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Physical Limits to Leaf Size in Tall Trees

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Leaf size in angiosperm trees vary by more than three orders of magnitude, from a few mm to over 1 m. This large morphological freedom is, however, only expressed in small trees and the observed leaf size range declines with tree height, forming well-defined upper and lower boundaries. The vascular system of tall trees that distributes the products of photosynthesis connects distal parts of the plant and forms one of the largest known continuous microfluidic distribution networks. In biological systems, intrinsic properties of vascular systems are known to constrain the morphological freedom of the organism. We show that the limits to leaf size can be understood by physical constraints imposed by intrinsic properties of the carbohydrate transport network. The lower boundary is set by a minimum energy flux, the upper boundary by a diminishing gain in transport efficiency.

The diversity in size, form and shape in the biological world is stunning, but limits to design freedom imposed by both intrinsic and extrinsic biophysical constraints are known to exist [1, 2]. Intrinsic constraints are determined by organism specific biological and morphological properties including cellular membrane properties, metabolic activity, and organism size and topology. Extrinsic constraints are set by the physical structure of the universe in which the plant lives and evolves; gravity, the strength of molecular bonds, viscosity, surface tension as well as environmental conditions such as solar radiation, wind, temperature, humidity, water, and nutrient availability. In the most forgiving environments, the limits to morphological diversity will be determined primarily by the intrinsic properties of the organism. Although such limits are common across the biological world [1, 3], only rarely are they discussed in the context of plants.

To support respiration and growth, plants continuously exchange materials and energy with their environment and distribute these across the plant body [4, 5]. Energy production in terrestrial plants is dominated by chlorophyll-based photosynthesis, and the process is primarily bound within leaves that must be exposed to sunlight to fulfill their function. The simple goal of light capture should favor large, flat leaves but constraints related to supporting the weight of the individual leaf as well as the entire tree crown [2], resisting winds [6], and lifting water [4], might limit their size and lead to variation in leaf size among different species (Figs. 1 and 2). Tall trees can have a competitive edge in the struggle to expose leaves to light, but trees with record heights (*Eucalyptus regnans* – 100 m, *Petersianthus quadrialatus* – 96 m or *Allantospermum borneense* – 90 m) are only found in environments characterized by the optimum conditions of closed canopy tropical rain forest where wind and water stress is minimal. In these environments, no extrinsic forces should limit leaf size. Remarkably, we find that leaf length in the tallest angiosperm trees is limited to a narrow range of 10–20 cm covering only a small portion

of the leaf sizes observed among trees in general (Fig. 2). We thus seek to explain this surprising decline in leaf size diversity with increasing tree height.

Lamina length of leaves l is highly variable among angiosperm tree species and varies from a few mm to over 1 m [7] (Figs. 1 and 2, Supplemental Material). The distribution shown in Fig. 2 is based on botanical descriptions covering 1925 species from 327 genera and 93 families. For each species, the data consist of a reported tree height h and range of leaf lamina length l , shown as the longest (\triangle) and shortest (∇) in Fig. 2. Lamina length of leaflets were used in the case of compound leaves. The data set includes almost all described native woody plant species from Sabah and Sarawak in Southeast Asia [8], one of the most diverse forest regions of the world, and major tree species from Australia and North America including the tallest recorded angiosperm tree species of the World.

A noticeable drop in variability at both ends of the leaf



FIG. 1. (Color online) Examples of leaf size variability. Typical leaf lamina length l (indicated by arrows) for a group of trees of height $h \leq 30$ m growing in North America. Leaf size varies from 3 cm in *Ulmus parvifolia* (Lacebark Elm) to 60 cm in *Magnolia macrophylla* (Bigleaf magnolia). For compound leaves (left), leaflet length was used (dashed arrow). See the Supplemental Material Fig. 1 for a complete list of species in the figure.

