Journal of Theoretical Biology 623 (2026) 112391

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

The evolutionary success of angiosperms: a foundation of bioenergetic surplus

Antonio F. Miguel [a,b]

[a] Institute of Earth Sciences, University of Evora, Evora, Portugal
[b] Complex Flow Systems Lab, ICT, Evora, Portugal

A R T I C L E I N F O

Keywords:
Angiosperms
Gymnosperms
Ferns
Plant hydraulics
Evolution
Leaf venation
Plant physiology
Constructal law

A B S T R A C T

The global ecological dominance of angiosperms represents a major evolutionary success. This study suggests that their ascendance is not due to a single trait but to a deeply integrated hydraulic design that maximizes performance and resilience. A model is developed, and based on the constructal law, the leaf vascular architecture of three major plant lineages, angiosperms, gymnosperms, and ferns is compared. The model evaluates performance based on two foundational parameters: the branching exponent which accounts for the supply efficiency, and the vein placement ratio, which controls water distribution.

The results demonstrate that the angiosperm architecture is superior across all modeled metrics. This design minimizes the energetic cost of water transport, ensures uniform water distribution, and enables rapid hydraulic responsiveness. Significantly, the model reveals that this profound efficiency generates a bioenergetic surplus that funds a resilient, redundant vascular network. This fault-tolerant design provides a decisive advantage against physical damage, ensuring that high photosynthetic capacity is a sustained reality rather than a fragile state. It is this synergistic system that provides a quantitative explanation for the enduring global supremacy of angiosperms.

1. Introduction

Angiosperms, or flowering plants, represent a staggering majority of plant life on Earth, comprising over 90% of all known plant species (Joppa, et al. 2011; Zwieniecki and Boyce, 2014; Benton et al, 2022). Their diverse forms, and ubiquitous presence in nearly every terrestrial ecosystem stand in contrast to the more ancient lineages of plants like gymnosperms (conifers, cycads, ginkgo), and ferns, which were the dominant terrestrial flora before the rise of angiosperms.

The fossil record indicates that the first angiosperms appeared in the early Cretaceous period, around 130–140 million years ago (Benton et al, 2022). By the end of the Cretaceous, angiosperms had become the dominant component of most terrestrial floras, a position they have held ever since (Benton et al, 2022). The remarkable success of angiosperms is attributable to a suite of interconnected innovations, both reproductive and vegetative. While their reproductive strategies provided a clear advantage, studies suggest that fundamental changes in their physiology, particularly in their leaves, may be crucial (Zwieniecki and Boyce, 2014).

The most conspicuous feature of angiosperms is the flowers that contain the plant's reproductive organs. Their colors, shapes, and scents have co-evolved with a vast array of pollinators, including insects, birds, and mammals, leading to highly efficient and targeted pollination (Buggs, 2021).

While reproductive features are undeniably important, the vegetative biology of angiosperms, especially their leaves, exhibits unique and highly advantageous traits. The key to this lies in their venation architecture and its connection to their physiology. Angiosperm leaves are characterized by a much higher density of veins compared to those of ferns and gymnosperms (Zwieniecki and Boyce, 2014). This dense network of veins, often forming a complex reticulate pattern, allows for a supply of water to the leaf tissues (Sack and Scoffoni, 2013). While classic models such as the West et al. (1999) framework emphasize metabolic scaling, and pipe-model theories focus on structural support, they often treat vascular architecture as a static consequence of size.

Furthermore, angiosperms uniquely maintain an anatomical arrangement where the distance between veins is not very different from the depth of the veins from the leaf surface (Zwieniecki and Boyce, 2014; Sack and Scoffoni, 2013; Roth-Nebelsick et al., 2001). This precise geometry seems to be the best way to deliver of water across the entire leaf surface, which is crucial for keeping stomata open for CO_2 uptake while minimizing water loss, thus maximizing photosynthetic efficiency

---

E-mail address: afm@uevora.pt.

https://doi.org/10.1016/j.jtbi.2026.112391
Received 4 October 2025; Received in revised form 23 January 2026; Accepted 27 January 2026

(Zwieniecki and Boyce, 2014).

The high vein density and placement in angiosperm leaves allows them to sustain higher rates of transpiration, which is directly linked to higher rates of CO_2 assimilation and photosynthesis (Zwieniecki and Boyce, 2014). This physiological advantage enabled angiosperms to outcompete ferns and gymnosperms, particularly in sunny and open environments where high photosynthetic rates are possible (Zwieniecki and Boyce, 2014). The reticulate venation of angiosperm leaves also provides a high degree of redundancy. If a part of the vein network is damaged, for instance by an herbivore, water can be rerouted through alternative pathways, ensuring that the rest of the leaf remains functional (Zwieniecki and Boyce, 2014). This resilience is also appointed as a factor in the longevity and overall productivity of angiosperm leaves.

Studies have shown that during the early Cretaceous, angiosperm lineages underwent a period of rapid genome reduction, a trend not observed in ferns and gymnosperms (Sack and Scoffoni, 2013; Roth-Nebelsick et al., 2001). This genomic innovation had profound consequences for cell biology and, consequently, for the entire plant's physiology. There is a strong positive correlation between genome size and cell size in plants (Brodribb et al., 2007; Walls, 2011). By downsizing their genomes, angiosperms were able to produce smaller cells. Smaller cells allowed angiosperms to pack more veins and stomata into a given leaf area (Simonin and Roddy, 2018). This is because smaller guard cells (the cells that form stomata) lead to a higher stomatal density, and smaller xylem cells allow for a denser network of veins without displacing photosynthetic tissue (Simonin and Roddy, 2018). The increased density of stomata and veins directly translates to a higher maximum potential for gas exchange, more CO_2 can be taken up for photosynthesis, and more water can be transported to support this process. This physiological boost enabled angiosperms to achieve faster growth rates.

The constructal law is a fundamental principle in physics that provides a unified explanation for the evolution of design in living systems. Its core importance lies in defining evolution and survival in physical terms: for any finite-sized flow system to persist in time (to live), its configuration must evolve to provide ever-easier access for the currents that flow through it (Bejan and Lorente, 2011). Unlike traditional descriptive models that characterize existing geometries, the constructal law serves as a predictive framework to investigate the thermodynamic trade-offs inherent in leaf venation. It identifies the physical direction of evolution by integrating the energetic costs of vascular branching with the distribution efficiency of vein placement into a single bioenergetic framework. By modeling the leaf as a thermodynamic system designed to maximize net carbon flux, this law may uncovers why specific designs, such as the hierarchical venation of angiosperms, are predictable outcomes of a physical law governing flow access rather than random biological occurrences.

