	1	40	Meinzer et al. (2001)
<i>Cecropia peltata</i>	Cecropiaceae	1	24	Meinzer et al. (2001)
<i>Kielmeyera coriacea</i>	Clusiaceae	3	4.3–7.7	
<i>Hura crepitans</i>	Euphorbiaceae	3	60–107	Meinzer et al. (2001)
<i>Dalbergia miscolobium</i>	Fabaceae	1	6.3	
<i>Dipteryx panamensis</i>	Fabaceae	2	41–118	Meinzer et al. (2001)
<i>Lonchocarpus latifolius</i>	Fabaceae	2	25–33	Meinzer et al. (2001)
<i>Platymiscium pinnatum</i>	Fabaceae	4	39–64	Meinzer et al. (2001)
<i>Prioria copaifera</i>	Fabaceae	1	68	Meinzer et al. (2001)
<i>Miconia ferruginata</i>	Melastomataceae	5	3.6–7.3	
<i>Trichilia tuberculata</i>	Meliaceae	4	24–27	Meinzer et al. (2001)
<i>Ficus insipida</i>	Moraceae	1	122	Meinzer et al. (2001)
<i>Virola surinamensis</i>	Myristicaceae	3	28–77	Meinzer et al. (2001)
<i>Eucalyptus globulus</i>	Myrtaceae	1	14.7	David et al. (1997)
<i>Eugenia coloradensis</i>	Myrtaceae	1	31	Meinzer et al. (2001)
<i>Guapira standleyanum</i>	Nyctaginaceae	1	69	Meinzer et al. (2001)
<i>Alseis blackiana</i>	Rubiaceae	5	22–38	Meinzer et al. (2001)
<i>Zanthoxylum belizense</i>	Rutaceae	3	55–68	Meinzer et al. (2001)
<i>Populus hybrid</i>	Salicaceae	1	13.7	Hinckley et al. (1994)
<i>Apeiba membranacea</i>	Tiliaceae	1	41	Meinzer et al. (2001)
<i>Luehea seemanii</i>	Tiliaceae	3	38–40	Meinzer et al. (2001)
<i>Qualea parviflora</i>	Vochysiaceae	2	5.2–5.9	

architecture and allometry play in dictating functional traits, and (3) show how the examples and approaches discussed can provide a series of common denominators for what at first sight may appear to be a baffling array of species-specific behaviors or “strategies”. The examples presented will focus on processes related to water economy, and carbon economy and growth, two areas in which substantial progress has recently been made in identifying convergent relationships.

Water economy

Whole-plant water use

It has recently been proposed that allometric scaling of plant vascular systems, and therefore water use, is universal (Enquist et al. 1998; West et al. 1999). For example, Enquist et al. (1998) found that total daily water use scaled with the 3/4 power of aboveground dry mass in a similar manner among 37 plant species. Consistent with this, Meinzer et al. (2001) reported common relationships between stem diameter and sapwood area and maximum sap flow in more than 20 co-occurring tropical forest tree species. When aboveground dry mass was estimated from stem diameter using the proportionality constant given by Enquist et al. (1998), the exponent describing the relationship between sapwood area and estimated biomass

was 0.74 (Meinzer et al. 2001). When the original data set of Meinzer et al. (2001) is extended to smaller stem diameters by including comparable measurements from additional species growing in other locations (Table 1), a common relationship between sap flux density (sap flow per unit sapwood area) and stem diameter persists (Fig. 1A). When sap flux density is plotted on a log scale to linearize the relationship, stem diameter accounts for 93% of the variation in sap flux density among 31 species for which comparable data were available (Fig. 1A, inset).

A number of mechanisms operating at the whole-tree level could be responsible for the curvilinear decline in sap flow with increasing stem diameter. If both tree height and total hydraulic resistance increased linearly with stem diameter, then hydraulic conductance, and therefore sap flux density, should decline in a manner similar to that seen in Fig. 1A, provided stomata regulate leaf water potential in a manner that maintains a relatively constant driving force as total resistance increases with path length. To test this hypothesis, a surrogate flux-resistance relationship was obtained by plotting the inverse of sap flux density against stem diameter (Fig. 1B). If the hypothesis were valid, then inverse sap flux density would increase linearly with stem diameter. However, the relationship obtained appeared to consist of two distinct linear phases, an initial phase in which inverse sap flux density increased relatively gradually with stem diameter

