Spatial networks / Réseaux spatiaux

The transport network of a leaf

Le réseau de transport d'une feuille

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A B S T R A C T

Modern leaves, the energy factories of plants, are the products of a 400-million-year evolutionary race towards improved efficiency and robustness. As such they have evolved two sophisticated transport systems, the xylem and the phloem, which irrigate the surface of the leaf blade, distribute water and nutrients, and collect the products of photosynthesis. In this review, we discuss the development and function of these two networks. Additionally, with a focus on the global topological and architectural features, we present an overview of the evolution of reticulation through the lens of transport network optimization theory and analyze some aspects of the physics of flow.

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R É S U M É

Les feuilles actuelles, les centrales énergétiques des plantes, sont la résultante d'une course de 400 millions d'années vers une efficacité et une robustesse accrues. En tant que telles, elles ont développé deux systèmes de transport sophistiqués, le xylème et le phloème, qui irriguent la surface du limbe de la feuille, distribuent l'eau et les nutriments, et recueillent les produits de la photosynthèse. Dans cette revue, nous discutons le développement et le fonctionnement de ces deux réseaux. En outre, en mettant l'accent sur leurs caractéristiques topologiques et architecturales globales, nous présentons un aperçu de l'évolution de la réticulation à travers l'optique de la théorie de l'optimisation des réseaux de transport et analysons certains aspects de la physique des flux.

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1. Introduction

The leaf is the energy factory of the plant, and clearly it is indispensable for its survival. Photosynthesis converts light energy to sugar, which in turn is transported to the photosynthetically inactive parts of the plant, such as the roots and the fruit, to sustain the organism and allow for growth. In fact, the vast majority of the land biomass is derived directly or indirectly from the leaf, and for this reason, land life as we know it would be inconceivable without it [1].

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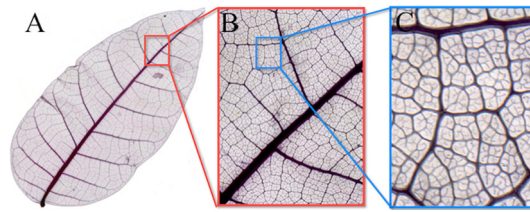
Fig. 1. Leaf vascular network of *Protium panamense*. The vascular system is composed by several orders of veins, forming a dense network of hierarchically nested loops. The leaf blade in panel (**A**) is approximately 12 cm in length. The zoomed-in section in panel (**C**) is approximately 1.5 mm across.

This review is devoted to one aspect of this formidable organ, its vascular network. The vascular network of the leaf is a transport network that is essential for the function of the entire organ. It functions as an irrigation system, replenishing the water that is lost during photosynthesis, as a nutrient collection and redistribution system, as a communication network [2] and furthermore, as a structural mesh to provide mechanical support. To achieve these functions, the vascular network of the modern angiosperm leaf is typically exceedingly complex, featuring several orders of hierarchically nested veins (Fig. 1).

This review will examine several aspects of the physics of this spatial network, focusing primarily in its function as a transport network. Unlike animals which achieve circulation using a pump (the heart), leaves carry out transport without active forcing, but by ingeniously exploiting various physical principles and by fine tuning the network properties to facilitate and control the flow.

We begin this review in Sec. 2 by examining the anatomy of the two main plant vascular systems in the leaf, the xylem and phloem, and the topological characteristics of the network they form. Then, in Sec. 3 we proceed to discuss aspects of their evolution and optimality of function. In Sec. 4 we consider the vascular network development, especially in the context of broad self-organizing principles and in Sec. 5 we continue to describe some modern tools to capture and quantify its architecture. Finally, in Sec. 6 we connect the vascular network of the leaf to other transport systems and briefly discuss potential universal design principles of biological transport networks.

This review is not meant to cover all aspects of vascular leaf physiology, and given its brevity is inevitably incomplete. However, we hope it will serve as a useful starting point for a non-plant biologist who wishes to study some basic physical aspects of the leaf vascular network and connect it to other transport systems of interest.