This study seeks to explain the dominance of angiosperms in most terrestrial floras in the light of the constructal law. We propose that their evolutionary success is attributable to an optimized architecture as flow systems, which conferred a significant competitive advantage and facilitated their global proliferation.

2. Materials and methods

2.1. The energetic cost of branching design in vascular networks

The branching vessels are found throughout the entire plant. Network of vessels applies to any fluid transport system, including the plant's vascular plumbing (the xylem) from the roots, through the stem, and into the finest veins of the leaves.

Consider a vein of length of radius r_0 splits into two daughter veins of radius r_1 and r_2. For the purposes of this scaling model, we assume symmetrical branching where both daughter vessels possess an equal radius. While asymmetrical branching occurs in nature, this idealized symmetry allows for a clear analytical focus on how the branching exponent (n) dictates the total resistance and metabolic cost of the network. Parent and daughter veins are related by (Miguel, 2024)

$$r_o^n = 2r_1^n \tag{1}$$

Notice that for angiosperm its architecture can be modeled with an exponent $n \sim 3$ (McCulloh et al., 2003), and for gymnosperm and fern the measured exponent is $n \sim 2.7$ (McCulloh and Sperry, 2006) and $n \sim 2.0$ (McCulloh and Sperry, 2005), respectively.

To quantify the metabolic cost of hydraulic transport, we model the total power dissipation (P) across a bifurcating vascular level. While the resistance of a single conduit is governed by the Hagen-Poiseuille law, the total energy required to drive a volume flow (Q) through a branching junction is defined by the work rate necessary to overcome the combined resistance of the hierarchy (Miguel, 2006)

$$P = \frac{Q^2 L}{r_o^4}\left(1 + \frac{1}{2}2^{4/n}\right) \tag{2}$$

where μ is the dynamic viscosity of water, L is the vessel length, Q is the parent volumetric flow rate, and r is the parent radius. The Q^2 term arises because power is the product of the pressure drop and the flow rate ($P = \Delta p\ Q$). By expressing the pressure drop in terms of laminar resistance (RQ), the power dissipation becomes RQ^2. This formulation allows us to isolate how the branching exponent (n) affects the total energetic tax of the network.

Consider now the radius after i generations. The radius of a single terminal vessel is

$$r_i = r_o\left(\frac{1}{2}\right)^{i/n} \tag{3}$$

The total area available for fluid delivery at the end of the network is the number of terminal vessels (2^i) multiplied by the area of a single terminal vessel

$$A_{total,i} = \pi r_o^2 2^{i(1-2/n)} \tag{4}$$

Eq. (4) shows that the total terminal area grows exponentially with the number of branching generations i, but the rate of this growth is determined entirely by the scaling factor in the exponent (1–2/n). If $n > 2$ the total terminal area increases with each branching generation, and if $n < 2$ total terminal area decreases, which is physically inefficient for supplying a volume. If $n = 2$ the total terminal area remains constant, equal to the initial area of the parent vessel.

2.2. A supply-demand framework for stomatal conductance

Consider that the flow system has two coupled components: a) a bifurcating vascular network that transports water from a primary vein (source) through i generations of smaller vessels to a set of terminal venules, and b) the leaf epidermis is divided into small patches or areoles, and each areole is supplied by one terminal venule and contains a population of stomata responsible for gas exchange.

According to the Hagen-Poiseuille equation, the hydraulic conductance of a cylindrical pipe is proportional to its radius to the fourth power, and the radius of a terminal venule after i branching generations is given by Eq. (3), yields

$$K_{ven} = r_o^4\left(\frac{1}{2}\right)^{4i/n} \tag{5}$$

Note that while this relationship represents a physical scaling law, we employ the equals sign to denote a normalized index. By fixing fluid properties, material constants, and baseline path lengths as unity, we transform the scaling proportions into a quantitative framework for comparative analysis. This normalization is applied consistently across all subsequent equations to isolate the geometric influence of the branching exponent (n) and the vein placement ratio (θ) on the relative efficiency of different plant lineages.

The maximum water flow that the venule can deliver is its

$$Q_{\max} = r_o^4 \left(\frac{1}{2}\right)^{4i/n} \Delta\Theta_{leaf} \tag{6}$$

where Q_{max} is the maximum volumetric flow rate (i.e., the total volume of water transported per unit time when the system operates at its peak hydraulic gradient), and Θ_{leaf} is the total water potential drop across the leaf.

If the total leaf area is A_{leaf}, each terminal venule has an areole of area defined by

$$A_{are} = \frac{A_{leaf}}{2^i} \tag{7}$$

where A_{are} is the areole of area

The maximum transpiration rate E_{max} from a single areole is (Monteith and Unsworth, 2013)

$$E_{\max} = k_{sto} \upsilon A_{are} \tag{8}$$

where k_{sto} is the stomatal conductance and υ is the vapor pressure deficit. The maximum transpiration capacity is defined as the total volume of water evaporated per unit leaf area per unit time (mmol m^{-2} s^{-1}). This parameter bridges the internal hydraulic supply (Q_{max}) with the external atmospheric demand. By normalizing transpiration to leaf area, we can evaluate how different vascular architectures (n and θ) support the metabolic requirements of the mesophyll tissue regardless of absolute leaf size.

An efficient design requires that the maximum supply must match the maximum demand $Q_{max} = E_{max}$ (i.e., constructal or maximum access). So, according to Eqs. (5)–(8)

$$k_{sto} \sim \frac{r_o^4}{A_{leaf}} 2^{i(1-4/n)} \tag{9}$$

The crucial term for comparing plant groups is the scaling exponent i (1–4/n). Notice that, for any network with $n < 4$, k_{sto} decreases as the network becomes more complex because the veins are tapering so quickly that the drop in the terminal venule's conductance is more severe than the reduction in the service area. However, the rate of this decrease is minimized when n is as large as possible.

2.3. Balanced resistance and optimal vein placement

Leaf's hydraulic network should supply water to all stomata as uniformly as possible. Uniform water supply prevents areas of the leaf from drying, which would cause stomatal closure and a loss of photosynthetic capacity (Taiz et al., 2015).

The creeping flow of water through the porous mesophyll from the vein to the evaporative surface can be described by the Darcy law. This total path can be divided into two primary resistance components acting in series. The resistance to water flowing upwards from the vein to the epidermal plane (vertical resistance), and the resistance to water spreading out horizontally across the epidermal plane to supply the region furthest from the vein (horizontal resistance). For vertical resistance, the path length is proportional to the vein depth, δ, and the cross-sectional area for this flow is proportional to the inter-vein distance, d (Fig. 1). On the other hand, for the horizontal resistance the path length is proportional to d, and the cross-sectional area for this flow is proportional to the vein depth, δ. As the total resistance is the sum of these two resistances

$$R \sim \frac{1}{\theta} + \theta \tag{10}$$

where θ is the vein placement ratio ($\theta = \frac{d}{\delta}$), d is the inter-vein distance (i.e., the horizontal path length water must travel across the epidermal plane), and δ is the vein depth (i.e., the vertical path length water travels from the vein to the evaporative surface).

