

Hydraulic limits on maximum plant transpiration and the emergence of the safety–efficiency trade-off

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Summary

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Received: 27 October 2012
Accepted: 27 November 2012

New Phytologist (2013) **198**: 169–178
doi: 10.1111/nph.12126

Key words: hydraulic limitation, safety–efficiency trade-off, soil–plant–atmosphere model, trait coordination, transpiration, vulnerability to cavitation, xylem conductivity.

- Soil and plant hydraulics constrain ecosystem productivity by setting physical limits to water transport and hence carbon uptake by leaves. While more negative xylem water potentials provide a larger driving force for water transport, they also cause cavitation that limits hydraulic conductivity. An optimum balance between driving force and cavitation occurs at intermediate water potentials, thus defining the maximum transpiration rate the xylem can sustain (denoted as E_{\max}). The presence of this maximum raises the question as to whether plants regulate transpiration through stomata to function near E_{\max} .
- To address this question, we calculated E_{\max} across plant functional types and climates using a hydraulic model and a global database of plant hydraulic traits.
- The predicted E_{\max} compared well with measured peak transpiration across plant sizes and growth conditions ($R = 0.86$, $P < 0.001$) and was relatively conserved among plant types (for a given plant size), while increasing across climates following the atmospheric evaporative demand. The fact that E_{\max} was roughly conserved across plant types and scales with the product of xylem saturated conductivity and water potential at 50% cavitation was used here to explain the safety–efficiency trade-off in plant xylem.
- Stomatal conductance allows maximum transpiration rates despite partial cavitation in the xylem thereby suggesting coordination between stomatal regulation and xylem hydraulic characteristics.

Introduction

Transpiration is linked to CO₂ assimilation through gas exchange between stomatal pores on leaves and the atmosphere (Farquhar & Sharkey, 1982). To sustain photosynthesis, water evaporation from leaves must be supplied from the soil through the soil-to-leaf hydraulic system (Hsiao, 1973; Enquist *et al.*, 1998; Brodribb, 2009). Water transport through the soil–plant–atmosphere continuum is driven by the difference in water potential between the atmosphere and the substomatal cavity (often approximated by the vapor pressure deficit). In turn, liquid-phase transport through the xylem causes water potential gradients to develop between the bulk soil and the leaves. When high atmospheric water demand increases transpiration, leaf and xylem water potentials decrease to a point where partial cavitation of the tissues may occur. As a result, steeper water potential gradients develop for a given flow rate. Under such conditions, for leaf water potential to remain sufficiently high to allow leaf functioning, stomatal conductance decreases and transpiration is reduced. Accordingly, cavitation provides a negative feedback (mediated by stomatal conductance) that bounds transpiration (Tyree &

Dixon, 1986; Tyree & Ewers, 1991; Sperry *et al.*, 2002). Changes in leaf area also contribute to control water fluxes, but such changes occur at longer time-scales than stomatal regulation and daily fluctuations in light and vapor pressure deficit (Maseda & Fernandez, 2006). When water potential is close to zero, the driving force causing water movement in the xylem is low, whereas at much more negative water potentials cavitation strongly reduces hydraulic conductance, so that in both cases transpiration is limited. However, as illustrated in Fig. 1, at intermediate values of water potential both driving force and conductance are sufficiently high to sustain a large water flux, thus determining conditions for maximum transpiration (Tyree & Sperry, 1988; Sperry *et al.*, 1998; Meyra *et al.*, 2011).

It might be inferred that plants evolved coordination mechanisms matching controls of stomatal aperture and leaf area development on the one hand and water transport capacity in the xylem (including roots development) on the other hand. We hypothesize that this coordination allows plants to operate near the maximum transpiration rate because using water more effectively would provide a competitive advantage, at least in water-limited ecosystems and when the vapor pressure deficit is high

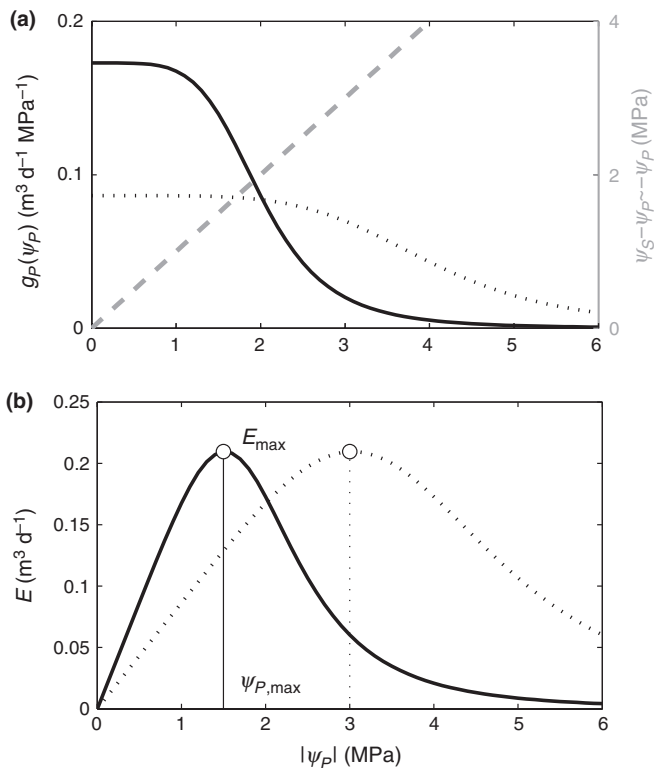


Fig. 1 Emergence of a maximum in transpiration at intermediate xylem water potentials. (a) Driving force for transpiration, expressed as water potential difference between the soil and the canopy ($\psi_S - \psi_P \approx -\psi_P$, gray dashed line) and xylem conductance ($g_P(\psi_P)$, black curves) for two sets of hydraulic characteristics (an efficient plant, solid line; a more conservative plant, dotted line). (b) The product of conductance and driving force results in transpiration $E = g_P(\psi_P)|\psi_P|$ (Eqn 3), which exhibits a maximum at the intermediate water potential $\psi_{P,\max}$ (open circles). In both panels, well-watered conditions are assumed so that ψ_S is much less negative than ψ_P ; $k_S = 1$ and $2 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$, $\psi_{50} = -4$ and -2 MPa (respectively for the more conservative and more efficient species; dotted and solid lines, respectively), $a = 5$, sapwood area $A_S = 0.01 \text{ m}^2$ and tree height $h = 10$ m. All symbols are also defined in Table 1.