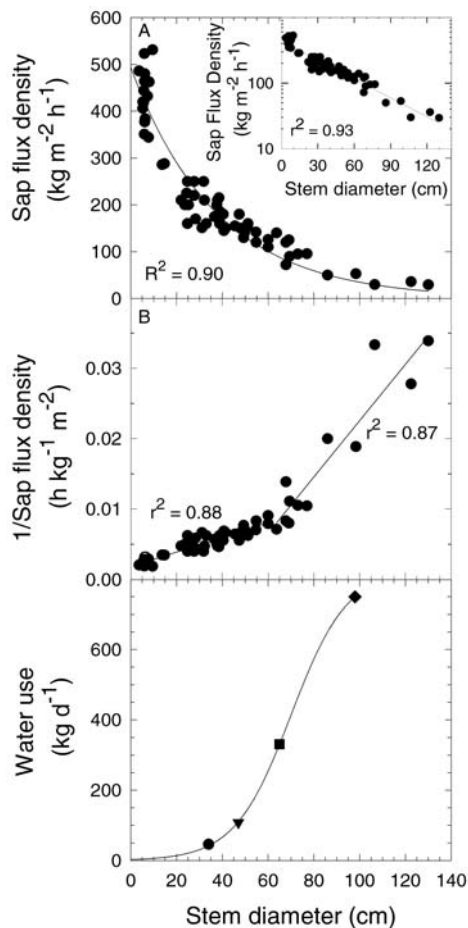


Fig. 1A–C Size-dependence of plant water use characteristics. **A** Maximum sap flux density in relation to stem diameter for one to five individuals of the 31 species listed in Table 1. All measurements were made with the heat dissipation method developed by Granier (1985, 1987) using 20-mm-long probes inserted in the outermost sapwood. *Inset*: sap flux density plotted on a log scale. **B** Reciprocals of the sap flux density measurements in **A**. **C** Total daily water use in relation to basal stem diameter for four co-occurring tropical forest tree species: (diamond) *Anacardium excelsum* (square), *Ficus insipida* (inverted triangle), *Schefflera morototoni* (circle) *Cordia alliodora*. Points are means of 22–56 days of measurements during the dry season. Standard errors are smaller than the symbols. Data obtained from James et al. (2002)

up to a threshold of ca. 60 cm, followed by an abrupt transition to a markedly steeper linear phase over the remaining range of stem diameter. At least three factors may have contributed to this biphasic relationship. First, maintenance of a constant driving force for water transport would require stomata to compensate for the gravitational component of water potential by allowing the daily minimum leaf water potential coinciding with the peak transpiration rate to fall by 0.1 MPa for every 10 m increase in tree height. However, if stomatal regulation is aimed at preventing leaf or stem water potential from falling below a threshold minimum value associated with excessive loss of xylem function due to cavitation, then there may be a height (stem diameter) threshold beyond which the maximum driving force

begins to decline because the increasingly negative gravitational component of water potential acts to diminish the net driving force with increasing height. In other words, as trees get taller, mechanisms of stomatal regulation that have evolved within the context of conserving whole-plant water transport may obscure fundamental scaling relationships that are based on physics alone. Second, changes in tree allometry that increase basal sapwood area relative to total leaf area would increase total water conducting capacity in relation to transpirational demand, thereby decreasing the flow rate per cross sectional area of xylem. Finally, as total stem water storage capacity increases with tree size, transient removal of water from storage above the point of sap flow measurement near the base of the tree would reduce maximum rates of sap flow recorded there (Goldstein et al. 1998). Although the water potential threshold mechanism is clearly consistent with the biphasic relationship in Fig. 1B, the latter two mechanisms would not invariably lead to linear increases in inverse sap flux density with increasing stem diameter.

All of the sap flow measurements reported in Fig. 1A were made with 2-cm-long probes inserted to a depth of a little over 2 cm in the sapwood. However, the observed decline in maximum sap flux density in the outermost 2 cm of sapwood does not necessarily imply a reduced rate of increase in total daily water use with increasing plant size, because sapwood area increases exponentially with stem diameter and because total water use depends on the radial profile of flow over the entire sapwood depth, which was greater than 20 cm in stems greater than about 60 cm in diameter (Meinzer et al. 2001). Substantial variation in radial profiles of sap flow has been reported both among and within species, and even circumferentially within the same stem. The patterns observed include maximal flow in the outermost sapwood followed by sharply declining flow with increasing depth, peak flow at some distance inside the vascular cambium, relatively constant flow across a broad range of depth, and alternating increases and decreases in flow with increasing depth (Phillips et al. 1996; Jiménez et al. 2000; Wullschlegel and King 2000; James et al. 2002). Furthermore, integrated daily water use is affected by stomatal regulation of daily courses of transpiration, which have been shown to be strongly size-dependent for a subset of the species represented in Fig. 1. Among these species, larger trees with greater stem water storage capacity sustain near maximal rates of flow for a substantially longer portion of the day than smaller trees (Goldstein et al. 1998).

James et al. (2002) measured sap flow at four to five points across the entire sapwood depth to obtain detailed radial profiles and used these to estimate total daily water use in one individual of three of the species represented in Fig. 1A plus one individual of a fourth co-occurring species. Each of the four types of radial profile described above was represented. When their data are plotted as a function of basal stem diameter, integrated daily water use is seen to increase sharply with stem diameter from

ca. 50 to 100 cm, the size of the largest individual in which sap flow was measured (Fig. 1C). A sigmoidal function was fitted to the data under the assumption of an intercept at the origin. Although a linear function provided an adequate fit to the data, its non-zero x -intercept was not biologically or empirically reasonable. In comparing Fig. 1A and C it is apparent that conclusions about the relationship between water use and tree size may be strongly dependent on the temporal and spatial scales over which water use is evaluated. The disparity between tree size-dependent patterns of water use at different scales probably reflects the size dependence of the influence of stem water storage on maximum rates of flow near the base of the stem (Fig. 1A) and on the fraction of the day during which transpiration remains near its maximum rate (Goldstein et al. 1998). Regardless of the scale, it is evident that substantial functional convergence exists in the relationship between water use and plant size among the taxonomically and architecturally diverse tree species represented in Fig. 1.