To find the minimum of this function (i.e., maximum flow access), we take its first derivative with respect to θ, set it to zero, and confirm that the second derivative is positive. Solving for θ yields $\theta = 1$ and $d = \delta$. The biological significance of the vein placement ratio (θ) lies in its role as a determinant of uniform leaf hydration. When d greatly exceeds δ ($\theta \gg 1$), as seen in many ferns and gymnosperms, horizontal resistance becomes dominant. This creates steep water potential gradients that force stomatal closure and limit carbon gain. Conversely, angiosperms typically maintain an anatomical arrangement where $\theta \sim 1$, ensuring a balanced resistance that maximizes the photosynthetic contribution of the entire leaf surface. This represents a convergent evolutionary target where the hydraulic resistances in both directions are balanced, that is, when the average distance between veins (d) is optimized to match their depth from the evaporative surface (δ).

Deviating from this equality ($d \neq \delta$) has physiological consequences. If plants typically exhibit $d > \delta$, the horizontal resistance is much greater than the vertical resistance, creating a steep water potential gradient across the leaf surface. This gradient causes stomata midway between veins to close under evaporative demand. As a result, large portions of the leaf surface become hydraulically limited and cannot contribute to

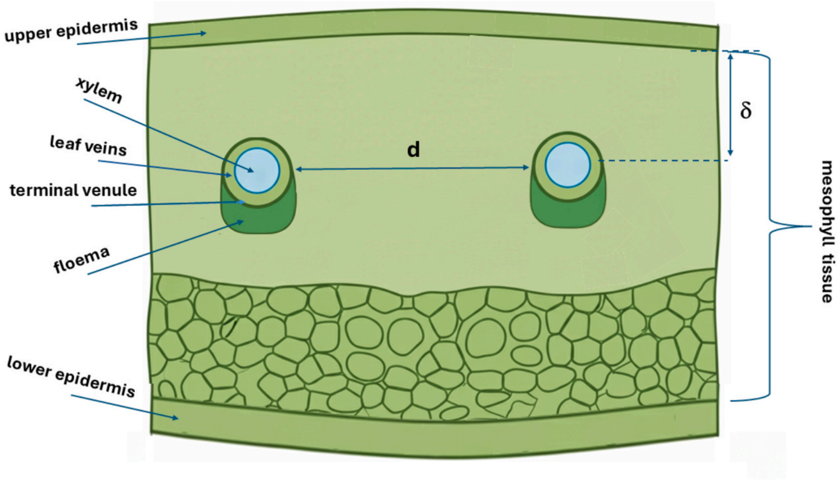

Fig. 1. Leaf hydraulic pathways and vein placement geometry, where total resistance is modeled as the sum of vertical resistance (proportional to vein depth, δ) and horizontal resistance (proportional to inter-vein distance, d) to show that optimal efficiency is achieved when the placement ratio (θ = d/δ) approaches unity, balancing these resistances for uniform water distribution.

carbon gain. Conversely, if vertical resistance were dominant ($d < \delta$), leaf hydraulic conductance would be limited by the thickness of the mesophyll. Consequently, adding more veins (reducing d) would provide no significant hydraulic benefit. This arrangement is not observed in nature.

2.4. Integrating vascular supply and distribution efficiency

A leaf is a thermodynamic system designed to obtain the maximum net carbon flux (Taiz et al., 2015; Nobel, 2009). This requires optimizing two coupled transport processes, the bulk flow of liquid water through the vascular network (hydraulic transport) and the exchange of gases (CO_2 in, H_2O out) through stomata (diffusive transport).

The performance of the leaf is the product of the capacity of the internal network to supply water and the efficiency of the terminal geometry to distribute it

$$k_{sto,\max} \sim \eta k_{sto,\mathrm{supply}} \tag{11}$$

where η is the terminal efficiency which quantifies the uniformity of water distribution at the leaf surface, and $k_{sto,sup}$ is given by Eq. (9).

The terminal efficiency is a normalized value that compares the best possible performance to the actual performance and can be defined as the ratio of the minimum possible resistance (i.e., for the constructal access) to the actual resistance. According to Eq. (10) and as the maximum flow access occurs for $\theta = 1$, we can write

$$\eta = \frac{R_{\min}}{R} = \frac{\left(\frac{1}{\theta}+\theta\right)_{\min}}{\left(\frac{1}{\theta}+\theta\right)} = \frac{2}{\left(\frac{1}{\theta}+\theta\right)} \tag{12}$$

where $R_{\min}$ is minimum flow resistance, and R is the plant actual resistance.

As the total leaf area is supplied by 2^i terminal veins we can write $d = A_{leaf}^{1/2} 2^{-i/2}$, and as veins are not standalone vessels their physical structure is embedded within the leaf's mesophyll tissue (i.e., the scale of its embedding (its depth) would be directly related to the scale of the object itself, its radius $\delta = r_o\, 2^{-i/n}$)and

$$\theta = \frac{A_{leaf}^{1/2}}{r_o} 2^{\left(\frac{1}{n}-\frac{1}{2}\right) i} \tag{13}$$

Then, Eq. (11) can be rewritten as

$$k_{sto,\max} \sim \frac{r_o^4}{A_{leaf}} 2^{\left(1-\frac{4}{n}\right) i} \frac{2}{\frac{1}{\theta}+\theta} \tag{14}$$

According to the constructal law, the design that maximizes the flow access is dependent on n. For $n < 4$, the exponent $(1 - 4/n)$ is negative and means that as the leaf grows more complex (as i increases), the water supply capacity per unit area decreases. To maximize performance, the plant needs to make this negative exponent as close to zero as possible, i.e., having n as large as possible when $n < 4$. The ratio of the distance between veins to their depth (θ) controls the distribution efficiency. This efficiency is maximized when the denominator is minimized, and it occurs when $\theta = 1$. If $\theta > 1$, it leads to greater hydraulic resistance and lower photosynthetic capacity. Analyzing n and θ together reveals the critical trade-offs in leaf design. Notice that, to maximize the net rate of CO2 assimilation, the plant must maximize both terms simultaneously. This means the ideal design combines the most efficient branching network (largest n approaching 4) with the most uniform water distribution geometry. For simple leaves (low number of branching generations i), the efficiency is dominated by the vein placement ratio θ, and $\theta \sim 1$ would perform better. For complex leaves (high i), the exponential term involving n becomes dominant. In this case, the penalty for having a smaller n grows exponentially, making a superior branching pattern more important than an optimal θ.