(Bejan *et al.*, 2008; Caylor *et al.*, 2009; Guswa, 2010). Even in mesic ecosystems, relatively dry days would require high rates of water transport to keep the leaves hydrated and fully functional, necessitating an efficient water transport system. Moreover, higher rates of transpiration reduce soil moisture faster following a rain event so that in the long term drainage and run-off are decreased and the use of available water by vegetation becomes more efficient (Rodríguez-Iturbe & Porporato, 2004). However, E_{\max} (maximum transpiration rate) is achieved under partial cavitation, raising the question as to whether plants operate near E_{\max} where partial cavitation occurs, or rather prevent water losses from reaching E_{\max} through stomatal regulation, thus maintaining relatively high water potentials and avoiding cavitation (Tyree & Sperry, 1988; Cruziat *et al.*, 2002).

The value of E_{\max} and the corresponding water potential depend on the shape of the xylem conductance–water potential relationship (Fig. 1; conventionally denoted as vulnerability curve). Plant species may be characterized as highly efficient if their saturated hydraulic conductivity (k_S) is high; however, a

xylem that efficiently transports water is often vulnerable to cavitation and its vulnerability curve is characterized by a less negative value of water potential at 50% loss of conductivity (ψ_{50}), as shown in Fig. 1(a) (solid curve). Alternatively, a species may be characterized by a less conductive, more resistant xylem that can more safely withstand cavitation (dotted curve in Fig. 1a). These patterns can be interpreted in terms of a ‘safety–efficiency’ trade-off of the water transport system (Hacke *et al.*, 2006; Meinzer *et al.*, 2010). The first combination of plant characteristics results in relatively high xylem water potentials that should prevent the occurrence of cavitation, while the second combination leads to more negative water potentials that, however, do not lead to substantial conductance loss.

Mechanistically, this trade-off between transport capacity and safety is thought to be caused by different vessel and intervessel pit structures. Hydraulically efficient xylem tends to have larger vessels with more interconnections than a ‘safer’, less efficient xylem. In angiosperms, the intervessel pits are also larger and more porous in hydraulically efficient species, resulting in a higher frequency of large pores that may seed embolism (Hacke *et al.*, 2006; Christman *et al.*, 2009; Lens *et al.*, 2011). In conifers, the more complex geometry of tracheids weakens the relationship between cavitation resistance and hydraulic efficiency (Pittermann *et al.*, 2006, 2012; Willson *et al.*, 2008). In addition, vessels in cavitation-resistant wood are reinforced to avoid implosion, resulting in higher wood density (Hacke *et al.*, 2001; Lens *et al.*, 2011; Pittermann *et al.*, 2012). The broad spectrum of xylem traits and growing conditions affecting the hydraulic properties of wood introduces strong variability in the k_S – ψ_{50} relationship (e.g. lack of trade-off among *Juniperus* species; Willson *et al.*, 2008). Nevertheless, some general patterns seem to emerge: conifers tend to have lower k_S but more negative ψ_{50} than angiosperms (Maherali *et al.*, 2004; Pittermann *et al.*, 2012) and tend to operate at lower xylem water potentials (Meinzer *et al.*, 2009). Within a plant functional group, safety–efficiency trade-offs have been noted across coexisting species, populations, ecosystems and climatic conditions (Hacke *et al.*, 2006; Corcuera *et al.*, 2011; Lens *et al.*, 2011; Fu *et al.*, 2012), as well as in individuals along the hydraulic pathway between the roots and the canopy (Meinzer *et al.*, 2010).

While other plant characteristics, in particular leaf and sapwood areas, affect transpiration (Whitehead *et al.*, 1984; Maseda & Fernandez, 2006), the focus here is on the role of size-independent hydraulic traits (k_S and ψ_{50}) used in determining the maximum rate of individual tree transpiration for a given plant size. Despite differences in these hydraulic traits between hydraulically efficient and hydraulically safe species (solid vs dotted lines in Fig. 1a), similar maximum transpiration rates may be achieved (Fig. 1b). Hence, it could be hypothesized that a safety–efficiency trade-off such that k_S and ψ_{50} are inversely correlated may allow similar peak transpiration rates for a given plant size. In other words, different hydraulic strategies might be functionally equivalent, thus explaining the wide (albeit coordinated) variability in k_S and ψ_{50} that has been observed within the same community (Markestijn *et al.*, 2011; Quero *et al.*, 2011; Fu *et al.*, 2012).

Table 1 Symbol definitions and units

Symbol	Definition	Units
a	Shape parameter of the vulnerability curve (Eqn 4)	–
A_S	Sapwood area	m^2
D	Vapor pressure deficit	mol mol^{-1}
E	Transpiration rate	$m^3 d^{-1}$
E_{\max}	Maximum transpiration (Eqn 7)	$m^3 d^{-1}$
k_P	Xylem hydraulic conductivity	$m^4 \text{MPa}^{-1} s^{-1}$
k_S	Specific conductivity	$\text{kg m}^{-1} \text{MPa}^{-1} s^{-1}$
g	Gravitational acceleration	$m s^{-2}$
g_P	Xylem hydraulic conductance (Eqn 4)	$m^3 \text{MPa}^{-1} s^{-1}$
$g_{P,\max}$	Maximum xylem conductance	$m^3 \text{MPa}^{-1} s^{-1}$
g_S	Stomatal conductance	$\text{mol m}^{-2} s^{-1}$
h	Canopy height	m
H	Total head, $H = \psi_P + \rho g z$	MPa
z	Vertical position	m
α	Ratio of hydraulic path length to vertical position	–
ρ	Density of liquid water	kg m^{-3}
ψ_P	Xylem water potential at the canopy height	MPa
$\psi_{P,\max}$	ψ_P at maximum transpiration (Eqn 5)	MPa
ψ_S	Soil water potential	MPa
ψ_{50}	ψ_P at 50% loss of conductivity (Eqn 4)	MPa