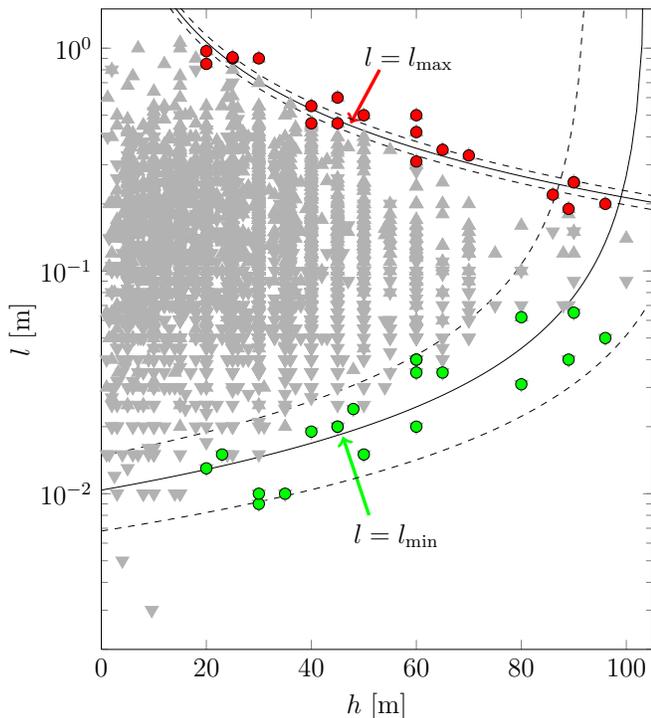


FIG. 2. (Color online) Variation in leaf size l with tree height h based on botanical data covering 1925 species from 237 genera and 93 families, see Supplemental Material Table I. Gray triangles show the reported range of leaf sizes for particular species as the longest (Δ) and shortest (∇) leaf lamina length plotted as a function of tree height h . Circles show the 5 longest (red, dark gray) and 5 shortest (green, light gray) leaves in each 20 m height bin for trees taller than $h = 20$ m. Solid lines are fits to Eq. (2) (upper limit) and Eq. (3) (lower limit) with parameters corresponding to a minimum flow speed of $u_{\min} \simeq 100 \mu\text{m/s}$ and energy output efficiency of $\sim 90\%$, see Fig. 3(a-b) and text for details. Dashed lines indicate 95% confidence intervals.

length spectrum can be found in increasingly taller tree species (Fig. 2). The observed decrease in maximum leaf length and the increase in minimum leaf length are both significantly different from expected changes based on a reduced number of species in the tall tree range. Further, the observed trends remain significant when considering only two large genera covering just 10% of the data set. See Supplemental Material Fig. 2, and Table II for detail on the statistical analysis.

It is well established that the leaf length variability in short trees reflects their adaptation to extrinsic micro- and macro-environmental forces and stresses [9]. However, the tallest trees are only found in the most suitable habitats, characterized by frequent fog and rain, high humidity and protection from wind. Thus the observed decrease in variability of leaf lengths and the existence of upper and lower limits to leaf length have no simple environmental explanation. It is therefore possible that the systematic variation of the limits to leaf size with tree

height is the consequence of an intrinsic constraint.

In the absence of environmental stress, any plant is limited by its ability to distribute the products of photosynthesis. The capacity of a leaf to export energy depends on the size of the leaf itself, and on the proportions of the plant as a whole, and may provide a candidate for the intrinsic constraint that limits leaf size. From many related biological transport problems, it is well known that the geometry of optimal distribution paths in closed or dendritic systems can be constrained by simple physical mechanisms that depend on organism size [1–3, 10–13]. In the following, we therefore seek to establish a relationship between the sugar export rate and the dimension of the distribution network.

Sugar transport in plants takes place in the phloem vascular system. Here, an aqueous solution of sugars, amino acids, proteins, ions, and signaling molecules flow through a series of narrow elongated cylindrical cells, known as sieve tube elements, lying end-to-end forming a microfluidic network spanning the entire length of the plant. The total solute concentration is $\sim 25\%$ wt/wt, and sugars, of which sucrose is the most abundant type, constitute 80% – 90% of this [14]. Although sugar transport is the primary role of the phloem it also plays a major role in the response to wounding and environmental stimuli [15]. The flow in the phloem is driven by differences in hydrostatic pressure between source (leaves) and sink (e.g., roots, fruits or other place of growth and storage) tissues, believed to be generated by gradients in osmotic potential between distal parts of the plant according to the Münch pressure flow hypothesis [16].