2. Vascular anatomy and architecture

The xylem is the transport system of the plant that brings water from the roots to the leaves to replenish the water that is lost during photosynthesis. Photosynthesis requires an exchange of gases between the leaf blade and the atmosphere. The stomata, typically situated at the abaxial surface of the leaf blade (see Fig. 2), need to be open to allow for this to happen. During the time that the leaf is photosynthetically active, water molecules escape from the mesophyll cell walls in the interior of the leaf, and eventually from the leaf blade through the opened stomata, in a process termed transpiration. In fact, in this respect, the typical leaf is remarkably wasteful in its water management: for each atom of carbon captured, up to 400 hundred molecules of water are lost through transpiration.

The water that evaporates from the leaf blade is replenished by the xylem network, which allows the leaf to remain hydrated even under conditions of high heat and low atmospheric humidity. The evaporation at the leaf creates capillary suction, creating tension in the continuous water column that is established between the xylem vascular network at the leaf, the petiole, the stem and finally to the roots. This tension results in the water being drawn from the soil and transported all the way to the leaves. The continuous water column is under negative pressure, and for this reason, it is susceptible to cavitation and embolisms, i.e. disruption of the continuity of the water column by air bubbles.

The xylem is ingeniously designed to mitigate the risks of embolisms and cavitation. The xylem of modern plants if composed of the lignified cell walls of two types of non-living cells, the tracheids and the vessel elements. These are elongated cells that are closely stacked, having perforations at their common walls (bordered pit pairs) and endings (perforation plates), as shown in Fig. 3, which allow for water to travel between the vessel elements. Although the perforation plates reduce the overall conductance of the vessels, they play a very important role in containing embolisms and protecting the integrity of the water column. Despite the complexity of the xylem at the cell level, when modeling the overall water transport in the leaf blade, it is sufficient to consider an overall, effective vessel conductance, which is a function of the vascular bundle thickness and captures the relationship between the flow and the water potential decrease, which governs the leaf hydraulics [3,4].

In contrast to the xylem, which is composed primarily of non-living cells, the phloem is metabolically active. The phloem is a complex system that is composed of transport cells (termed sieve elements), parenchyma cells (typically used for food storage), and companion cells (which support the metabolic function of the sieve elements) [3]. The purpose of the phloem is to redistribute the sugars created through photosynthesis at the leaf to the rest of the plant, but also to act as a communications system. The movement of sap, the sugar solution in the phloem, is driven by osmotic pressure gradients, and require osmotic pumping units.
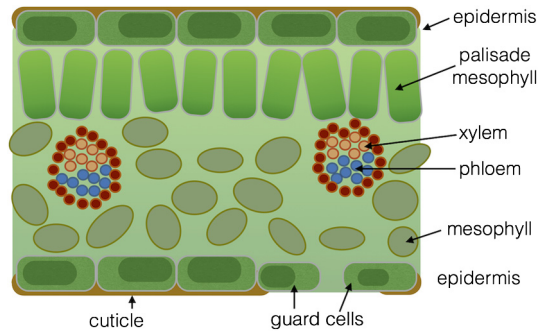
Fig. 2. Anatomy of a leaf blade (cross-sectional view). The water evaporates through the stomata at the bottom of the leaf blade, and is replenished by the xylem in the vascular bundle.
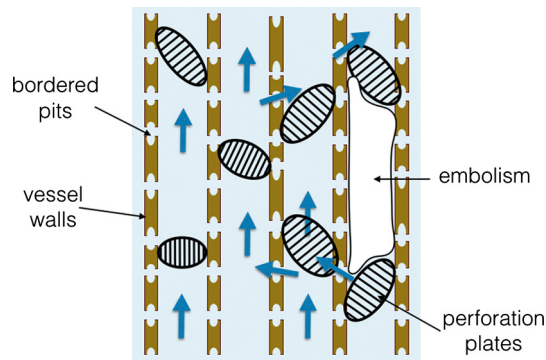
Fig. 3. Xylem anatomy. The bordered pits and perforation plates permit water transport while containing embolisms. Figure redrawn from [3].
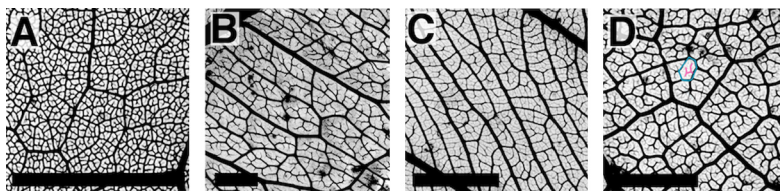