The question that is first addressed is whether individual plants worldwide operate near the maximum rate of transpiration regardless of their ecosystem of origin. Second, we assess whether maximum transpiration is conserved across plant functional types and ecosystems and explore the consequences of a stable maximum transpiration rate in terms of hydraulic safety–efficiency trade-offs. To quantify transpiration, a minimalist model of water flow through plant xylem was employed. As a point of departure from earlier numerical modeling studies of water transport in the soil-to-leaf system (Tyree & Sperry, 1988; Sperry *et al.*, 1998, 2002; Bohrer *et al.*, 2005; Chuang *et al.*, 2006), an analytical representation of the plant hydraulic characteristics (i.e. xylem conductivity and vulnerability curve) is presented based on widely reported hydraulic traits (collected in a database encompassing *c.* 750 data points relative to nearly 550 species or varieties). The simplicity of this approach allows analytical expressions for the maximum rate of transpiration to be derived, thereby facilitating the testing of model predictions against observed peak transpiration rates.

Materials and Methods

A simplified description of transpiration based on Darcy’s law and frequently measured xylem hydraulic characteristics is presented first (see Theory section; symbols are defined in Table 1). This simplified model is used to compute analytically the values of maximum transpiration rate that can be achieved by the plant hydraulic system, which are then compared with independent sap-flow measurements from individuals of different size and species (see Data analysis and parameterization section).

Theory

The water flux through a stem segment, E , can be calculated in analogy to Darcy’s law as (Sperry *et al.*, 1998; Bohrer *et al.*, 2005; Chuang *et al.*, 2006),

$$E = -k_P(\psi_P) \frac{\partial H}{\partial z}, \quad \text{Eqn 1}$$

where $k_P(\psi_P)$ is the sapwood hydraulic conductivity; ψ_P is the water potential in the plant xylem at height z ; H is the total head, computed as $H = \psi_P + \rho g z$ (ρ is the density of liquid water and g is the gravitational acceleration). For analytical tractability, a lumped representation of the soil–plant–atmosphere continuum is adopted here, in which a single value of conductance and a lumped representation of the plant water potential are assumed to be representative of water transport in the whole plant. Following this simplified framework, and neglecting any capacitive effects, the hydraulic gradient $\partial H / \partial z$ is approximated as the difference between hydraulic head at height z and in the bulk soil, divided by the path length, assumed here to be proportional to z (Whitehead *et al.*, 1984; Jones & Sutherland, 1991; Mencuccini, 2003; Novick *et al.*, 2009). This approximation results in

$$E = k_P(\psi_P) \frac{\psi_S - \psi_P - \rho g z}{\alpha z}, \quad \text{Eqn 2}$$

where the proportionality coefficient α is in general larger than unity because the actual hydraulic path from the root tips to the point of cavitation is larger than the vertical distance from the ground.

Because the aim is to quantify the maximum transpiration rate allowed by the plant hydraulic system (regardless of stomatal regulation and atmospheric demand), we focus here on water transport under well-watered conditions so that $|\psi_S| \ll |\psi_P|$, resulting in $\psi_S - \psi_P \approx -\psi_P$. This assumption also implies that the root water potential is much smaller in magnitude than $|\psi_P|$. Hence, for these restricted conditions, only $|\psi_P|$ is the relevant water potential term driving water movement in the soil–plant system. In addition, high rates of transpiration occur at water potentials about one order of magnitude larger (in absolute value) than gravitational potential in trees shorter than *c.* 20 m, as is the case in most datasets used here, so that $|\rho g z / \psi_P| \ll 1$. Finally, it can be assumed that cavitation occurs first in the most distal parts of the plant (Zimmermann, 1978; Tyree & Ewers, 1991; Nardini & Salleo, 2000). This approximation is also consistent with the typical cavitation measurements, which are often performed in young branches near the plant top. Hence, we set $\alpha z \approx h$, where the canopy height h approximates the hydraulic path length between the roots and the canopy (Whitehead *et al.*, 1984; Schäfer *et al.*, 2000; Mencuccini, 2003; Novick *et al.*, 2009). It is important to note that the hydraulic path length is probably longer than the linear distance between the ground and the canopy top owing to roots and branching aboveground. Both this approximation and the assumption of negligible root water potential might lead to overestimated transpiration fluxes. Under

these assumptions, water transport is solely controlled by xylem water potential (the driving force) and xylem properties, which are responsible for the pressure drop along the soil–leaf continuum. Accordingly, the transpiration rate (Eqn 2) can be simplified to

$$E \approx g_p(\psi_p) |\psi_p|, \quad \text{Eqn 3}$$

where the xylem conductance is $g_p = k_p/h$. Because g_p is a decreasing function of xylem water potential ψ_p (see Fig. 1a), the transpiration flux defined by Eqn 3 admits a local maximum (denoted by E_{\max} , Fig. 1b) at an intermediate value of ψ_p , which we denote by $\psi_{p,\max}$. Around this value of water potential, the driving force is sufficient to sustain the water flow but not negative enough to cause substantial cavitation (Sperry *et al.*, 1998; Meyra *et al.*, 2011).