2.5. Hydraulic architecture and carbon assimilation

The photosynthetic capacity is related with the rate of carbon fixation, which is made possible by the CO_2 acquired through open stomata (Taiz et al., 2015; Nobel, 2009). The net rate of CO_2 assimilation is fundamentally limited by the diffusion of CO_2 into the leaf through the stomata. This can be described by (Taiz et al., 2015; Nobel, 2009)

$$\Omega \sim k_{CO2}\left(C_{amb} - C_{\mathrm{int}}\right) \tag{15}$$

where Ω is the net rate of CO_2 assimilation, C_{amb} is the ambient CO_2 concentration, C_{int} is the intercellular CO_2 concentration, and k_{CO2} is the conductance to CO_2 which is directly proportional to the stomatal conductance for water vapor (Eq. (11)). Thus, to maximize photosynthetic capacity, the plant must maximize its sustainable stomatal conductance that depends on the distribution efficiency and supply capacity. As shown before, the supply capacity depends on the vascular architecture defined by n and i. According to the Hagen-Poiseuille equation, the hydraulic conductance of a single vessel is proportional to its radius to the fourth power, and the radius of a terminal venule after i generations is $r_i = r_o^4\, 2^{-4i/n}$. Then, the total hydraulic conductance of the leaf's terminal vessels (2^i) is the sum of all individual conductance ($\sim r_i^4$) and

$$K_{total} \sim 2^{\left(1-\frac{4}{n}\right) i} r_o^4 \tag{16}$$

Now we combine the Eqs. (11), (12), (15) and (16) that results in

$$\Omega \sim \frac{r_o^4}{A_{leaf}} 2^{\left(1-\frac{4}{n}\right) i} \frac{2}{\left(\frac{1}{\theta}+\theta\right)} \left(C_{amb} - C_{\mathrm{int}}\right) \tag{17}$$

As before, the design that maximize the net rate of CO_2 assimilation is dependent of i and n. The $\theta = 1$ maximize the flow access and the argument that the most uniform water distribution occurs when the average distance between veins is equal to their average depth from the evaporative surface. Angiosperms are observed to uniquely maintain this anatomical arrangement where $\theta \sim 1$, preventing areas of the leaf from drying out and maximizing the photosynthetic contribution of the entire leaf surface. Ferns and gymnosperms typically have $\theta \gg 1$, leading to significant hydraulic limitation and reduced photosynthetic capacity.

For any network where $n < 4$, the exponent $(1 - 4/n)$ will be negative. This means that as the leaf becomes more complex (i.e., as i increases), the supply capacity per unit area inevitably decreases. The goal is to make this decrease as slow as possible. To do this, we must make the negative exponent as close to zero as possible.

2.6. Hydraulic time constant and system responsiveness

Another interesting quantity is the hydraulic time of system responsiveness. Let's define a constant hydraulic time as the product of the total hydraulic resistance and the leaf's hydraulic capacitance

$$\tau_R = R_{total} Z_{leaf} \tag{18}$$

where τ_R is the hydraulic time constant, and Z_{leaf} is the leaf's hydraulic capacitance

The overall performance of the leaf depends on both the vascular supply and the efficiency of water distribution at the terminals. Total resistance is the inverse of the total hydraulic conductance. As mentioned, the net rate of CO_2 (Eq. (17)) is directly proportional to the leaf's effective conductance. Thus,

$$R_{total} = \frac{A_{leaf}}{r_o^4}\left(\frac{1}{\theta}+\theta\right)2^{-1-\left(1-\frac{4}{n}\right)i} \tag{19}$$

The leaf capacitance is proportional to the total surface area of the vein network, which is dominated by the vast number of terminal vessels. According to Eq. (4), we can write

$$Z_{leaf} \sim A_{total,i} = \pi r_o^2 2^{\left(1-\frac{2}{n}\right)i} \tag{20}$$

Substitution of Eqs. (19) and (20) in Eq. (18) yields

$$\tau_R = \frac{\pi A_{leaf}}{r_o^2}\left(\frac{1}{\theta}+\theta\right)2^{\frac{2}{n}i} \tag{21}$$

According to Eq. (21) τ_R has a minimum value when $\theta = 1$. Besides, as θ deviates from 1 (either becoming larger or smaller) increases the hydraulic time constant. A larger branching exponent n results in a smaller hydraulic time constant. Analyzing the parameters n and θ together reveals the critical trade-offs in plant leaf design. For simple leaves (low i) and small differences on n, the efficiency is dominated by the θ. The plant with the optimal $\theta \sim 1$ would likely have a shorter time constant. For complex leaves (high i), the exponential term becomes dominant. The penalty for having a smaller n grows exponentially, makes a much more significant problem. The superior branching pattern becomes more important, and it would likely have a better time constant, even if its θ is not equal to 1.

2.7. *Performance-cost trade-off of network redundancy*

The photosynthetic capacity is related with the rate of carbon fixation, which is made possible by the CO_2 acquired through open stomata (Taiz et al., 2015; Nobel, 2009). Besides, the water lost through stomata to gain CO_2 is controlled by stomatal conductance (Taiz et al., 2015; Nobel, 2009).

Consider that the total hydraulic conductance of a leaf is limited by two major resistances in series: the resistance of the vein xylem and the resistance of the pathways outside the xylem. Thus,

$$\frac{1}{K_{leaf}} = \frac{1}{K_x}+\frac{1}{K_{ox}} \tag{22}$$

where K_{leaf} is the hydraulic conductance of a leaf and K_x hydraulic conductance of the xylem.

The maximum rate of transpiration that the leaf can sustain before suffering from dangerous levels of dehydration (i.e., before leaf water potential drops to a critical point where damage occurs) can be written as (Sperry and Tyree, 1988).

$$E_{trasn,crit} = K_{leaf}(\psi_{steam} - \psi_{crit}) \tag{23}$$

where $E_{trans,crit}$ is the critical transpiration rate the leaf's water supply can support, Ψ_{stem} is the water potential of the stem at the base of the leaf (−0.5 MPa (Brodribb and Cochard, 2009) for a typical water potential of a stem during the day), and Ψ_{crit} is the critical leaf water potential at which stomata are forced to close to prevent hydraulic failure.