Fig. 4. Examples of the diversity of leaf network morphology in the Burseraceae family. Highest order venation morphology in (**A**) *Protium ovatum*, (**B**) *Protium madagascariense*, (**C**) *Pouteria filipes*, (**D**) *Canarium betamponae*. In (**D**), one areole (smallest loop) is marked (blue) together with freely ending veins (red). Scale bars correspond to 2 mm. (Adapted from [5].)

In the leaf blade, the xylem and phloem run parallel to each other, together forming the vascular bundle. The xylem is situated in the adaxial (top) side of the blade, further away from the stomata at the bottom, and the phloem at the abaxial (bottom). Together, the xylem and phloem form an integrated system of transport (Fig. 2), similar to a complex traffic system of two way streets and highways. Water enters at the petiole at the base of the leaf, it is distributed via the complex system of tracheids and vessel elements, escapes through the cell walls, part of it evaporates and is lost through transpiration, and part of it is reloaded along with sugar in the phloem, and eventually exits the leaf blade again through the petiole.

The actual variability of the leaf vascular networks is immense, even among closely related species. In Fig. 4 we show some examples of higher order vascular structures from species in the Burseraceae family; large variability similarly exists in the lower order structures. Despite this diversity, general organizing principles exist, e.g. according to the flowering plant group (dicotyledonous or monocotyledonous) the species belongs to. Dicotyledonous species typically have reticulate venation with a single primary vein in the middle of the leaf blade and several secondaries emanating from it, while the monocotyledonous leaf venation is dominated by several parallel veins. Hierarchy and reticulation are almost invariably present in the venation of both monocots and dicots.

Although the microscopic anatomy of the vascular bundle is very important for determining the leaf hydraulics, for the rest of this review, we will not consider the cellular physiology of the leaf vein. Instead, we will treat the bundle of vessel elements in each vascular segment of the leaf as a single conductive element, described by an effective resistivity, and focus on the network properties of the leaf vasculature.
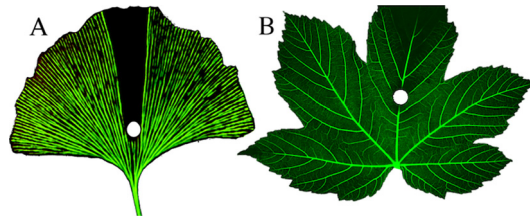
Fig. 5. Irrigation of damaged leaves and the effect of loops. (**A**) A ginkgo leaf lacks anastomoses, and damage will disconnect large downstream sectors of the leaf from the petiole. (**B**) The vascular network of a maple leaf remains connected even after major damage. The fluorescent dye will eventually reach the entirety of the blade.

3. Evolution and optimality

The current form of the modern, highly reticulate leaf is the product of million of years of evolution. As evidenced by the rich fossil record, primitive leaves featured venation dominated by simple, non-hierarchical and roughly parallel longitudinal veins or dichotomously branching systems, and lacked hierarchical venation or anastomoses; these more advanced traits appeared independently in many disjoint groups [6]. Along with the appearance and increase of reticulation came an explosive increase in vascular density [7], especially after the emergence of angiosperms. In fact, leaf vascular density has been found to correlate with climate, in particular growing season temperature and atmospheric CO_2 concentration [8], and paleoclimate [9].

The reason for this shift towards a more complex network is that the leaf vascular system is crucial for the leaf, and therefore under tremendous evolutionary pressure to be efficient. There is close correlation between various leaf vascular traits and photosynthetic efficiency [10,11]. Evolving an improved vascular system allowed angiosperm plants to adapt to atmospheric conditions that increased the hydraulic cost of photosynthesis, either from decreasing CO_2 or atmospheric humidity. Major shifts in vascular architecture that improved leaf conductance permitted higher transpiration rates, and eventually allowed the plant to photosynthesize longer, and more efficiently.