The effect of water potential on plant conductance is typically modeled by reducing the saturated xylem conductance, $g_{p,\max}$, by an empirical factor accounting for the loss of conductivity caused by progressive cavitation (Jones & Sutherland, 1991; Sperry *et al.*, 1998). Among the different (but conceptually equivalent) possible empirical functions, the following inverse polynomial expression is employed here for convenience (Fig. 1a),

$$g_p(\psi_p) = g_{p,\max} \left[1 + \left(\frac{\psi_p}{\psi_{50}} \right)^a \right]^{-1}, \quad \text{Eqn 4}$$

where ψ_{50} represents the xylem water potential at 50% loss of conductivity and a is a shape parameter linked to the sensitivity of xylem conductance to changes in water potential at $|\psi_{50}|$ (i.e. $\partial(g_p/g_{p,\max})/\partial\psi = -a(4|\psi_{50}|)^{-1}$).

The upper bound for transpiration is the maximum theoretical water transport capacity along the soil-to-leaf system, which is computed by imposing $\partial E/\partial\psi_p = 0$ in Eqn 3. The water potential at maximum transpiration is then found as

$$\psi_{p,\max} = \psi_{50}(a-1)^{-\frac{1}{a}}, \quad \text{Eqn 5}$$

at which the maximum transpiration rate is achieved (from Eqn 3),

$$E_{\max} = g_p(\psi_{p,\max}) |\psi_{p,\max}|. \quad \text{Eqn 6}$$

In Eqn 6, the conductance under maximum water transport (at $\psi_p = \psi_{p,\max}$) is computed from Eqn 4 as $g_p(\psi_{p,\max}) = (1 - 1/a)g_{p,\max}$, where $1/a$ is the fractional loss of conductivity under such conditions. Combining Eqns 5 and 6 yields the maximum transpiration rate as a function of plant hydraulic traits,

$$E_{\max} = g_{p,\max} |\psi_{50}| a^{-1} (a-1)^{1-\frac{1}{a}} \quad \text{Eqn 7}$$

Eqn 7 predicts a proportionality of maximum transpiration and the product of saturated xylem conductance and the water

potential at 50% cavitation, indicating that both traits are equally important in defining water transport. The proportionality constant, $a^{-1}(a-1)^{1-\frac{1}{a}}$, varies little (between 0.5 and 0.7), suggesting that the slope parameter a is of secondary importance in the definition of E_{\max} , although it controls the fractional loss of conductivity when transpiration is maximized.

This derivation partly differs from the approach by Sperry *et al.* (1998), who defined the maximum transpiration ('critical transpiration' in their notation) as the water flux on the brink of catastrophic xylem failure. Their maximum transpiration rate is obtained by increasing E up to the critical level and not by changing the water potential as it is done in Eqn 5. From a physical perspective, the vapor pressure deficit drives transpiration at the leaf level, triggering changes in both stomatal conductance and leaf water potential. In the present approach, stomatal conductance is not explicitly modeled, so either E or the water potential in the most distal compartments of the plant can be varied. When E increases above the maximum (critical) value, no water potential can be found that still satisfies Eqn 2 (as shown in Fig. 2b), implying complete xylem dysfunction (Sperry *et al.*, 1998). By contrast, the approach proposed here is based on changes in xylem water potential, so that a transpiration value can always be defined as ψ_p becomes more negative, but its value remains upper-bounded by E_{\max} , at which no catastrophic failure occurs. Instead, transpiration declines smoothly beyond $\psi_{p,\max}$ creating a well-defined plateau (Fig. 1b), similar to the results of Meyra *et al.* (2011). Despite these differences in the mathematical approach, both Sperry *et al.* (1998) and the model proposed here predict a maximum in transpiration rate for moist soil conditions that only varies with xylem properties and plant size.

Data analysis and parameterization

The model is parameterized to describe transpiration of individual trees, which can be compared with typical sap-flow measurements. Published sapwood-specific conductivities, k_S ($\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$), are employed so that the plant maximum conductance can be computed as $g_{p,\max} = k_S A_S / (\rho h)$, where A_S is the sapwood area (m^2), ρ is the density of water (kg m^{-3}), and h is the canopy height (m). Values of sapwood-specific conductivity k_S and of the two parameters of the vulnerability curves (a and ψ_{50}) were obtained from a collection of wood trait data from literature sources, and grouped according to plant functional types (deciduous and evergreen woody angiosperms and conifers) and climate (data sources are listed in the Supporting Information, Table S1). Climate at each site was characterized based on the description in each publication or in few instances using the reported rainfall and temperature or global climate maps. For simplicity, species from riparian areas in dry ecosystems were considered as part of the more mesic biomes for the same thermal regime.

Only estimates of saturated hydraulic conductivity obtained after flushing of the samples (to refill embolized vessels) or vulnerability curves that did not exhibit native embolism were considered (i.e. curves that do not show cavitation at the least negative pressures). Other factors (such as wood sample age) were