Stomatal control of transpiration

Fluctuations in leaf water potential (Ψ_L) are determined by variation in the transpiration flux density (E) and the hydraulic conductance of the soil-to-leaf pathway (G_t) if all other relevant variables such as soil water potential surrounding the roots remain constant. The upper end of the operating range of Ψ_L is thus governed by the soil water potential surrounding the roots and the lower end by the sensitivity stomata exhibit in regulating transpiration in response to variation in the leaf-to-air vapor pressure deficit (VPD) and G_t . It seems reasonably well established that the progressive closure of stomata in response to increasing VPD is linked to sensing of E rather than VPD (Mott and Parkhurst 1991; Monteith 1995; Meinzer et al. 1997a). Sensing of E implies a feedback response to transpiration-induced changes in the water status of leaf tissue. However, stomatal limitation of transpiration in response to increasing evaporative demand may exhibit feedback or feedforward (Farquhar 1978) characteristics with respect to regulation of bulk leaf water status depending on the location of the leaf cells experiencing transpiration-induced changes in their water status. For example, stomatal sensing of cuticular transpiration via changes in the water status of guard cells or other epidermal cells could result in feedforward regulation of bulk leaf water status if stomatal transpiration decreases with increasing evaporative demand, whereas sensing of stomatal transpiration would always have feedback characteristics with respect to bulk leaf water status (Meinzer 2002). Recent studies point to considerable convergence in responses of stomatal conductance (g_s) to VPD and G_t . Some interpretations of separate and combined stomatal responses to these variables and their implications for transpiration are discussed below.

Although there is considerable variation among species in the rate at which g_s decreases with increasing VPD

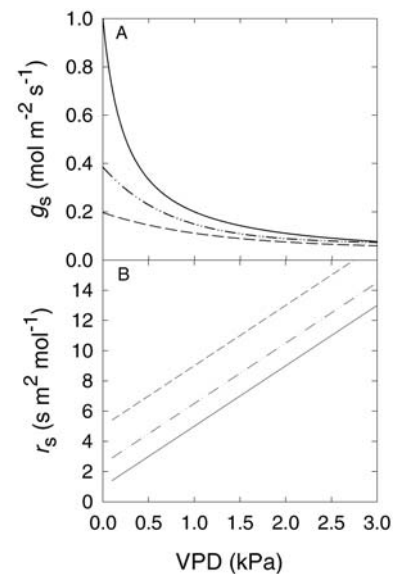


Fig. 2 A Hypothetical relationships between stomatal conductance and VPD for three species differing in maximum values of g_s at low VPD. B Relationships in A plotted as stomatal resistance ($r_s=1/g_s$)

(Schulze and Hall 1982), an exponential decline in g_s with increasing VPD is a common feature shared by most species. Oren et al. (1999) have exploited this characteristic relationship to demonstrate that the sensitivity of g_s to VPD is proportional to the magnitude of g_s at low VPD in the same manner across a broad range of species and conditions. Their results were consistent with predictions of a hydraulic model that assumes stomatal regulation of Ψ_L . However, there is an important distinction between the responsiveness or sensitivity of g_s to increasing evaporative demand and the responsiveness of the stomatal guard cells themselves. The three hypothetical species response curves in Fig. 2A are consistent with increasing sensitivity of g_s to VPD as the magnitude of g_s at low VPD increases. Yet, when the reciprocal of g_s , stomatal resistance (r_s), is plotted against VPD, three lines with identical slopes, but different y-intercepts (maximum values of g_s) are obtained (Fig. 2B). Because r_s changes linearly with pore radius, parallel linear responses of r_s to VPD imply identical sensitivity of stomatal aperture to variation in VPD (functional convergence). Thus, dramatic differences in the sensitivity of g_s to increasing evaporative demand may not necessarily reflect intrinsic differences in individual guard cell responsiveness. Differences in stomatal density, pore depth, or G_t among the three hypothetical species could account for differences in minimum r_s (maximum g_s) at low VPD. On the other hand, differences in the responsiveness of g_s to VPD among species may indeed reflect differences in the sensitivity of stomatal aperture if the slope of the relationship between r_s and VPD differs.

The distinction between sensitivity of g_s and of the stomata themselves to evaporative demand may seem academic because transpiration is not just a function of stomatal aperture, but of g_s , which integrates individual

pore area, pore depth and stomatal density. Nevertheless, analyzing stomatal behavior and properties over a range of scale could reveal convergence in physiological functioning and allow one to partition apparent differences in responsiveness of g_s among different mechanisms such as stomatal density, soil-to-leaf hydraulic constraints, and intrinsic differences in guard cell behavior when confronted with comparable stimuli. Although the preceding considerations indicate that definitive conclusions cannot be drawn concerning intrinsic differences and similarities in stomatal guard cell properties among species based on analysis of the behavior of g_s alone, there is evidence of considerable convergence among species with regard to responses of g_s to VPD when leaf boundary layer conditions and appropriate normalizing factors are taken into account (Bunce 1985; Meinzer et al. 1995, 1997b; Oren et al. 1999).