In fact, there are several aspects of the leaf vascular architecture that have been shown to optimize conductance. The typical distance between veins is proportional to the angiosperm leaf blade thickness, as predicted by an optimization model that takes into account flow saturation [12,13]. Vessel scaling (the ratio of hydraulic radii of all conduits at consecutive ranks as a function of the ratio of the number of conduits present at a subsequent rank) conforms with Murray's law, further bolstering the claim that the leaf vascular has been optimized for conductance [14] (see also [15,16]). Murray's law, first shown in the context of animal vascular networks, stems from the fact that a biological transport network will naturally evolve to be maximally efficient given a certain material cost to build and maintain the network. Murray's law predicts that the inner radius of the mother vessel r_p cubed will be equal to the sum of all inner radii of the daughter vessels downstream r_i raised to the third power:

$$r_p^3 = \sum_i r_i^3 \tag{1}$$

In [17], the authors have found that the distribution of tracheids along the length of pine needles scales with the square root of the distance of the needle tip, consistent with optimal distribution of transport conductivity that minimizes pressure drop per given investment in xylem. Pine needles have thus evolved an optimal water delivery distribution system that allows them to maximize needle length for given pressure drop Δp and thus improve their photosynthetic performance. The phloem distribution in pine needles, although driven by different mechanisms, follows a similar law and is consistent with transport energy minimization. This suggests that conductive efficiency is more important than communication speed at the leaf level [18].

Evidence for optimization exists beyond the scalings found for local traits: the leaf vascular network is an integrated unit, and optimality predicts global trait–trait scaling relationships for the leaf blade size, the density of the lower vascular orders and other geometrical traits [19–21,4].

The importance of topology becomes evident when considering the complex networks that irrigate broad leaf blades, in contrast to the one dimensional pine needle vascular system. The tree topology is the most cost efficient architecture, however damage to a single edge can lead to a very large portion of the system getting disconnected from the topological root of the tree, especially when the damaged edge is near the root. This is demonstrated in Fig. 5, where we damage a ginkgo leaf and show that fluid marked with a fluorescent dye cannot reach the area of the leaf blade downstream of the damage. A maple leaf, featuring dense loops (not easily visible in the resolution of Fig. 5) allows the fluid to bypass the injury site and eventually irrigate the entire leaf blade.

In [22] we show that minimizing the average water potential drop $\sum \Delta p_i$ while keeping the construction cost of the network constant, produces networks that are similar to dicotyledonous leaves, if the network is required to be robust to damage. The construction cost K is generically a function of the conductances of each vessel C_e, i.e. $K = \sum_e C_e^\gamma$. The exponent γ depends on how the material cost and conductance of the vessel scale with the radius. It is a proxy for the
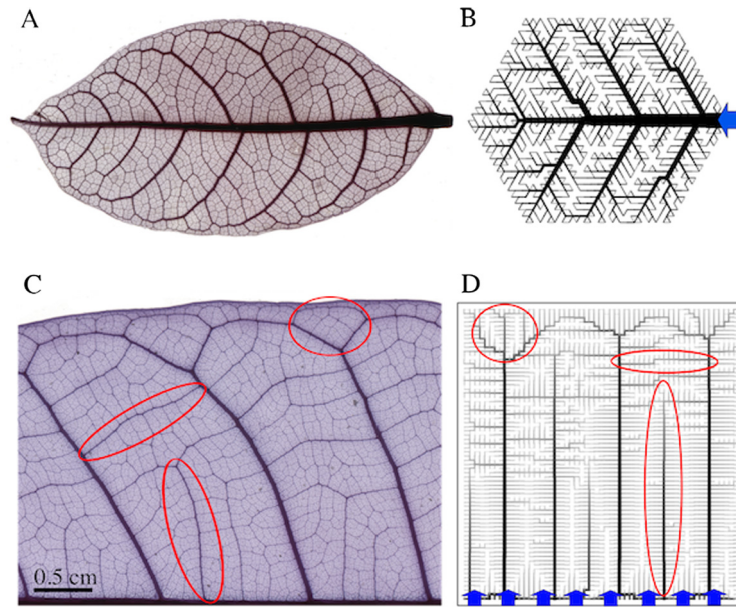
Fig. 6. Optimization models successfully predict the structure of dicotelydonous leaf venation. (**A**) Dicot leaf *Canarium nitidifolium*. (**B**) Transport network, optimized to minimize the average pressure drop, while required to remain connected under any edge removal. The flow input (source) is denoted with the blue arrow. Every node of the network is a sink. (**C**) Detail of a *Protium pittieri* leaf. (**D**) Transport network, optimized to minimize the average pressure drop, while required to remain connected under any edge removal. To emulate the main vein at the leaf section shown in (**C**), the entire bottom row of the simulated network is designated as input nodes (denoted with the blue arrows). Every node of the network is a sink. The red circles point to the architectural similarities between the natural and simulated networks, such as the intersecondary veins. (Adapted from [5].)