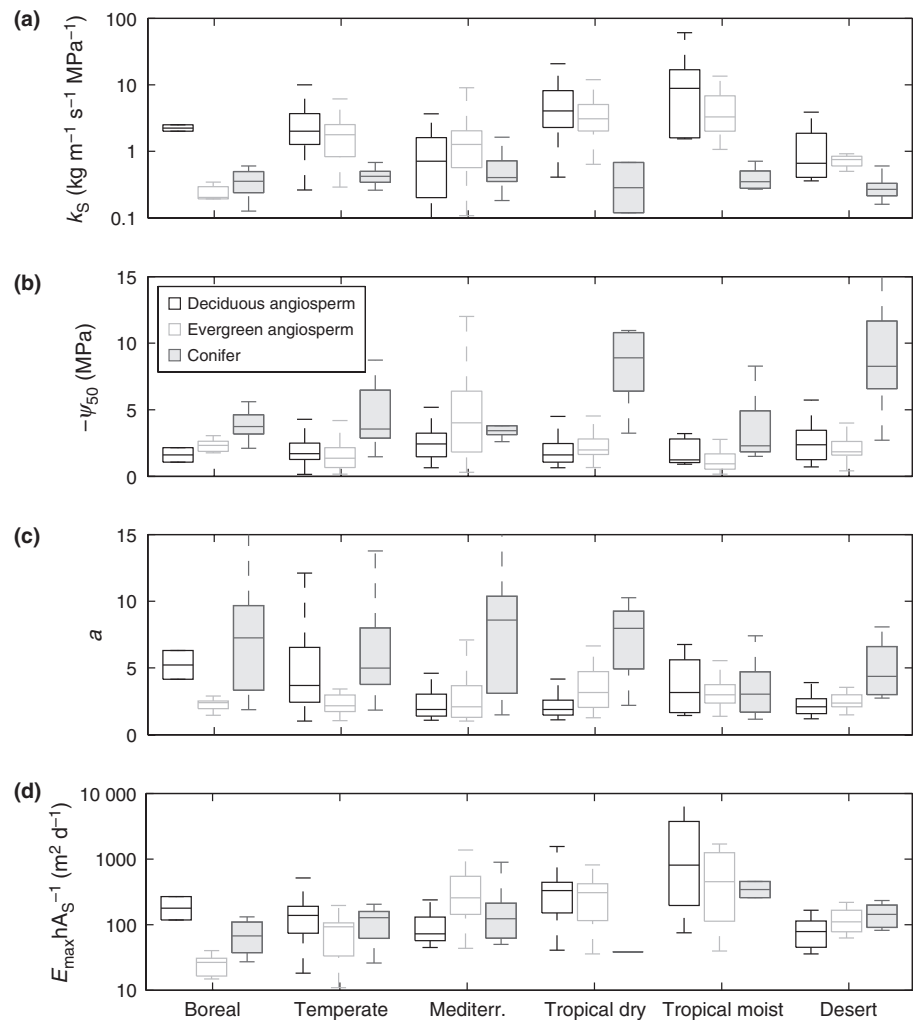


Fig. 2 Hydraulic traits and maximum transpiration rates across climates and plant types. Box plots of (a) sapwood-specific hydraulic conductivity, k_S (used to compute $g_{P,max} = k_S A_S / (\rho h)$), (b) water potential at 50% loss of conductivity, ψ_{50} , (c) shape factor for the vulnerability curve, a , and (d) maximum transpiration (normalized per unit sapwood area and tree height, see Eqn 7, to eliminate the effect of plant size) for all the major biomes and plant types considered. In each box, the central mark indicates the median, the edges indicate the first and fourth quartiles (Q_1 and Q_3), and the whiskers represent the extreme values, computed as $Q_1 - 1.5(Q_3 - Q_1)$ and $Q_3 + 1.5(Q_3 - Q_1)$.

not controlled and might contribute to the variability of the dataset. Vulnerability curves obtained from plants under different treatments (e.g. irrigated vs natural rainfall regime, or transplants in different soils) were considered separately, whereas measurements for the same species, site and treatment, but retrieved on different dates, were lumped into a single vulnerability curve. Where vulnerability curves obtained with different methods were published, we selected the one covering the largest range of water potentials, regardless of method (in all these methodological comparisons differences among approaches were small). Each vulnerability data set was fitted to Eqn 4 by nonlinear least-square regression to obtain a and ψ_{50} . The assembled database encompasses nearly 750 data points (*c.* 550 species and cultivars) spanning all major biomes. The hydraulic trait database is available from the TRY initiative for plant traits (<http://www.try-db.org/TryWeb/Home.php>, see Kattge *et al.*, 2011).

For model evaluation at the scale of an individual tree, published sap flow-based peak transpiration estimates from different biomes and plant types were collected (Table S2). These tree-level transpiration measurements can, in principle, be related to stomatal conductance (e.g. Schäfer *et al.*, 2000; Novick *et al.*, 2009), but because of a lack of environmental and plant data in several of the selected studies we restricted our analysis to water fluxes through

the xylem and only qualitatively refer to the corresponding stomatal conductance values. To ensure well-watered conditions, only sap-flow measurements after rainfall events or from irrigated trees were selected. Maximum transpiration data were either retrieved from the peak values reported in the original publications, or estimated from mean daily fluxes assuming a parabolic daily cycle of 12 h (this specification results in a peak transpiration rate that is *c.* 1.5 times the daily mean value). A perfect match between species used for the sap-flow measurements and species in our database was not always possible. In such cases, we used genus-averaged traits to match at least the genus of the sampled species.

All hydraulic traits and the estimated maximum transpiration rates were log-transformed to preserve normality before statistical analyses. Differences between mean hydraulic traits were tested using *t*-test and unbalanced ANOVA, implemented in MATLAB (MathWorks, Natick, MA, USA). Reduced major axis regressions and confidence intervals for the slope were computed as in Niklas (2006).

Results and Discussion

Before addressing the first question on the occurrence of maximum transpiration, we consider the global patterns in the plant

hydraulic parameters that determine E_{\max} (i.e. k_S , ψ_{50} , and a , see Fig. 2). As already noted (Maherali *et al.*, 2004, 2006; Meinzer *et al.*, 2009; Pittermann *et al.*, 2012), conifers have lower k_S and more negative ψ_{50} than angiosperms ($P=0.05$). Among ecosystems, conifer and angiosperm k_S and ψ_{50} are different ($P=0.05$) in mesic temperate and tropical ecosystems and in deserts (ψ_{50} only in the latter biome). Leaf habit does not show consistent patterns, although in some ecosystems deciduous angiosperms have been found to be more hydraulically efficient than evergreen ones (Fu *et al.*, 2012). A tendency for larger k_S is also apparent in tropical ecosystems, whereas Mediterranean and desert ecosystems generally have low k_S . Patterns in the shape parameter, a , are less clear, but conifers have significantly larger a overall ($P=0.05$). Much of the variability in these traits, however, occurs across species within any ecosystem and plant type, yielding a range of maximum transpiration rates (Fig. 2d).