In addition to achieving relative homeostasis of Ψ_L by limiting transpiration with increasing evaporative demand, numerous studies have shown an active stomatal coordination of transpiration with variation in G_t (Meinzer 2002 and references therein) that serves to limit the operating range of Ψ_L within a given species. As with stomatal responses to humidity, stomatal coordination of transpiration with variation in the hydraulic properties of the soil-to-leaf pathway is likely to involve feedback sensing of changes in water status in yet to be identified portions of the leaf. Stomata sometimes overcompensate for reductions in G_t by limiting transpiration enough to cause Ψ_L to increase leading to feedforward regulation with respect to bulk leaf water status (Meinzer and Grantz 1990). When perturbations of the root environment contribute to changes in G_t , chemical as well as hydraulic signals may be involved (Tardieu and Davies 1992; Tardieu et al. 1993).

Studies reporting common relationships between g_s and G_t among co-occurring species point to considerable convergence with regard to coordination of stomatal and hydraulic properties (Meinzer 2002). In some cases, the shared relationship between g_s and G_t is curvilinear, with g_s becoming asymptotic at the highest values of G_t observed (e.g. Meinzer et al. 1995; Andrade et al. 1998), whereas in other cases the shared relationship between g_s and G_t is linear (e.g. Comstock 2000; Nardini and Salleo 2000). Because stomatal regulation of Ψ_L apparently involves sensing of transpirational fluxes (stomatal or cuticular), VPD and G_t should dominate in determining g_s if other variables remain constant. Responses of g_s to simultaneous variation in VPD and G_t may thus describe a response surface shared by co-occurring species. Consistent with this, apparently distinct responses of g_s and E to variation in VPD among co-occurring tropical forest canopy species converged (Meinzer et al. 1997b; Andrade et al. 1998) when the data were multiplied by the branch level ratio of leaf area to sapwood area, a surrogate measure of leaf area-specific hydraulic resistance (Tausend et al. 2000). The results of this normalization procedure, which transforms vapor phase conductances and fluxes from a leaf area to a

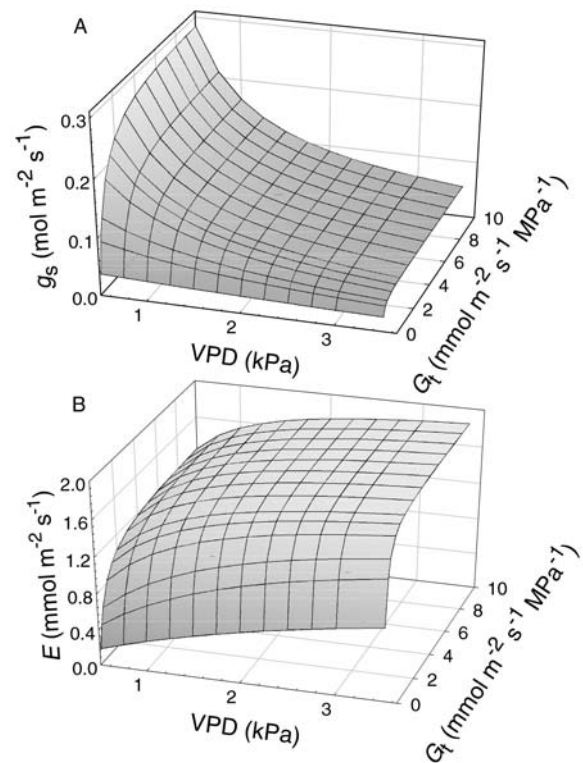


Fig. 3 **A** Stomatal conductance (g_s) as a function of leaf-to-air VPD and hydraulic conductance of the soil-to-leaf pathway (G_t). Conditions: slope of linear increase in stomatal resistance with increasing VPD is 5, and $g_s = a(1 - e^{-bG_t})$, where a is maximum g_s at zero VPD ($1 \text{ mol m}^{-2} \text{ s}^{-1}$) and b is 0.4. **B** Transpiration (E) as a function of VPD and G_t calculated as $E = \text{VPD}[1/(1/g_s + 1/g_b)]$, where g_s is obtained from Fig. 4A and g_b (leaf boundary layer conductance) is held constant at $2 \text{ mol m}^{-2} \text{ s}^{-1}$.

sapwood area basis, are congruent with the data presented in Fig. 1 and by Meinzer et al. (2001). In addition, Franks and Farquhar (1999) found that 13 species representing different growth forms and habitats shared a common relationship between stomatal sensitivity to VPD and an index of hydraulic conductance in the vicinity of the guard cells. These convergent relationships between stomatal behavior, transpiration and hydraulic properties among co-occurring species are intriguing given the probable divergence in other features such as hydraulic architecture and vulnerability of xylem to cavitation.