The energy flux E (energy per unit time per unit area of vasculature) mediated by the movement of sugar molecules may be quantified by considering the flow speed u of the carrier liquid, since the energy flux can be expressed as $E = kcu$. Here, c is the concentration of sugar in the phloem sap and k is the energy content per sugar molecule. The flow speed u will depend on the geometric parameters of the problem, in particular on the height of the tree h , length of the leaf l and the radius of the phloem sieve element r . A well established method for estimating the hydraulic properties of plant vasculature is to use an Ohmic analogy to describe the fluidic network [17]. We thus follow Pickard [17] and Jensen *et al.* [18, 19] and consider the plant as consisting of three parts: A source (leaf), a stem, and a sink (root, fruit or other places of growth and storage), and assign a hydraulic resistance to each of these. This compartmentalized model reflect that water enters the phloem tubes in the leaf, then flows down along the stem, and finally exits the tubes at the sink. To enter the phloem in the leaf, water must traverse a semipermeable membrane and thus the resistance $\mathcal{R}_{\text{source}} = 1/(2\pi r l L_p)$ is inversely proportional to the phloem wall area $2\pi l r$ and the hydraulic permeability of the membrane L_p . The choice of the leaf lamina length l as the characteristic

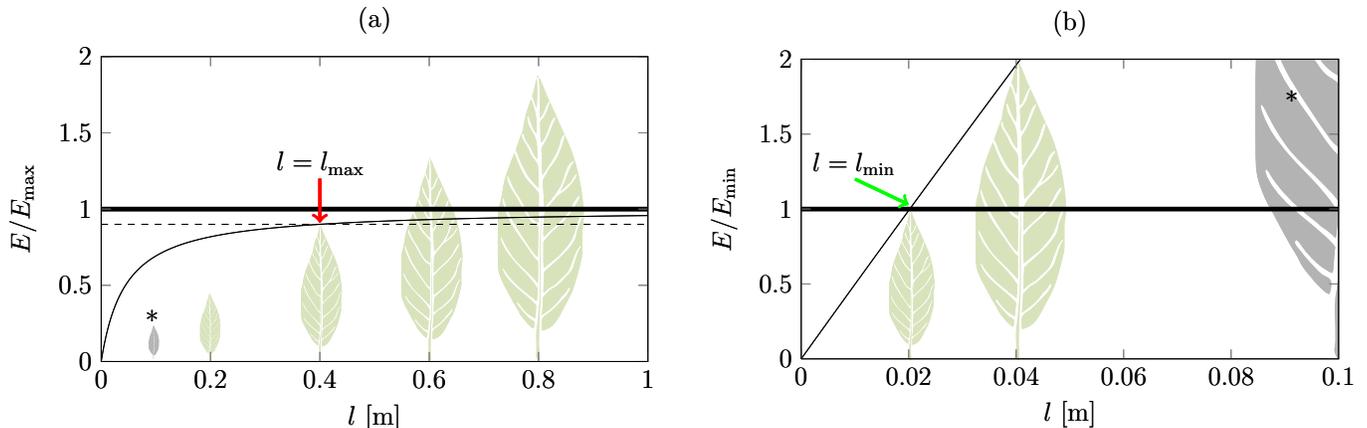


FIG. 3. (Color online) Limits to leaf size in tall trees. (a) Mechanism for the upper limit on leaf size. Energy flux E plotted as a function of leaf size l (thin black line). As the leaf becomes longer, the energy flux slowly approaches a maximum value $E_{\max} = kcr^2\Delta p/(8\eta h)$ set by the height of the tree (thick black line). In the case of a $h = 50$ m tree, the gain in net energy export is very small beyond $l = 40$ cm, where the energy flux is 90% of E_{\max} (dashed line) and the leaf length must double to $l = 80$ cm in order to obtain a 5% increase in net energy flux E . This leads to the prediction of maximum leaf size l_{\max} given in Eq. (2). (b) Mechanism for lower limit on leaf size. Energy flux E plotted as a function of leaf size l (thin black line). As the leaf length increases, the energy flux increases above a minimum required energy flux $E_{\min} = kcu_{\min}$ (thick black line) which is assumed to be independent of tree height. This leads to the prediction that the leaf size l_{\min} at which $E = E_{\min}$ is given by Eq. (3). Here, the case of a $h = 50$ m tree, where $l_{\min} \simeq 2$ cm, is shown. In (a) and (b), gray leaves marked with (*) have the same size.