This maximum sustainable water flow can be related to the maximum opening of the stomata. The rate of transpiration is proportional to the stomatal conductance and to the dryness of the air (vapor pressure deficit). By assuming that the maximum transpiration rate is determined by the hydraulic limit, the maximum sustainable stomatal conductance can be written as (Monteith and Unsworth, 2013)

$$k_{stomatal,crit} \sim \frac{E_{trans,crit}}{\zeta_{vpd}} \tag{24}$$

where $k_{stomatal,max}$ is the maximum opening of the stomata, and ζ is the vapor pressure deficit (1.5 kPa (Lane and Martin, 2010)).

Photosynthesis is a direct function of how much CO_2 enters the leaf (i.e., of $k_{stomatal,max}$) and the difference of CO_2 concentration the air and inside the leaf. According to Fick's Law of diffusion the maximum photosynthetic capacity is given by (von Caemmerer and Farquhar, 1981).

$$J_{photo,\max} \sim \frac{k_{stomatal,crit}}{1.6}\left(C_{CO2,air} - C_{CO2,in}\right) \tag{25}$$

where $J_{photo,max}$ maximum photosynthetic capacity, $C_{CO2,air}$ is the ambient CO_2 concentration in the atmosphere (420 μmol/mol (Keeling, 2025)), and $C_{CO2,in}$ is the CO_2 concentration inside the leaf ($C_{CO2,in}/C_{CO2,air} \sim 0.7$ (Wong et al., 1979)).

The dendritic network performs the main task of distributing water from the source outwards. This requires energy to build and operate it. Angiosperm plants present also a redundant network. This consists of the additional, cross-linking veins that form loops (anastomoses) and provide robustness and damage control (Taiz et al., 2015; Nobel, 2009). This requires a secondary investment in terms of energy.

Consider that the total energy cost is due to the energy required to build and operate the dendritic network (E_{dend}) and the energy required to build the cross-linking veins that form loops (E_{redun})

$$E_{total} = E_{dend} + E_{redun} \tag{26}$$

where the cost to build the essential dendritic network is given by the product of cost function that represents the efficiency of the branching pattern, and an intrinsic material costs that represent the intrinsic energy cost for a plant to produce its water-conducting tissue (xylem).

Consider that each plant has a fixed, general budget of N units to invest in its leaf venation, and gymnosperms and ferns invest zero in redundancy. So, their entire budget N is consumed by their dendritic network.

The previous analysis shows that the cost function is lowest at the $n = 3$, and considering that

$$E_{dend} = w(|n-3|+1) \tag{27}$$

where w is the intrinsic material costs that represent the intrinsic energy cost for a plant to produce its water-conducting tissue (xylem). Notice that the term $(|n-3|+1)$ represents the design penalty, which is minimized (equal to 1) at the optimal branching exponent of $n = 3$, consistent with the results obtained before, and increases as the architecture deviates from this ideal.

The E_{redun} can be viewed as a fraction of E_{dend} and approached as $E_{redun} = \chi\, E_{dend}$, with χ defined as factor that accounts for an extra cost for their safety. Thus, the net performance index as the photosynthetic return for the total energy investment can be defined as

$$\phi = \frac{J_{photo,\max}}{E_{total}} \sim \frac{\Omega}{E_{total}} = \frac{\frac{r_o^4}{A_{leaf}}2^{\left(1-\frac{4}{n}\right)i}\frac{2}{\left(\frac{1}{\theta}+\theta\right)}}{w(|n-3|+1)(1+\chi)} \tag{28}$$

Eq. (28) shows the net performance index as depending of n, θ and χ.

2.8. *Robustness against damage*

The key advantage of a redundant network is robustness against damage. Therefore, an index that accounts for performance under environmental stress is required to be defined.

The previous section measures performance under ideal conditions, but it is important to evaluate the robustness of a redundant network to damage. To create a more realistic model of plant performance, we quantify the return on investment by measuring the expected photosynthetic output against the total energy cost of building the vein network, defining the following index

$$\phi_{res} = \frac{J_{photo,udm}}{E_{total}} \tag{29}$$

where ϕ_{res} is the resilience performance index and $J_{photo,ud}$ is photosynthetic return under damage.

The expected photosynthetic return represents the average performance of a leaf under the risk of damage. It represents a weighted average of the two possible states for any given section of the leaf: undamaged or damaged. Considering p the damage probability (i.e., likelihood that any part of the leaf's vascular network might fail due to external factors), a fraction of the leaf (1-p), is expected to remain undamaged. In this state, it operates at its maximum potential, which is the critical stomatal conductance (Eq. (24). The remaining fraction of the leaf p is expected to be damaged and its function is reduced. It operates at a fraction of its maximum potential, given by $k_{stomatal,max}$ $f_k(n)$ where $f_k(n)$ is fraction of hydraulic conductance that is retained in a leaf section after a vein is damaged. Notice that it measures the network's ability to continue supplying water to the tissue downstream of a break and is full dependent on the physical architecture of the leaf's vein network. Thus, Eq. (29) can be rewritten as

$$\begin{aligned}\phi_{res} &= \frac{k_{stomatal,crit}\left[1 - p(1 - f_k(n))\right]}{E_{total}} \\ &= \frac{\frac{r_o^4}{A_{leaf}} 2^{\left(1-\frac{4}{n}\right)i} \frac{2}{\left(\frac{1}{\theta}+\theta\right)}}{w(|n-3|+1)(1+\chi)} \left[1 - p(1 - f_k(n))\right] \end{aligned} \tag{30}$$

Eq. (30) accounts for investment in redundancy (χ) and the boost system reliability via $f_k(n)$ allowing to calculate the return on investment when the may damage occur ($p > 0$).

3. Results and discussion

3.1. The bioenergetic foundation

The evolution of plant hydraulic systems is governed by the need to optimize the transport of water from roots to leaves while minimizing the metabolic expenditure required for construction and operation. While the dominance of angiosperms is undoubtedly driven by a suite of reproductive and vegetative innovations, our results suggest that these traits are supported by a foundational hydraulic efficiency. By integrating distinct physical models into a single framework, we can quantify how two foundational architectural traits, the branching exponent (n) and the vein placement ratio (θ), produce a cascading effect that magnifies performance differences across plant lineages. This approach, grounded in constructal law that says that the successful natural systems evolve designs that provide maximum access for the flows passing through them, allows us to analyze and explain the ecological dominance of one of plant lineages.

While other models may describe static hydraulic architectures or metabolic scaling, the constructal law explains the process of design generation, allowing us to quantify the bioenergetic surplus that fuels evolutionary innovations like genome reduction. The main advantage of this approach is its ability to connect foundational physics directly to ecological dominance; however, a limitation is its focus on global system optimization over local cellular variability. By defining success through flow access, this framework provides a physical basis to rank the relative efficiency of diverse lineages, explaining why even subtle improvements in architecture (as seen between ferns and gymnosperms) lead to measurable differences in ecological persistence.