Using species- and genus-specific hydraulic traits, the theoretical maximum transpiration rates were computed using Eqn 7 for individuals in which peak transpiration had been measured, allowing us to directly address the question of whether plants operate near E_{\max} . The theoretical maximum transpiration reasonably predicts the observed peak transpiration rates over a wide range of plant sizes, species, functional types and climates (Fig. 3a, $R=0.88$, $P<0.001$). The model is unable to precisely predict peak transpiration in each individual because xylem properties and transpiration are generally not measured in the same tree. However, the lack of strong bias in the model predictions suggests that, on average, woody species operate close to the maximum transpiration sustained by their hydraulic system. This result is consistent with a previous study (Tyree & Sperry, 1988), although others have shown that the difference between maximum and actual peak transpiration depends on species and their leaf to root area ratio (Sperry *et al.*, 2002). Note that in Fig. 3(a), plant size (in terms of sapwood area) contributes to the variability and introduces some degree of autocorrelation between measured and modeled rates, but it does not affect model bias. A more stringent test is provided in Fig. 3(b), where measured and

modeled transpiration fluxes per unit sapwood area are compared. Also in this case the theoretical maximum transpiration reasonably captures the measured rates ($R=0.59$, $P<0.001$), with no significant statistical bias (the mean of the residuals is not significantly different from zero at $P=0.05$; see the inset of Fig. 3b). We note, however, that transpiration rates of some boreal species are overestimated, possibly because the vapor pressure deficit during the measurement period was not high enough to allow reaching the theoretical maximum transpiration rates.

The model also predicts that $1/a$ equals the fraction of conductivity lost under maximum transpiration. Hence, larger values of a imply larger losses of conductivity when E_{\max} is reached. Based on this model prediction, loss of conductivity in angiosperms and conifers is estimated, respectively, as *c.* 36% and 22% in well-watered conditions. These values are broadly consistent with typical xylem pressures near $1/3$ of ψ_{50} observed worldwide, indicating substantial cavitation (Meinzer *et al.*, 2009) and are also in agreement with the observation of larger safety margins in conifers than in angiosperms (Meinzer *et al.*, 2009; Johnson *et al.*, 2012). In particular, the estimated loss of conductivity in dry tropical forest angiosperms ($a=3.7$ from Fig. 2c, fractional loss of conductivity $1/a=0.27$) compares well with observations that in this ecosystem xylem water potential under nondrought conditions corresponds to 24–40% cavitation (Meinzer *et al.*, 2008). Furthermore, field measurements of peak ultrasound acoustic emissions (UAE) may also be used to test the prediction that the fractional loss of conductivity equals $1/a$. For example, in *Alnus cordata* ($a=3$), maximum midday UAE occurs at $\psi_p \approx -1.3$ MPa, corresponding to 0.3–0.4 fractional loss of conductivity (Tognetti & Borghetti, 1994), which is in good agreement with the predicted value of $1/a=0.33$ for this species. Hence, based on evidence from different experimental observations, we conclude that, on average, plants achieve peak transpiration rates that are well approximated by the theoretical maximum transpiration sustained by their xylem.

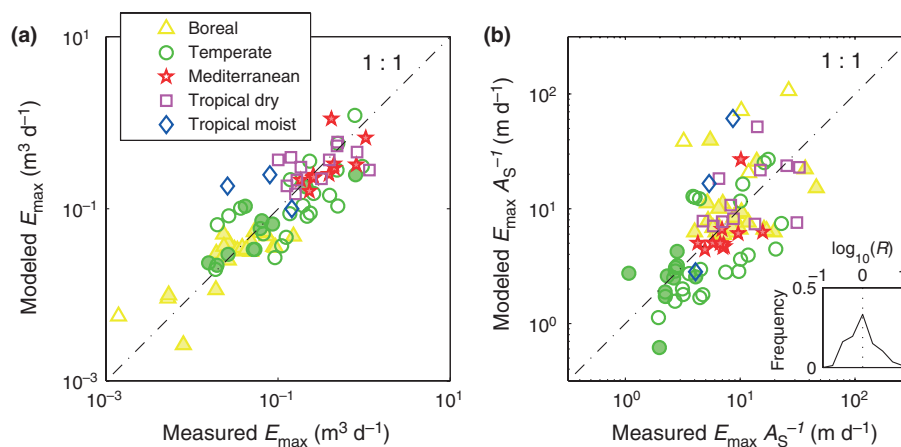


Fig. 3 Test of maximum transpiration hypothesis. Comparison between measured and modeled maximum transpiration (E_{\max} , Eqn 7) expressed as total sap flow of individual trees (a) and sap flow per unit sapwood area (b). The inset shows the frequency plot of the residuals R ; filled and open data points indicate conifers and angiosperms, respectively.

Compared with the large variations exhibited by the individual hydraulic traits that determine E_{\max} (Fig. 2a,c), the theoretical maximum transpiration rate (normalized with respect to plant size) is relatively conserved across plant types, with no significant differences between angiosperms and conifers at $P=0.05$ (Fig. 2d). Earlier studies did suggest that long-term mean transpiration (likely correlated with E_{\max}) may be a ‘conserved’ hydrological variable in a given climate (Roberts, 1983). Here we interpret the low variability in E_{\max} across plant types as a consequence of the trade-off between conductivity and water potential at 50% cavitation. Because E_{\max} is proportional to the product of k_S and $|\psi_{50}|$ (Eqn 7), to sustain a given maximum transpiration rate, a plant can either adopt the combination of high transport efficiency and low resistance to cavitation (i.e. high k_S and low $|\psi_{50}|$), or low efficiency and high resistance (low k_S and high $|\psi_{50}|$), consistent with a safety–efficiency trade-off. This trade-off is also mediated by the slope of the vulnerability curve, through parameter a , although the effect of a on E_{\max} is less important than the effect of $|\psi_{50}|$ (in fact, the factor $a^{-1}(a-1)^{-\frac{1}{a}}$ in Eqn 7 varies much less than $|\psi_{50}|$ across species and climates). In particular, the contrasting hydraulic strategies adopted by angiosperms and conifers lead to similar E_{\max} in any given ecosystems. With regard to climatic effects, tropical moist ecosystems exhibit significantly higher E_{\max} than boreal, temperate and arid ecosystems ($P=0.05$; Fig. 2d). Plants in seasonally dry ecosystems (Mediterranean and tropical) have intermediate E_{\max} , while boreal ecosystems attain the lowest values, consistent with lower average vapor pressure deficit. Angiosperms from Mediterranean and tropical