An example of a hypothetical surface describing responses of g_s to various combinations of VPD and G_t is shown in Fig. 3A. To generate the surface, a typical asymptotic response of g_s to increasing G_t , and a typical exponential decline in g_s with increasing VPD were assumed (see figure legend for additional conditions and assumptions). Although differences among features such as stomatal density, hydraulic architecture, and plant size may cause individual species to exhibit distinct operating ranges of g_s , substantial functional convergence would be inferred if operating ranges for a group of species conformed to a shared response surface. Analysis of physiological operating ranges defined by single or

multiple variables may provide insights as to which anatomical, structural and other features play the most important roles in constraining the range of physiological options available to co-occurring species. When the response surface of g_s shown in Fig. 3A is used to generate a response surface for E assuming a constant value for boundary layer conductance (g_b) of $2 \text{ mol m}^{-2} \text{ s}^{-1}$, E is seen to remain relatively constant over a large range of combinations of VPD and G_t (Fig. 3B). The relative homeostasis of E above threshold values of VPD and G_t is not readily inferred from the response surface of g_s , and is attributable largely to the decoupling influence of the boundary layer (Jarvis and McNaughton 1986) at higher values of g_s and to reductions in maximum g_s at low VPD as G_t declines.

Convergence in stomatal regulation of transpiration in response to variation in VPD and G_t (Fig. 3B) would require constraints on the range of variation in the combination of leaf traits that determine total leaf conductance to water vapor (stomatal plus boundary layer). These constraints should result in a trade-off between stomatal pore frequency and individual pore diffusive path length mediated by the influence of leaf size on g_b and therefore on the stomatal decoupling coefficient, Ω (Jarvis and McNaughton 1986). For example, the response surface in Fig. 4 was generated to explore possible combinations of stomatal frequency, stomatal pore diffusive path length, and leaf size that would lead to convergence in maintenance of the transpiration rate at $1.5 \text{ mmol m}^{-2} \text{ s}^{-1}$ under the conditions specified in the figure legend. It is apparent that the influence of leaf size on g_b strongly constrains the combinations of stomatal frequency and pore length that would lead to similar transpiration rates on a leaf area basis in small versus large leaves. The simulation in Fig. 4 is consistent with general observations of lower g_s in species with small leaves and high g_b (e.g. conifers) than in species with large leaves and low g_b . Surveys of leaf size, stomatal frequency and pore length among co-occurring species across a range of environments should reveal the extent to which combinations of these features are constrained by convergence in regulation of transpiration.

Influence of wood density

In addition to its widely recognized consequences for mechanical properties and commercial utilization of wood, wood density is an important determinant of xylem water transport properties and whole-plant water relations. Hacke et al. (2001) reported highly significant correlations between wood density and the xylem pressure threshold for 50% loss of hydraulic conductivity by cavitation among several species exhibiting a relatively broad range of wood density. Although the relationships were distinct for angiosperms and conifers, all species within each group appeared to share a common relationship between density and xylem resistance to cavitation.

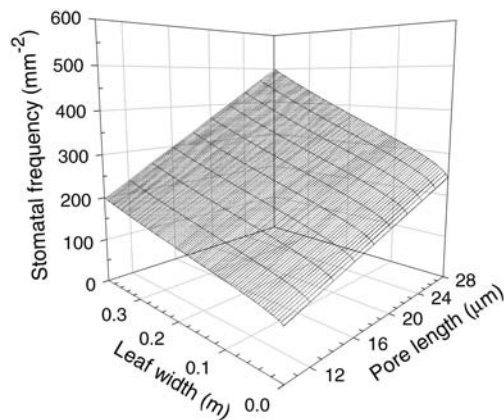


Fig. 4 Combinations of stomatal pore frequency and pore diffusive path length necessary to maintain a constant transpiration rate of $1.5 \text{ mmol m}^{-2} \text{ s}^{-1}$ as leaf size, and therefore boundary layer conductance, varies. The transpiration rate was obtained from the response surface in Fig. 3B at VPD=1.0 kPa and $G_t=5.0 \text{ mmol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$. Other conditions for the simulation were wind speed= 0.5 m s^{-1} , stomatal pore radius= $2.5 \text{ }\mu\text{m}$. Boundary layer conductance was estimated from leaf size and wind speed, and stomatal conductance was estimated from stomatal frequency and pore length as described by Nobel (1991)

The gain in cavitation resistance with increasing wood density appears to be associated with a cost in terms of reduced hydraulic conductivity. In a study of six co-occurring Hawaiian dry forest species, Stratton et al. (2000) noted a 5-fold increase in wood specific hydraulic conductivity (k_s) associated with a relatively small decrease in wood density from ca. 0.65 to 0.5 g cm^{-3} . The six species shared a single, linear relationship ($r^2=0.98$) between k_s and wood density. It is likely that wood density determines a suite of whole-plant water relations characteristics in addition to xylem cavitation resistance and k_s . For example, in their study of Hawaiian dry forest species, Stratton et al. (2000) observed additional correlations between wood density and minimum annual Ψ_L , diel variation in Ψ_L , and the Ψ_L corresponding to turgor loss as determined from pressure-volume curves. Results of a survey of wood density and diel variation in Ψ_L among 27 species reinforces a role for wood density in determining patterns of regulation of whole-plant water balance (Fig. 5). Diel variation in Ψ_L ($\Delta\Psi_L$) initially increased gradually with wood density up to a value of ca. 0.5 g cm^{-3} followed by a more rapid, steady increase in $\Delta\Psi_L$ over the remaining range of data. It is possible that the relationship between $\Delta\Psi_L$ and wood density is sigmoidal, but $\Delta\Psi_L$ data for species with wood density greater than 0.9 g cm^{-3} were not found. The strength of the relationship in Fig. 5 is remarkable given that for nearly all of the species, values of wood density and $\Delta\Psi_L$ were not available for the same individuals. Typical values of wood density were obtained from published lists and the literature was surveyed for reports of $\Delta\Psi_L$ (Table 2). The criteria applied to selecting values of $\Delta\Psi_L$ (see Table 2) limited the number of species that could be included in the survey. Nevertheless, it is notable