length scale is motivated by detailed studies of leaf venation patterns which reveal that the distance along the vasculature from any point in the leaf to the leaf base is proportional to l [20], a result that does not depend on leaf shape. In the stem, phloem sap flows through what is essentially a single cylindrical tube of radius r and length h , so the stem resistance is $\mathcal{R}_{\text{stem}} = 8\eta h/(\pi r^4)$, where η is the viscosity of the sap, typically five times greater than water $\eta \simeq 5$ mPas [21]. At the sink, sugar is used for metabolism, growth or storage, and water exits the phloem by crossing a semipermeable membrane. We may therefore write for the sink resistance $\mathcal{R}_{\text{sink}} = 1/(2\pi r s L_p)$ where s is the length of the sink region. Since sugar is consumed throughout the plant, the sink length is typically much greater than the leaf length ($s \gg l$) and so the sink resistance will be much smaller than the leaf resistance, i.e. $\mathcal{R}_{\text{sink}} \ll \mathcal{R}_{\text{source}}$. From these simple considerations, we are now able to express the characteristic sugar transport speed u in terms of leaf size l , stem length h , and phloem tube radius r

$$u = \frac{1}{\pi r^2} \frac{\Delta p}{\mathcal{R}} = \frac{2r^2 L_p l}{r^3 + 16\eta L_p l h} \Delta p \quad (1)$$

where the hydraulic resistance $\mathcal{R} = \mathcal{R}_{\text{source}} + \mathcal{R}_{\text{stem}}$ and Δp is the osmotic pressure difference driving the flow, set up by differences in sugar concentration between source and sink. For most trees, sugar loading into the phloem vasculature is believed to be a passive, diffusion mediated process, and the available pressure differential $\Delta p \simeq 1$ MPa does not scale with tree height and may be

treated as an independent parameter [22, 23]. Eq. (1) predicts that for a fixed tree height h and leaf length l , the flow velocity u is at a maximum when the phloem tube radius r scales as $r \propto (L_p \eta l h)^{1/3}$, a relation which is well documented in many herbaceous plants [18] and in some trees [19]. For trees taller than $h \simeq 20$ m, however, the sieve element radius r appears to never grow larger than $r \simeq 20 \mu\text{m}$, presumably because of constraints on the size/volume of the sieve-element/companion cell complex [19, 24, 25].

For constant sieve element radius r , the flow speed u in Eq. (1) decreases monotonically with tree height h due to the added resistance to flow in the stem. The dependence on leaf size, however, is more complicated. Initially, the flow speed u increases linearly with leaf size. A larger leaf leads to a greater flow speed because the flow accelerates along the vasculature in the leaf due to osmotic exchange of water, acting as tributaries to a river. As the leaf grows very large, however, the leaf resistance becomes small compared to the stem resistance $\mathcal{R}_{\text{source}} \ll \mathcal{R}_{\text{stem}}$, and ultimately the flow speed can never exceed the value $u_{\max} = r^2 \Delta p / (8\eta h)$.

From Eq. (1), we find an expression for the energy flux E in terms of leaf size l and tree height h : $E = kcu = 2kc\Delta p r^2 L_p l / (r^3 + 16\eta L_p l h)$. Since the plant invests considerable amounts of energy in constructing and maintaining photosynthetic tissue, it is reasonable to assume that it will refrain from constructing larger leaves once the energy flux E approaches the maximum energy output $E_{\max} = kcu_{\max} = kcr^2\Delta p / (8\eta h)$. At this point,

the gain in energy output from increasing the leaf size is small (see Fig. 3(a)), and likely no longer sufficient to offset the cost of building and maintaining the leaf. We therefore assume that an increase in leaf size will stop once the energy output E has reached a fraction $E \sim (1 - \tau)E_{\max}$ (where $\tau \ll 1$) of the maximum obtainable. This leads to a maximum predicted leaf length of

$$l_{\max} = \frac{1}{16} \frac{r^3}{\tau L_p \eta} \frac{1}{h} \quad (2)$$

as illustrated in Fig. 3(a).