climates might have developed higher maximum transpiration than plants in colder climates for a number of reasons. Allowing large transpiration in response to high vapor pressure deficit and maximizing fluxes when soil moisture becomes available, while avoiding dry conditions through phenological strategies, are plausible explanations. In tropical dry forests, high efficiency can be achieved by drought-deciduous species that escape the effects of drought by reducing their leaf area (Bucci *et al.*, 2005). By contrast, in arid ecosystems values of E_{\max} are, on average, comparable to more mesic temperate forests (Fig. 2d), possibly because under dry conditions a conservative water-use strategy or drought avoidance might be more advantageous. Accordingly, more efficient water transport systems than in mesic climates would not be required, despite the greater atmospheric demand. These comparisons are based on individual-tree, normalized E_{\max} values; hence, ecosystem-level transpiration fluxes are also mediated by changes in the density of individuals and their size.

If efficiency and safety were perfectly complementary, a constant E_{\max} for a given plant size would be expected. Because maximum transpiration can be expressed as the product of xylem conductivity and xylem water potential at maximum transpiration, $E_{\max} = g_P(\psi_{P,\max})|\psi_{P,\max}|$, a constant E_{\max} would imply that $g_P(\psi_{P,\max}) \approx |\psi_{P,\max}|^{-1}$. Fig. 4 shows that conductance (converted to conductivity units) and water potential are inversely correlated ($R=-0.58$, $P<0.001$), providing statistically significant support for the safety–efficiency trade-off hypothesis (this correlation stems in part from the inverse relationship between k_S and $|\psi_{50}|$ across species; see for example Maherali *et al.*, 2004). However, the slope of the reduced major axis regression, equal to -1.41 ± 0.10 , is significantly steeper than -1 ($P=0.05$), indicating that safety and efficiency do not perfectly compensate each other to sustain maximum transpiration. The reported xylem characteristics allow E_{\max} to range between 0.02 to $1 \text{ m}^3 \text{ d}^{-1}$ for a tree with $A_S/h = 10^{-3} \text{ m}$ (comparable to values reported by Wullschlegel *et al.*, 1998), with boreal conifers and some angiosperms from temperate climates positioned towards the lower end of the range and angiosperms from temperate and tropical forests at the higher end (see also Fig. 2d). Moreover, consistent with the hypothesis that conifers have a more conservative water use and operate at lower ψ_P than angiosperms (Maherali *et al.*, 2004; Meinzer *et al.*, 2009), $\psi_{P,\max}$ tends to be more negative and $g_P(\psi_{P,\max})$ tends to be lower in conifers than in angiosperms.

Our results also suggest a substantial coordination between the plant water supply system (controlled by xylem properties and sapwood area) and water lost from the leaves (set by stomatal conductance, leaf area and air dryness), which allows transpiration to match the maximum theoretical rate in periods of high atmospheric demand. In particular, the consistency between measured and modeled peak transpiration rates implies that at least under well-watered conditions stomata allow partial cavitation to achieve maximum rate of water transport, which is consistent with theoretical studies (Jones & Sutherland, 1991) and empirical evidence (Meinzer *et al.*, 2009). For given leaf and sapwood areas, the rates of water supplied to leaves through the xylem ($E_{\max} \sim g_{P,\max}|\psi_{50}|$, see Eqn 7) and the rate of water loss from

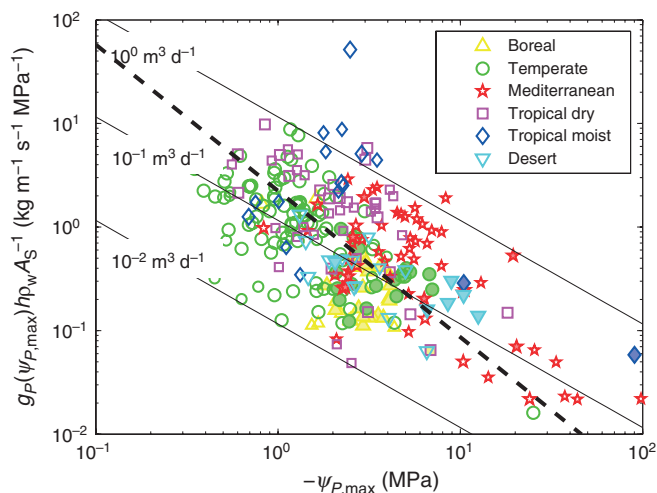


Fig. 4 Scatter plots of conductance ($g_P(\psi_{P,\max}) = (1 - a^{-1})g_{P,\max}$, here converted to conductivity units), and driving force ($\psi_{P,\max} = \psi_{50}(a - 1)^{-\frac{1}{a}}$) when transpiration is maximum ($R = -0.58$, $P < 0.001$). Transpiration per unit sapwood area and unit plant height can be calculated as the product of these two quantities (Eqn 3), so that contours of constant E_{\max} are lines with slope of -1 in this log–log representation (thin lines). Filled and open data points indicate conifers and angiosperms, respectively; for angiosperms, small symbols refer to evergreen species, large symbols to deciduous species. The thick dashed line is a reduced major axis regression of all data points ($y = 2.23|x|^{-1.41}$); numerical values for individual tree transpiration (thin lines) are obtained by assuming $A_S = 0.01 \text{ m}^2$ and $h = 10 \text{ m}$.