3.2. Comparative energetic constraints and distribution

To provide a clear and quantitative comparison, this analysis utilizes empirically-supported parameters that represent the dominant architectural strategies of each lineage. While basal angiosperms exhibit ancestral traits with $\theta \gg 1$, derived angiosperms (which represent the overwhelming majority of modern species) uniquely maintain an anatomical arrangement where $\theta \sim 1$ (Zwieniecki and Boyce, 2014). For our comparative model, we utilize θ values that reflect the broad ecological archetypes of each group: $\theta \sim 2.5$ for derived angiosperms, $\theta \sim 6$ for gymnosperms, and $\theta \sim 10$ for ferns (Zwieniecki and Boyce, 2014; Brodribb et al., 2007). While ferns exhibit significant architectural diversity, the higher θ values observed in many ancestral designs impose the hydraulic limitations discussed in the following sections.

The branching exponent (n) is decisive in determining the energetic tax or operational expense of the plant's hydraulic pump. Each plant group is fundamentally constrained by its unique hydraulic architecture. To provide a clear and quantitative comparison, this analysis will use the following empirically-supported parameters: angiosperms exhibit a $n \sim 3$ (McCulloh et al., 2003) and θ typically ranging between 1.5 and 4 (Brodribb et al., 2007; Zwieniecki and Boyce, 2014); gymnosperms show a $n \sim 2.7$ (McCulloh and Sperry, 2006) and θ ratio typically between 5 and 15 (Brodribb et al., 2007; Zwieniecki and Boyce, 2014); and ferns possess the evolutionarily oldest design with $n \sim 2$ (McCulloh et al., 2003) and a θ value consistently greater than 10. Using these values, $n = 3$ and $\theta = 2.5$ for angiosperms, $n = 2.7$ and $\theta = 6$ for gymnosperms and $n = 2$ and $\theta = 10$ for ferns (Zwieniecki and Boyce, 2014; Brodribb et al., 2007), we analyze how these traits cascade into advantages in cost, capacity, and resilience. These values serve as the primary inputs for calculating the energetic and hydraulic indices presented in Table 1.

The data in Table 1 illustrates that the angiosperm architecture yields the lowest possible energetic cost and the most uniform distribution geometry. In the following sections, we analyze how these fundamental differences cascade into major advantages regarding photosynthetic capacity, system responsiveness, and long-term resilience.

To isolate the hydraulic consequences of network architecture, our comparative analysis focuses on the scaling effects of the branching exponent (n) and the vein placement ratio (θ). Other physiological parameters, such as leaf area (A_{leaf}) and intrinsic material costs (w), are treated as baseline constants to ensure that observed differences in performance indices are a direct result of the integrated vascular geometry rather than species-specific size variations.

This evolutionary success begins at the most basic constraint on any living organism, the constructal flow access that impacts the energy budget. The model of energetic cost quantifies the raw operational expense of the hydraulic pump, a baseline tax on a plant's resources (Eq. (2). Here, the branching exponent n is decisive. The angiosperm value of $n \sim 3$ yields the lowest possible cost factor of 2.26. This represents a design that has evolved to move water with maximal energetic efficiency. In contrast, the designs of ferns ($n = 2$, cost $= 3.0$) and gymnosperms ($n = 2.7$, cost $= 2.40$) impose a permanent energetic tax on their physiology.

It is important to note that the physical architecture defined by n and δ does not act in isolation from the internal anatomy of the conduits. The

Table 1
Bioenergetic and hydraulic performance indices for major plant lineages, summarizing the fundamental branching (n) and distribution (θ) parameters used to model energetic cost, flow resistance, and system responsiveness across evolutionary archetypes.

Parameter / Index	Angiosperms	Gymnosperms	Ferns
Branching Exponent (n)	3.0	2.7	2.0
Vein Placement Ratio (θ)	2.5	6.0	10.0
Cost Factor P (from Eq. (2)	2.26	2.40	3.0
Flow Resistance (R) (from Eq. (10)	2.9	6.17	10.1
Time constant (τ_R) (from Eq. (18)	$\sim 2.9 \times 2^{0.67i}$	$\sim 6.17 \times 2^{0.74i}$	$\sim 10.1 \times 2^{i}$

transition from the high-resistance tracheids found in ferns and gymnosperms to the wide, efficient vessel elements of angiosperms is a primary anatomical driver of hydraulic capacity. Within our framework, this anatomical evolution can be viewed as the structural mechanism that allows angiosperms to achieve the high-performance branching exponent $n \sim 3$. While gymnosperms and ferns are often constrained by the higher resistance of tracheids, the lower-resistance vessels of angiosperms permit a more efficient tapering logic, reducing the overall energetic tax on the plant's hydraulic pump.

While some studies suggest that ferns can achieve a branching exponent of $n \sim 3$ within individual vascular bundles (McCulloh and Sperry, 2005), they remain limited by a lack of hierarchical network integration. More importantly, the ecological success of a lineage is not determined by a single parameter in isolation. As shown in Table 1, gymnosperms possess a lower branching exponent ($n \sim 2.7$) than the theoretical ideal due to the dual role of tracheids in providing both hydraulic transport and mechanical support (McCulloh and Sperry, 2006). However, gymnosperms significantly outperform ferns because of their superior vein placement ratio ($\theta \sim 6$ vs. $\theta > 10$). This suggests that the evolutionary step up from ferns to gymnosperms was driven primarily by improvements in distribution geometry (θ), whereas the leap to angiosperm dominance required the simultaneous optimization of both n and θ.

Beyond this baseline operational cost, efficient design must also master the geometry of delivery. The model of balanced resistance assesses the effectiveness of this final, critical step (Eq. (10). The extremely high resistance values for ferns ($\theta = 10$, $R = 10.1$) and gymnosperms ($\theta = 6$, $R = 6.17$) indicate a deeply damaged geometry that creates hydraulic deficit locations within the leaf, rendering large portions photosynthetically useless. The lower resistance of angiosperms ($\theta = 2.5$, $R = 2.9$) ensures a much more uniform hydraulic landscape, allowing the entire leaf surface to operate as a cohesive, productive system. Consequently, according to the principle of balanced resistance, adding more veins beyond the point where $\theta \sim 1$ provides diminishing hydraulic benefits for water distribution. This equilibrium represents the convergent evolutionary target for the majority of derived Eudicots (broad-leaved angiosperms). However, functional distinctions exist within the angiosperm clade, particularly regarding high-productivity Monocots. While Eudicots converge on geometric balance, C4 grasses (e.g., *Andropogon gerardii*) frequently exhibit $\theta < 1$. This deviation does not represent hydraulic inefficiency but rather a specialized adaptation: the extremely high vein densities are required to support specialized Kranz anatomy and rapid phloem loading (Ocheltree et al., 2014). Thus, while Eudicots optimize for the construction-distribution balance of $\theta \sim 1$, these specialized Monocots prioritize minimized diffusion distances ($\theta < 1$) to sustain maximum carbon flux.