Although having several small leaves in place of one large may seem advantageous, it is worth noticing that the flow speed u and hence energy flux E generated by each leaf grows linearly with leaf size when l is small (i.e. when $L_p \eta l h \ll r^3$, see Eq. (1)). Thus for small leaves, no significant gain in energy export can be obtained by replacing one big leaf with two smaller leaves. Having smaller leaves does, however, affect translocation speed. To facilitate efficient transport of signaling molecules and to ensure that at least some energy is delivered to the receiving sink we propose that the flow speed must exceed some minimum value u_{\min} . If not, the plant would be unable to effectively use the phloem as an information path and have difficulties delivering a minimum energy flux $E_{\min} = kcu_{\min}$ to the sink, thereby defying the purpose of laying down the vascular network in the first place. To estimate this minimum flow speed, we note that vascular systems are formed because cell-to-cell diffusion is insufficient as a transport mechanism over long distances [1, 26]. With typical plant cell sizes in the range of $d = 10 \mu\text{m} - 100 \mu\text{m}$, diffusion and advection of sugars are equally effective over these length scales when the Peclet number $Pe = vd/D = 1$ [26], where v is the flow speed and D is the diffusion coefficient ($D = 0.5 \times 10^{-9} \text{ m}^2/\text{s}$ for sucrose [27]). We therefore expect $v \simeq D/d = 5 \mu\text{m}/\text{s} - 50 \mu\text{m}/\text{s}$ to provide a lower estimate of the minimum flow speed u_{\min} .

Assuming $u = u_{\min}$ we find from Eq. (1) that the leaf size l_{\min} at which this speed is first obtained is given by

$$l_{\min} = \frac{1}{16} \frac{r^3}{L_p \eta} \frac{1}{(h_{\max} - h)} \quad (3)$$

as illustrated in Fig. 3(b). In Eq. (3), we have expressed the minimum leaf size in terms of $h_{\max} = r^2 \Delta p / (8 \eta u_{\min})$, the tree height at which it is no longer possible to obtain the flow speed u_{\min} due to resistance to flow in the stem.

To quantify the lower and upper boundary of the leaf length data set in Fig. 2 we used the five longest and five shortest leaves within 20 m tree height bins. In the analysis we focused only on trees taller than 20 m since observational data indicates that the sieve element radius is constant above this height [19] in which case Eqns. (2) and (3) are relevant. The upper boundary

can be fitted to Eq. (2) with a line reflecting nearly 90% of maximum energy outflow from an infinitely long leaf, ($\tau = 0.094 \pm 0.004$, $R^2 = 0.89$, $N = 20$, $p < 0.05\%$). The lower boundary can be fitted to Eq. (3) with a minimum flow speed of approximately $u_{\min} = 100 \mu\text{m}/\text{s}$ ($u_{\min} = 96 \pm 5 \mu\text{m}/\text{s}$, $R^2 = 0.95$, $N = 20$, $p < 0.05\%$), see Fig. 2. The trend of the boundaries remains valid for subsets of the data covering just 10% of the species (2 genera), suggesting that the observed pattern is not strictly phylogenetic but truly driven by intrinsic physical effects (Supplemental Material Fig. 2). The determined value of u_{\min} is compatible with minimum observed flow rates from multiple species [28, 29], and with our estimate of diffusion limited transport at the cell-to-cell level. With estimates of the driving pressure ($\Delta p = 1 \text{ MPa}$) and membrane permeability ($L_p = 5 \times 10^{-14} \text{ m/s/Pa}$) derived from the literature [22, 30] we find that tree height h_{\max} at which the flow speed u_{\min} can no longer be obtained is $h_{\max} = 104 \pm 6 \text{ m}$.

This question considered in the present paper is part of a greater class of problems questioning how physical laws affect the size and shape of living organisms. We propose a simple physical model that explains the observed limits to leaf size and the lack of very long and very short leaves on tall trees. The limits to leaf size can be understood by physical constraints imposed by intrinsic (biological and geometrical) properties of the carbohydrate transport network. The lower boundary of the leaf size is set by the minimum energy flux (Eq. (3)), the upper boundary by a diminishing gain in transport efficiency (Eq. (2)). Both established boundaries meet at $h \sim 100 \text{ m}$, very close to the maximum angiosperm tree height ever recorded [7], providing a biophysical interpretation of the absolute limit to tree height.

The broad range of leaf lengths found in short trees reflect variation driven by environmental factors within limits set by the sugar transport network. Environments characterized by e.g. water stress or high winds generally lead to a decrease in leaf size [31], which may eventually approach the lower boundary $l_{\min}(h)$. In harsh environments, tree height can therefore be limited by leaf length, since small leaves are unable to support the required minimum flow in taller trees. This provides a new explanation for the lack of tall trees in environments with limited water resources. On the other hand, environments most suitable for plant growth allow trees to explore the upper boundary of leaf lengths where further growth does not benefit energy export rates. This may explain the endemic occurrence of the tallest trees in the most forgiving environments, including tropical rain forest or foggy river ravines.

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