the canopy ($E_{\max} \sim g_{S,\max} D_{\max}$, where $g_{S,\max}$ is the canopy-level stomatal conductance and D_{\max} the vapor pressure deficit in conditions of maximum transpiration) can be equated, obtaining the relationship $g_{P,\max} |\psi_{50}| \sim g_{S,\max} D_{\max}$. This proportionality indicates that the coordination between maximum liquid- and gas-phase conductances is also mediated by vulnerability to cavitation and air dryness (this relationship could not be validated because of lack of specific data independent of the sap flow measurements). Coordination among the conductances of different organs has been observed across species (Meinzer, 2002; Mencuccini, 2003; Santiago *et al.*, 2004; Choat *et al.*, 2011; Manzoni *et al.*, 2013), leading to the hypothesis that it may represent an optimal strategy that balances risk of cavitation and efficient water transport.

The coordination between liquid- and gas-phase transport in plants is also supported by coordinated changes across species in the water potential at stomatal closure and at incipient cavitation (Cruiziat *et al.*, 2002; Brodribb *et al.*, 2003). During dry periods, in conservative water users, stomata tightly regulate water losses, whereas in drought-resistant species transpiration is allowed even as leaf and xylem water potentials decrease and cavitation develops. Liquid-phase leaf conductance has also been hypothesized to control water fluxes by acting as a hydraulic valve that reduces transpiration through partial cavitation before other tissues become damaged (Johnson *et al.*, 2011). Similar to stomatal control, this decrease in leaf conductance may improve the water status of the stem and branches by increasing ψ_P . Our results suggest that under well-watered conditions, changes in both stomatal and leaf conductances allow ψ_P to reach values close to $\psi_{P,\max}$, corresponding to some degree of cavitation that primarily depends on the slope of the vulnerability curve (i.e. the fractional loss of conductivity can be estimated by $1/a$).

The proposed model and estimates of maximum transpiration rely on two main assumptions: the capacitance of the transporting tissues is neglected and soil moisture is assumed to be non-limiting for water transport in the root zone. Regarding the first assumption, stem capacitance buffers the fluctuations in water potential of terminal branches and leaves, thus reducing the occurrence of sudden pressure drops that might trigger catastrophic cavitation. As a result, peak transpiration is maintained longer and water potential is less variable in species with higher stem capacitance (Goldstein *et al.*, 1998; Meinzer *et al.*, 2008). Despite these effects of capacitance on the temporal dynamics of transpiration, peak rates do not seem to be significantly affected. When normalizing water fluxes with respect to plant size, peak transpiration appears conserved (Meinzer *et al.*, 2008) or even declines (Goldstein *et al.*, 1998) as size and capacitance increase. Similarly, explicit numerical simulations in which capacitance was considered also suggest that maximum transpiration rates are minimally affected by the dynamics of water storage or capacitance (Bohrer *et al.*, 2005). Hence, we surmise that steady-state flow with no capacitance remains a reasonable assumption when the goal is restricted to computation of maximum transpiration rates rather than the diurnal variations of transpiration.

Relaxing the assumption of high soil moisture, the soil-to-root, xylem and stomatal conductances would decline as the soil dries

between rainfall events, resulting in lowered transpiration rates (Cruiziat *et al.*, 2002; Manzoni *et al.*, 2013). In these conditions, the transpiration that best balances driving force and cavitation is predicted to be lower, but to be attained at more negative water potentials than in well-watered conditions (results not shown). The former prediction is consistent with previous results, whereas the latter is in contrast (Sperry *et al.*, 1998), possibly because of the different mathematical approach adopted here. These transpiration values will be critically affected by the soil–root conductance, which in turn depends on soil moisture, root distribution and soil texture (Hacke *et al.*, 2000; Jackson *et al.*, 2000; Katul *et al.*, 2003; Siqueira *et al.*, 2008), as well as the leaf-to-root area ratio (Sperry *et al.*, 1998, 2002).

In conclusion, a minimalist model of water transport along the soil-to-leaf system was developed to explore whether plants operate close to maximum transpiration rates when soil water is not limiting. The model describes transpiration rate as driven by a water potential difference (i.e. the driving force) and controlled by the transport properties of the xylem (conductivity and vulnerability to cavitation). At intermediate water potentials, the balance between driving force and cavitation induced by steep water potential gradients is optimal and a maximum transpiration rate can be achieved. This maximum transpiration rate can be obtained by both a highly conductive but highly vulnerable xylem and a less conductive but less vulnerable one. Accordingly, species with different xylem hydraulic properties may still achieve a water transport rate that matches atmospheric demand, indicating near-functional equivalence across plant types in a given climate. Overall, model predictions of maximum water fluxes match independent observations, suggesting that plants may have evolved coordinated controls on stomatal conductance and leaf area development, xylem properties and the climatic conditions that set the atmospheric evaporative demand. We surmise that such coordination allows the highest water transport capacity of the xylem tissues. This maximum rate of transpiration is achieved under partial cavitation, suggesting that stomatal regulation may allow some loss of xylem conductivity in well-watered conditions. Coordination between leaf and xylem transport should be further explored to test its occurrence as a potential optimal ecological strategy not only under well-watered conditions, but also under varying water availability.

Acknowledgements

This work was supported by the US Department of Energy (DOE) through the Office of Biological and Environmental Research (BER) Terrestrial Carbon Processes (TCP) program (DE-SC0006967) and NICCR (DE-FC02-06ER64156), the Agriculture and Food Research Initiative from the USDA National Institute of Food and Agriculture (2011-67003-30222 and 2012-68002-19795) and the National Science Foundation (AGS-1102227, EAR-1013339, IOS-0920355, and CBET-1033467). We also thank Hafiz Maherali for sharing his data and three anonymous reviewers for constructive critique.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 List of literature sources for the wood trait database

Table S2 Dataset used to validate the maximum transpiration model

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