3.3. The bioenergetic surplus and resilience

The efficiency of the primary vascular network generates a bioenergetic surplus that permits high-risk evolutionary innovation. These foundational efficiencies in cost and geometry are not independent features. They unite to determine the leaf's integrated performance and its final ecological output. The model for carbon assimilation (Ω) connects the architecture directly to the leaf's primary purpose that is to growth (Eq. (15). The key insight is that performance is a product (not a sum) of supply and distribution efficiency. Consequently, the limitations of ferns in both n and θ cause a multiplicative breakdown of their photosynthetic potential, while the angiosperm's superiority in both areas results in a superior rate of carbon fixation. However, in nature, a very dynamic system power is not sufficient without agility. The hydraulic time constant (τ_R) model illustrates the understanding of a plant's adaptability (Eq. (18). The long-time constants of ferns ($\tau \sim 10.1 \times 2^{i}$) and gymnosperms ($\tau \sim 6.17 \times 2^{0.74i}$), comparing with angiosperms ($\tau \sim 2.9 \cdot 2^{0.67i}$), imply slow, unresponsive systems. Angiosperms by minimizing both resistance and capacitance, possess an agile system that allows them to efficiently manage the constant trade-off between gaining carbon and losing water, a crucial advantage in fluctuating environments.

This analysis, culminating in a design that is both powerful and agile, leads to the final and most essential aspect of the angiosperm strategy, its optimization for long-term viability. The performance-cost model shows that the supreme efficiency of the angiosperm's primary network ($n = 3$) generates a bioenergetic extra (Eq. (28)). It is precisely this extra that funds their most decisive adaptation, the resilience. The final model of robustness against damage is critical for explaining long-term dominance (Eq. (30)). The dendritic networks of ferns and gymnosperms are inherently fragile, lacking redundancy, any localized damage from herbivores (near certainty with rates around 7–10% (Turcotte et al., 2014)) results in catastrophic failure for all downstream tissue. In contrast, angiosperms invest their surplus in a redundant, meshed network. This design provides fault tolerance, acting as a form of biological insurance that allows water to be rerouted around damage. This ensures that the leaf's high photosynthetic potential is not fragile but a sustained reality.

A large genome carries a high metabolic cost (Lynch and Marinov, 2015). While reducing it offers permanent energy saving, the evolutionary process itself is risky. The bioenergetic surplus is the critical factor that permits evolutionary innovation (Lane and Martin, 2010). A fern or gymnosperm, operating on a tight energy budget, cannot afford the risk. So, they are trapped to pay the high maintenance cost of their genomic factory. The angiosperm, as mentioned, has a surplus capital from its superior hydraulics network (n and θ), and could afford to take this risk. Thus, the constructal values of n and θ provide the permission slip from evolution. They evolved with freedom to provide easier and greater access to what flows in different conditions. This means that they create a state of profound capital security and resilience, that seems to be the one and only condition under which the high-risk, high-reward strategy of genome reduction becomes viable.

All this contributes to the dominance of angiosperms. It is not the result of a single trait but of an integrated collection of co-evolved optimizations that align perfectly with constructal law. They provide a cascading advantage: a low-cost, efficient blueprint enables superior photosynthetic output and agility, and the economic surplus generated allows for a crucial investment in a resilient, fault-tolerant structure. It is this complete, multi-layered evolution in direction of easier access to what flows that creates a system that is powerful, efficient, responsive, and robust, and provides the essence for their supremacy over the global landscape.

3.4. Limitations of the model

While the present model identifies fundamental bioenergetic scaling laws, it relies on several simplifying assumptions that warrant discussion. First, the vascular network is modeled as a series of bifurcating vessels. While real leaves exhibit complex branching and looping, this dendritic framework captures the primary energetic costs associated with hierarchical fluid transport. Second, we assume that water delivery to the mesophyll occurs predominantly via terminal venules. While leakage from higher-order veins exists, the terminal vessels represent the vast majority of the network's surface area and the primary site of distribution efficiency. Third, the goal of uniform water distribution is presented as the constructal ideal for maximizing carbon gain. We acknowledge that phenomena such as stomatal patchiness represent biological responses to heterogeneous stress that fall outside this steady-state optimization. Similarly, while the model identifies $n \sim 3$ and $\theta \sim 1$ as the constructal targets, not all successful angiosperms follow this specific framework. High-productivity lineages, such as C4 grasses, may exhibit $\theta < 1$ to support specialized Kranz anatomy (Ocheltree et al., 2016). The model's strength lies in identifying the global system optimization toward which derived angiosperms have converged, rather than accounting for every instance of local cellular variability.

Finally, for the purpose of quantifying bioenergetic trade-offs, we assume zero investment in redundancy for ferns and gymnosperms. While these lineages may possess localized loops, they lack the ubiquitous, hierarchical mesh found in angiosperms, which provides the unique resilience and damage-control capacity discussed in this study. This model also clarifies the comparative success of non-angiosperm lineages. Although ferns represent an older evolutionary template, they possess a more primitive branching exponent (n ~ 2.0) and an inefficient vein placement ratio (θ ~ 10.0), resulting in a flow resistance (R ~ 10.1) significantly higher than that of gymnosperms (n ~ 2.7, θ ~ 6.0, R ~ 6.17). This confirms that gymnosperms follow the hydraulic template for efficiency more closely than ferns, providing a physical basis for their greater relative success.

This bioenergetic framework is well-exemplified by the genus Psilotum, which belongs to the fern lineage (Monilophytes). Consistent with the ancestral hydraulic template (McCulloh and Sperry, 2005), Psilotum exhibits a dichotomous branching architecture characterized by an exponent of n ~ 2.0, rather than the constructal ideal of n ~ 3. Furthermore, it operates with a high resistance distribution geometry that fails to achieve the optimal vein placement ratio of θ ~ 1 observed in derived angiosperms. Crucially, Psilotum lacks the reticulate (looping) vein networks found in angiosperms (Schulte et al., 1987), meaning it lacks the robustness against damage required to mitigate hydraulic failure, further constraining its ecological dominance.