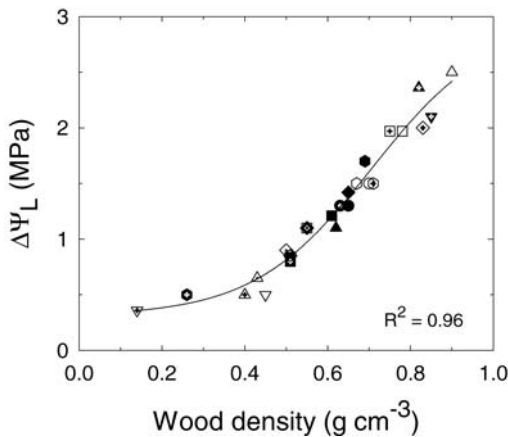


Fig. 5 Relationship between diel variation in leaf water potential ($\Delta\Psi_L$) and wood density for 27 species. See Table 2 for species and sources of data

that a simple physical characteristic of wood can account for such a large fraction of variation in physiological regulation of the maximum driving force for water movement among diverse species growing in environments ranging from the humid tropics to deserts.

The preceding examples indicate that variation in wood density is strong predictor of variation in a suite of characteristics related to efficiency and integrity of xylem water transport, regulation of leaf water balance, and avoidance of turgor loss. However, these correlations raise questions concerning the ultimate sources of variation in these features. It is logical to infer that in species with high wood density, and therefore low k_s , a greater driving force for water movement would be required to sustain rates of photosynthetic gas exchange comparable to those of co-occurring species with lower wood density, but this possible constraint presumably would not prevent a species with high wood density from having a less negative minimum Ψ_L set point than another species with similar wood density growing in a different environment, especially if the opportunity for seasonal partitioning of carbon assimilation exists. Transient release of stored water from wood is also likely to play a role in dampening diel fluctuations in Ψ_L in species with low-density wood because wood saturated water content and density are negatively correlated. Although it is reasonable to suggest that the increased cavitation resistance associated with high wood density is an advantageous feature for plants growing in arid environments, the available data indicate that species with a broad range of wood density co-exist in both arid and humid environments (e.g. Alden 1995; Brown 1997). Thus, despite potential environmental influences, the range of wood density exhibited by a given species is likely to have genetically determined components associated with its intrinsic growth allometry (Enquist et al. 1999, see below) and with architectural features of its root system that influence the magnitude of plant water deficits during xylem element expansion and wall thickening. Regardless of the causes of differences in

wood density among species, this feature constrains physiological options related to plant water economy, leading to broad functional convergence.

Carbon economy and growth

At the leaf level, general relationships among fundamental leaf traits such as photosynthetic capacity and nitrogen content (Field et al. 1983), and photosynthetic capacity and leaf life-span (Chabot and Hicks 1982) have been known for some time. Because much of the work on which these relationships are based has been carried out with individual species or small groups of co-occurring species, the degree to which they are universal has remained uncertain. However, in a recent groundbreaking paper, Reich et al. (1997) demonstrated that universal constraints, or trade-offs, among fundamental leaf traits such as nitrogen content, life-span, photosynthetic capacity and leaf mass per area apply across hundreds of species native to a wide range of biomes from the tropics to tundra. In a subsequent study, Reich et al. (1998) reported that leaf dark respiration rate on a mass basis was also well predicted by leaf nitrogen content on a mass basis, leaf mass per area, and leaf life-span across 69 species native to multiple temperate and tropical biomes. Further analysis of potential biome-specific differences in the slopes and intercepts of relationships among the fundamental leaf traits listed above indicated that although their y-intercepts usually differed, their slopes were similar (Reich et al. 1999). The results of Reich et al. (1997, 1998, 1999) are consistent with those of an earlier global scaling exercise by Schulze et al. (1994) in which global relationships between maximum stomatal conductance ($g_{s,max}$) and leaf nitrogen content, maximum surface conductance and $g_{s,max}$, and maximum surface CO_2 assimilation rate and maximum surface conductance were derived. Taken together, these findings point to convergent evolution among populations that has led to universal relationships among functional traits at the global scale with important implications for interpreting and modeling vegetation properties such as productivity across a broad range of scale.

In a theoretical analysis of the linkages of the function of leaves with their composition and morphology, Roderick et al. (1999a) proposed that the mass of nitrogen per unit mass of liquid is relatively constant within leaves, and that the surface area to volume ratio of leaves is proportional to their liquid content. In a follow-up study (Roderick et al. 1999b), measurements made on a group of 27 species were consistent with these predictions. Furthermore, maximum photosynthetic rate on a liquid volume basis was predicted to increase linearly with the leaf surface area to volume ratio in the same manner for all 27 species.