economy of scale: a small γ means the cost of vessels increases slowly with the conductance, so it is preferential to combine many smaller vessels that transfer fluid in a similar direction with a larger one. Conversely, a large γ means the cost of vessels increases sharply with the conductance, so building larger vessels leads to diminishing returns, and a flatter architecture is more cost efficient. Leaves are thought to have a $\gamma \sim 0.25$–0.5, so a hierarchical network architecture is optimal. The requirement that the network is robust, i.e. remains percolated when individual edges are removed, leads to an optimal network that features dense loops. In Fig. 6 we show in more detail how this optimization model can predict various features of dicotyledonous leaf venation, such the secondary vein connections near the leaf margin. The importance of anastomoses and redundancy of the leaf vascular network has been similarly investigated in several different contexts, both theoretically and experimentally [23–25].

Here we need to mention that the structure of the leaf vascular network plays an important role for the mechanical properties of the leaf blade [26]. However, these mechanical aspects are out of the scope of this review.

4. Development and growth

The highly ramified vasculature of modern plants develops through a sequence of developmental phases that are highly variable between species (a variability that is intimately interwined with the fact that the vascular topology is also very diverse), but some distinct developmental phases are typically followed [27]. In modern dicots, the midvein provascular strand first appears, growing from the base of the leaf primordium to its tip. Then the secondary veins extend from the midvein and grow towards the margin, followed by the tertiary and higher order veins that get patterned while the leaf blade surface is expanding. Typically vascular ramifications take place first at the tip of the leaf, but the details of this process are highly variable, overlapping, and species dependent.

The development of monocot venation, which is dominated by parallel veins, similarly follows a hierarchical sequence. First, the midvein and the large lateral veins appear near the base and grow towards the tip of the leaf, followed by the intermediate longitudinal veins, and last, the higher order lateral and longitudinal veins that establish the ramification.

The mechanistic understanding of the developmental process of how leaf vascular networks acquire their highly efficient form is not well understood, despite focused attention by the scientific community. One reason is that the biochemistry of leaf vascular development is very complex and largely unknown. One of the most widely accepted frameworks for understanding vascular patterning is auxin canalization [28].

Auxin canalization, as the name suggests, involves the plant hormone auxin which is typically produced at the shoots of the plant and is transported to the rest of the plant body. Critical to the transport of auxin in the plant is a trans-membrane efflux carrier protein called PIN1, which facilitates the exit of auxin from the cells. The position of PIN1 proteins in the cell membrane can itself be polar and depends on the presence of auxin (via its concentration or its flux), this way generating a
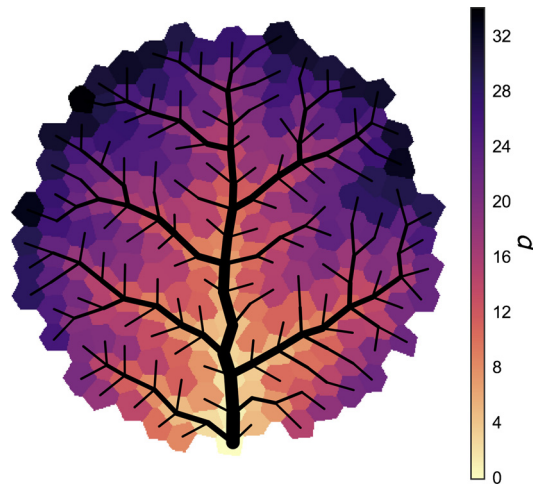
Fig. 7. Globally optimum network produced by the locally adaptive rule of Eq. (2). (Adapted from [29].)