4. Conclusion

The global dominance of angiosperms is a direct consequence of an integrated and deeply synergistic design that perfectly embodies the principles of constructal law. Their success is not the result of a single superior trait, but of a cascade of co-evolved optimizations in order to easier access to what flows. At its core, the angiosperm leaf is built upon a foundation of profound efficiency. Its vascular architecture, defined by an optimal branching exponent (n ~ 3) and vein placement ratio (θ ~ 1), minimizes the costs of both construction and operation.

This hydraulic efficiency provides the bioenergetic foundation for superior photosynthetic power and the agility required to thrive in dynamic environments. Furthermore, the freedom to evolve designs that maximize flow access does more than just enhance peak performance, it builds systemic resilience. The bioenergetic surplus generated by its efficient primary network funds a meshed, reticulate system of minor veins. This redundancy provides critical fault tolerance and serves as a form of biological insurance against environmental damage.

While this architecture represents an additional construction cost, the payoff is enormous, ensuring that high performance is a sustained reality rather than a fragile state. This integrated strategy creates a system that excels in ideal conditions and endures over the long term. Ultimately, it is this total superiority in maximizing and sustaining the access of flows (water, carbon, and energy) that explains the unparalleled success of angiosperms across the global landscape. By serving as a foundational driver, this constructal design provided the bioenergetic capital necessary for the lineage to develop the reproductive and vegetative advantages that define their unparalleled success and enduring reign across the Earth.

CRediT authorship contribution statement

Antonio F. Miguel: Writing – review & editing, Writing – original draft, Validation, Resources, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

The author declares that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

Bejan, A., Lorente, S., 2011. The constructal law and the evolution of design in nature. Phys. Life Rev. 8, 209–240.

Benton, M.J., Wilf, P., Sauquet, H., 2022. The Angiosperm terrestrial revolution and the origins of modern biodiversity. New Phytol. 233, 2017–2035.

Brodribb, T.J., Cochard, H., 2009. Hydraulic failure defines the recovery and point of death in water-stressed conifers. Plant Physiol. 49, 575–584.

Brodribb, T.J., Feild, T.S., Jordan, G.J., 2007. Leaf maximum photosynthetic rate and venation are linked by hydraulics. Plant Physiol. 144, 1890–1898.

Buggs, R.J.A., 2021. The origin of Darwin's "abominable mystery". Am. J. Bot. 108, 22–36.

Joppa, L.N., Roberts, D.L., Pimm, S.L., 2011. How many species of flowering plants are there? Proc. Biol. Sci. 278, 554–559.

Keeling, C.D., 2025. The Keeling Curve. Scripps CO_2 Program, Scripps Institution of Oceanography. https://keelingcurve.ucsd.edu.

Lane, N., Martin, W., 2010. The energetics of genome complexity. Nature 467, 929–934.

Lynch, M., Marinov, G.K., 2015. The bioenergetic costs of a gene. Proc. Natl. Acad. Sci. 112, 15690–15695.

McCulloh, K.A., Sperry, J.S., 2005. The evaluation of Murray's law in *Psilotum nudum* (Psilotaceae), an analogue of ancestral vascular plants. Am. J. Bot. 92, 985–989.

McCulloh, K.J., Sperry, J.S., Adler, F.R., 2003. Water transport in plants obeys Murray's law. Nature 421, 939–942.

McCulloh, K.A., Sperry, J.S., 2006. Murray's law and the vascular architecture of plants. In: Herrel, A., Speck, T., Rowe, N.P. (Eds.), Ecology and Biomechanics. Boca Raton, FL, USA, CRC Taylor & Francis, pp. 85–100.

Miguel, A.F., 2006. Constructal pattern formation in stony corals, bacterial colonies and plant roots under different hydrodynamics conditions. J. Theor. Biol. 242, 954–961.

Miguel, A.F., 2024. Low dissipative configuration in flow networks subject to constraints. Physica D 467, 13426.

Monteith, J.L., Unsworth, M.H., 2013. Principles of Environmental Biophysics, fourth ed. Academic Press.

Nobel, P.S., 2009. Physicochemical and Environmental Plant Physiology, fourth ed. Academic Press.

Ocheltree, T.W., Nippert, J.B., Prasad, P.V., 2016. A safety vs efficiency trade-off identified in the hydraulic pathway of grass leaves is decoupled from photosynthesis, stomatal conductance and precipitation. New Phytol. 210, 97–107.

Ocheltree, T.W., Nippert, J.B., Prasad, P.V.V., 2014. Stomatal responses to changes in vapor pressure deficit reflect tissue-specific differences in hydraulic conductance. Plant Cell Environ. 37, 132–139.

Roth-Nebelsick, A., Uhl, D., Mosbrugger, V., Kerp, H., 2001. Evolution and function of leaf venation architecture: a review. Ann. Bot. 87, 553–566.

Sack, L., Scoffoni, C., 2013. Leaf venation: structure, function, development, evolution, ecology and applications. New Phytol. 198, 983–1000.

Simonin, K.A., Roddy, A.B., 2018. Genome downsizing, physiological novelty, and the global dominance of flowering plants. PLoS Biol. 16, e2003706.

Sperry, J.S., Tyree, M.T., 1988. Mechanism of water stress-induced xylem embolism. Plant Physiol. 88, 581–587.

Schulte, P.J., Gibson, A.C., Nobel, P.S., 1987. Xylem anatomy and hydraulic conductance of *Psilotum nudum*. Am. J. Bot. 74, 1438–1445.

Taiz, L., Zeiger, E., Moller, I.M., Murphy, A., 2015. Plant Physiology and Development, sixth ed. Sinauer Associates, Sunderland.

Turcotte, M.M., Davies, T.J., Thomsen, C.J., Johnson, M.T., 2014. Macroecological and macroevolutionary patterns of leaf herbivory across vascular plants. Proc. R. Soc. B 281, 20140555.

von Caemmerer, S., Farquhar, G.D., 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta 153, 376–387.

Walls, R.L., 2011. Angiosperm leaf vein patterns are linked to leaf functions in a global-scale data set. Am. J. Bot. 98, 244–253.

West, G.B., Brown, J.H., Enquist, B.J., 1999. A general model for the structure and allometry of plant vascular systems. Nature 400, 664–667.

Wong, S.C., Cowan, I.R., Farquhar, G.D., 1979. Stomatal conductance correlates with photosynthetic capacity. Nature 282, 424–426.

Zwieniecki, M.A., Boyce, C.K., 2014. Evolution of a unique anatomical precision in angiosperm leaf venation lifts constraints on vascular plant ecology. Proc. R. Soc. B 281, 20132829.