Consistent with the preceding examples of convergence in regulation of carbon economy at the leaf level, we have observed that CO_2 assimilation and g_s co-vary in a similar manner among nine C_4 grass and dicotyledons

Table 2 List of species for which wood density and diel variation in leaf water potential ($\Delta\Psi_L$) data are plotted in Fig. 5. The values of $\Delta\Psi_L$ reported represent those for sapling to adult field-grown plants experiencing typical rather than extreme soil water status for their habitat type

Species	Family	Wood density (g cm ⁻³)	Source	$\Delta\Psi_L$ (MPa)	Source
<i>Acer negundo</i>	Aceraceae	0.50	Alden (1995)	0.90	Kolb et al. (1997)
<i>Acer saccharum</i>	Aceraceae	0.63	Alden (1995)	1.30	Loewenstein and Pallardy (1998)
<i>Spondias mombin</i>	Anacardiaceae	0.40	Brown (1997)	0.50	Meinzer unpublished data
<i>Annona glabra</i>	Annonaceae	0.51	Zotz et al. (1997)	0.85	Zotz et al. (1997)
<i>Ceiba pentandra</i>	Bombacaceae	0.27	Brown (1997)	0.50	Zotz and Winter (1994)
<i>Pseudobombax septenatum</i>	Bombacaceae	0.14	Simpson and Sagoe (1991)	0.36	Machado and Tyree (1994)
<i>Goupia glabra</i>	Celastraceae	0.70	Brown (1997)	1.50	Granier et al. (1992)
<i>Diospyros sandwicensis</i>	Ebenaceae	0.65	Stratton et al. (2000)	1.30	Stratton et al. (2000)
<i>Acacia greggii</i>	Fabaceae	0.85	http://waynesword.palomar.edu/plsept99.htm	2.10	Nilsen et al. (1984)
<i>Cercidium microphyllum</i>	Fabaceae	0.55	http://waynesword.palomar.edu/plsept99.htm	1.10	Halvorson and Patten (1974)
<i>Eperua falcata</i>	Fabaceae	0.78	Brown (1997)	1.97	Huc et al. (1994)
<i>Proxopis glandulosa</i>	Fabaceae	0.82	Alden (1995)	2.36	Nilsen et al. (1981)
<i>Nothofagus menziesii</i>	Fagaceae	0.51	http://www2.fpl.fs.fed.us/TechSheets/techmenu.html	0.80	Sun et al. (1995)
<i>Quercus alba</i>	Fagaceae	0.71	Alden (1995)	1.50	Ginter-Whitehouse et al. (1983)
<i>Quercus incana</i>	Fagaceae	0.83	http://www.forestworld.com/wow/wowonline_home.html	2.00	Donovan et al. (2000)
<i>Quercus petraea</i>	Fagaceae	0.75	http://www.forestworld.com/wow/wowonline_home.html	1.97	Breda et al. (1995)
<i>Juglans nigra</i>	Juglandaceae	0.51	Alden (1995)	0.85	Ginter-Whitehouse et al. (1983)
<i>Liriodendron tulipifera</i>	Magnoliaceae	0.43	Alden (1995)	0.65	Roberts et al. (1978)
<i>Swietenia macrophylla</i>	Meliaceae	0.44	Brown (1997)	0.50	Barker et al. (2000)
<i>Eucalyptus marginata</i>	Myrtaceae	0.67	http://www2.fpl.fs.fed.us/TechSheets/techmenu.html	1.50	Stoneman et al. (1997)
<i>Metrosideros polymorpha</i>	Myrtaceae	0.51	Stratton et al. (2000)	0.85	Stratton et al. (2000)
<i>Fraxinus excelsior</i>	Oleaceae	0.69	http://www.forestworld.com/wow/wowonline_home.html	1.70	Cochard et al. (1997)
<i>Nestegis sandwicensis</i>	Oleaceae	0.65	Stratton et al. (2000)	1.42	Stratton et al. (2000)
<i>Rhizophora mangle</i>	Rhizophoraceae	0.90	Simpson and Sagoe (1991)	2.50	Melcher et al. (2001)
<i>Nesoluma polynesicum</i>	Sapotaceae	0.61	Stratton et al. (2000)	1.21	Stratton et al. (2000)
<i>Pouteria sandwicensis</i>	Sapotaceae	0.62	Stratton et al. (2000)	1.10	Stratton et al. (2000)
<i>Tectona grandis</i>	Verbenaceae	0.55	Simpson and Sagoe (1991)	1.10	Whitehead et al. (1981)