feedback loop where auxin establishes polar PIN1 concentrations which in turn facilitate the flow of auxin. The auxin canalization hypothesis suggests that this positive feedback loop establishes paths of auxin flux by a self-organization process, which subsequently causes cellular differentiation and eventually the formation of the vascular bundles.

The auxin canalization hypothesis has produced a large suit of models that each captures (and makes assumptions about) different aspects of the molecular biology that drives this process. The flux based models generally read:

$$\frac{dK_{ij}}{dt} = f(q_{ij}) + \rho_o - \mu K_{ij} \tag{2}$$

where K_{ij} is the PIN1 concentration in the membrane section of a cell i neighboring a cell j, ρ_o is the basal rate of PIN1 production, μ is the rate of PIN removal, q_{ij} is the flux of auxin between the two cells, and $f(x)$ is the positive feedback term. The specific form of $f(x)$ plays an important role in determining the morphology of the vascular pattern.

The auxin canalization equation (2) belongs to a broader class of "use-it-or-lose-it" equations, such as the one used for the slime mold *Physarum polycephalum*, which is likely behind the shared morphological features between dicotelynodous leaves and physarum. The authors in [29] show that Eq. (2) in a growing tissue can produce a vascular network that is globally optimal for dissipation. This network exhibits a hierarchy of vessels that is reminiscent of dicotelydonous leaves, as shown in Fig. 7.

Auxin canalization in its most simple instantiation cannot produce closed loops or replicate several of the features seen in leaf vascular networks without fine tuning or other assumptions [30–32,28,33,34]. The auxin canalization equation can however produce loops if the auxin production is fluctuating [35]. The extent of the fluctuation will control the loopiness of the final vascular structure.

Auxin canalization for the most part disregards the effects of mechanical forces in vascular patterning. In [36], Couder first proposed that the loopy vascular phenotypes commonly found in modern plants are the result of a crack-like pattern formation process that takes place potentially due to a growth rate mismatch between the epidermis and the mesophyl. Since mechanical stress is a tensorial field, models that consider mechanics can natively close loops [37–39]. Tissue mechanics has also been considered as factor in determining the angle between anastomosing veins [40]. It is likely that both auxin canalization and mechanics play an important role in vascular differentiation in the leaf [41].

Vascular patterning has also been considered in the computer science community, in an effort to algorithmically produce realistic looking leaves [42].

5. Measurement and phenotyping

Connecting theory with observation and experiment and better understanding the physiological properties that control the development and function of the leaf vascular network requires reliable and detailed data, as well as methods to properly quantify and characterize the vascular phenotypes. Traditionally, network characterization would take place by manually identifying some named phenotypic traits [43]. These phenotypic traits include vein density, extent of reticulation, type of edges etc., and point to the striking diversity of leaf vascular form [44].

Since 1980 there has been interest in constructing an algorithmic method for vascular phenotyping [45]. In the recent years, efforts have shifted towards automated, high throughput phenotyping of form, but also characterization based on machine learning. These methods typically rely on high volumes of data, and online data repositories have been established to house user generated cleared leaf catalogs [46]. The first step towards an automated extraction of leaf form from cleared
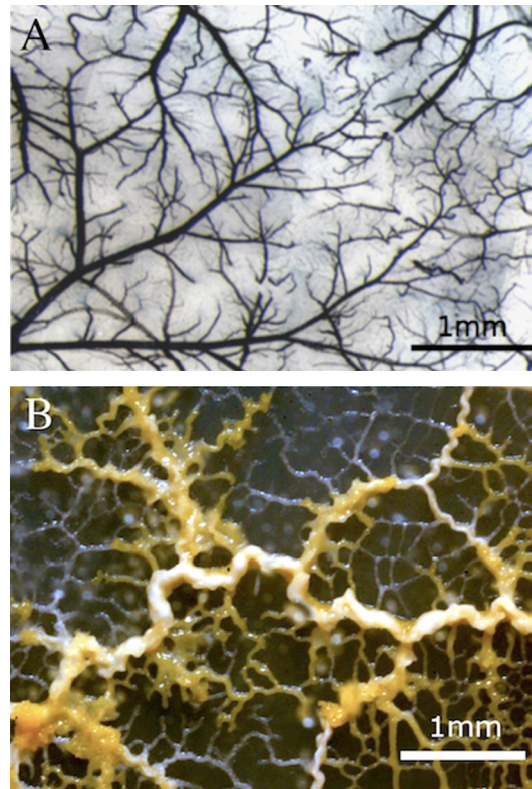
Fig. 8. Hierarchy and loops in biological transport networks. (**A**) Surface arterial vasculature of the mouse cortex. (Image courtesy M. Adams and P. Drew.) (**B**) *Physarum polycephalum*.

leaf images relies on algorithms that perform the network vectorization, namely the representation of the bitmap image data by a list of nodes (accompanied by their two dimensional locations) and weighted edges that connect them [47–49]. Of course, reliable vectorization of the data necessitates a high resolution digital image of the original network, and caution needs to be exercised when there are imaging limitations [50].

The vectorized image of the network is then used to analyze phenotypic traits, to understand aspects of vascular development [51], correlate them with environmental of genetic factors, and much more. Recently, several groups have started to shift their attention to the topology of the network, and attempted to define phenotypic traits that capture aspects of the venation that are related to the hierarchy, as e.g. in [52] and in [53]. Given that the leaf vascular network is degree constrained, a lot of the traditional metrics that have been used to quantify complex networks, such as clustering or betweenness centrality are of limited use (see, e.g., [54]). However, characteristics such as the angle between vascular segments can reveal important information about the mechanics during development [40]. Similarly, the aspect ratio of the leaf areoles (the smallest closed loop in a leaf) is a useful statistic to characterize leaf venation, similar to the shape of a city block, used in quantification of city patterns [55]. In [56] we found that the topology of the hierarchical, nested vascular structure of the leaf defines a new phenotypic trait that is orthogonal to the widely used geometric phenotypic traits such as vein density. Further, we used machine learning to show that a small set of geometric and topological phenotypic traits can be used to identify leaves from fragments, this way defining a venation "fingerprint". The usage of machine learning does not require a vectorized network: Wilf et al., in [57], used computer vision and artificial intelligence to analyze and classify leaf images into families and orders by learning a codebook of visual elements that represent leaf shape and venation patterns.

6. The leaf vascular network as a transport network

The leaf vascular network is a spatially embedded transport network [58] that shares a lot of functional requirements and developmental constraints with other biological transport networks such as animal vasculature and the slime mold *Physarum polycephalum*, shown in Fig. 8. These commonalities in function and development lead to inevitable analogous traits in structure. These traits include hierarchy, where broad vessels achieve transport efficiently over large distances and smaller vessels are used to perfuse the tissue at smaller scales, and loopiness that provides robustness to damage and optimal function in the presence of fluctuations. However, these considerations do not apply only to living networks, but also to man made, engineered networks such as road networks and natural networks as, for example, fluvial systems. For

this reason, leaves can be used as a model system to generate and develop new understanding about the function and topology of living transport networks and for producing new engineering paradigms for man-made distribution systems.

Low cost gene sequencing, as well as new high throughput microscopy techniques now for the first time permit the acquisition of unprecedented amounts of data on plant genetics and leaf vascular structure. This data, coupled with the new machine learning techniques that are rapidly become mainstream in all fields of science promise quantum leaps in our knowledge about leaf vascular networks. However, for this promise to truly materialize and translate to a knowledge of how transport is actually achieved and optimized in the plant leaf, we need to understand the fundamental physical mechanisms that drive and control the flow, the functions that the plant needs to optimize as well as the constraints, costs and compromises that will inform the models to predict the network form. The next few steps towards unraveling the puzzles of plant physiology and ecology can only be achieved with joint efforts from biology, computer science and physics.

Acknowledgements

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