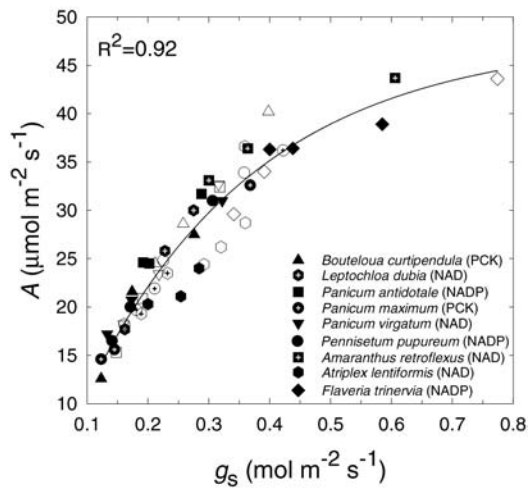


Fig. 6 Relationship between assimilation (A) and stomatal conductance (g_s) for six C_4 grass and three C_4 dicotyledons grown in a glasshouse (lat. $21^{\circ}21'N$) at different levels of salinity (*filled symbols*) and nitrogen (*open symbols*) availability. Measurements were made on attached leaves sealed in the ventilated, thermoelectrically cooled cuvette of a steady-state gas exchange system (PACsys 9900; Data Design Group, La Jolla, Calif.). The CO_2 concentration was maintained at $350 \mu\text{mol mol}^{-1}$, leaf temperature at $30^{\circ}C$, and photosynthetic photon flux density at $1,200 \mu\text{mol m}^{-2} \text{s}^{-1}$. The species represent all three known C_4 biochemical subtypes (*NAD*, *NAD*-malic enzyme, *NADP*, *NADP*-malic enzyme, *PCK*, phosphoenolpyruvate carboxykinase). Meinzer and Zhu (unpublished data)

grown at different levels of salinity and nitrogen availability (Fig. 6). The nine species represented all three known C_4 metabolic subtypes. Besides pointing to highly conserved coupling between g_s and photosynthetic capacity, these results suggest that C_4 species may share common response mechanisms to multiple, and quite distinct, environmental stresses. The relatively low degree of scatter around the regression line in Fig. 6 is partly attributable to the measurements being made under similar leaf chamber environmental conditions with the same instrumentation on plants grown in the same glasshouse. In comparing the results in Fig. 6 with other data in the literature, potential disparities among studies in light and temperature conditions need to be taken into account. Nevertheless, the relationship between assimilation and g_s in Fig. 6 appears to be consistent with that observed for the C_4 dicotyledon *Atriplex triangularis* (Osmond et al. 1980) and the C_4 grass *Bothriochloa caucasia* (Dougherty et al. 1994).

In addition to their relevance for water economy at the whole-plant scale, quarter-power allometric scaling models based on plant mass have revealed striking convergence in the size-dependence of growth. Niklas and Enquist (2001) have demonstrated that annualized growth rates scale as the $3/4$ -power of body mass over 20 orders of magnitude among plant groups that include algae, aquatic ferns, dicotyledons, monocotyledons and conifers. Consistent with this, Enquist et al. (1999) found that growth rate scaled with the $3/4$ power of mass among 45

co-occurring tropical tree species, and species-specific relationships with identical slopes but different intercepts collapsed onto a common line when changes in diameter were normalized by the corresponding values of wood density. In view of the preceding examples of the impact of wood density on several aspects of plant-water relations, the latter finding reinforces the notion that a simple physical property of plant tissue can both determine a suite of plant functional characteristics, and reveal functional convergence among a broad range of species when applied as a normalizing variable. Enquist and Niklas (2001) have extended allometric theory from the whole-plant to the ecosystem scale by showing that, with some exceptions, the number of individuals per unit area scales as the $-3/4$ -power of aboveground biomass.

Conclusions

The preceding examples indicate that simple normalizing variables related to plant size, architecture and tissue biophysical properties could reveal substantial convergence in plant function at multiple scales. However, the existence of widespread functional convergence should not be taken to imply that species do not matter. Although regulation of basic processes related to water and carbon economy may exhibit remarkable convergence, unique attributes related to functions such as reproductive biology and secondary compound production are the rule rather than the exception. Nevertheless, characterizing the trade-offs that determine where individual species operate on multidimensional response surfaces describing their modes of resource acquisition and response to the environment will enhance understanding of their roles and performance in ecosystems. For example, some of the approaches outlined here could improve our understanding of the traits that contribute to the success of invasive species in specific environments and vegetation types, leading to better predictions of their invasive potential under given conditions.

The universal scaling models described in the previous sections are likely to be powerful tools for identifying and understanding broad scale convergence in plant functional relationships. Existing data typically yield exceptionally high linear coefficients of determination ($r^2 > 0.90$) when plotted on log-log plots, but closer inspection of these plots reveals that the range of the dependent variable can be an order of magnitude at a given value of the independent variable. This degree of uncertainty is obviously problematic if the goal is to obtain a precise prediction of plant behavior under specific conditions. However, the tendency for logarithmic plots to obscure significant variability should not be interpreted as a sign that these models are fundamentally flawed or of limited utility. Rather than being an indicator of weakness of the underlying theory, variability of the functional attribute being predicted serves as a useful starting point for identifying and characterizing additional independent axes of variation. Once this is accomplished, the models

can be adjusted appropriately to enhance the reliability of their predictions under specific sets of adequately defined conditions.

The recent findings summarized here strongly suggest that there may be a limited number of physiological solutions to a given problem of plant adaptation to the environment. Comparative ecophysiological studies will therefore benefit from consideration of the constraints that plant anatomical, structural and chemical attributes place on physiological functioning. At a minimum, comparative studies of species responses to the environment should include measurements at more than a single scale, and sufficient information on plant size, allometry and tissue biophysical properties to allow the observed responses and behavior to be normalized. Increased uniformity with regard to measurement protocol and selection of normalizing variables would facilitate meta-analyses of data from independent studies.

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