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EVOLUTIONARY PATTERNS OF LEAVES: PALEOBOTANY AND CONSTRUCTAL LAW

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Paleobotany has been making the evolution of living structures that gave rise to present-day plants with thin planar leaves increasingly clear. And it tells us a fascinating story with many chapters to write and enigmas to decipher. The evolution of the structures that gave rise to present-day leaves with dense venation is one of those enigmas for which Constructal Law can offer a consistent, scientifically based, and beautiful explanation.

In this article, we show how it is possible to understand the evolution of the shape and venation of the structures that gave rise to present-day leaves. We aim to promote "easier and easier access" to all the energy and mass currents that allow photosynthesis and subsequent redistribution of products throughout the leaf system within a constraints framework (optimization of solar radiation capture and access to water and nutrients).

Keywords: Paleobotany; Leaf evolution; Venation patterns; Constructal Law.

1. INTRODUCTION

Bejan´s Constructal Law [1] is increasingly establishing itself as a reference paradigm in the evolution of animate and inanimate systems. Applications of Constructal Law to the evolution of natural systems is a hot topic that has been covered in multiple publications, some recent [2].

Paleobotany offers us a varied record of the evolution of plant leaves from microphylls, small and simple leaves, to megaphylls, larger and more complex leaves, over billions of years. Quoting Kenrick [3]: "The fossil record shows that megaphylls evolved from the photosynthetic branching systems of early vascular plants that became flattened and later webbed to produce a broad lamina in several groups by the end of the Devonian" (see. Fig 1). However, as noted by Tomescu [4]: "current understanding of plant phylogeny and leaf development fails to shed light on the origin of microphylls and supports several independent origins of megaphylls.".

This paper shows how Constructal Law can provide a convincing explanation for this question.

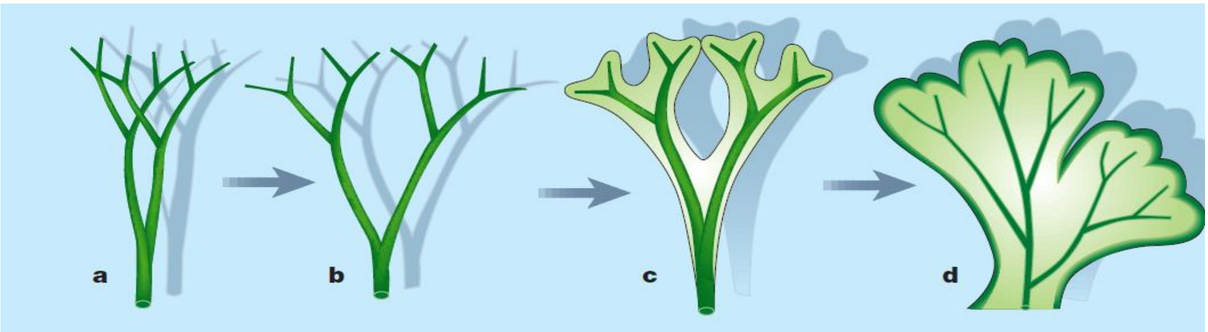

Fig. 1 – Evolution of leaves from microphylls: (a) Dichotomous branching; (b) Widening for maximum exposition to sunlight; (c) Transition to a planar leaf; (d) Fully developed planar leaf. (reprinted from ref. [3]).

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2. **FLOW ACCESS IN A DICHOTOMOUS BRANCHING MICROPHYLL**

Leaf is a plant construct that performs several functions: (i) it is the plant's powerhouse where molecules essential to the plant's life are manufactured through photosynthesis; (ii) it is the panel that collects the solar energy that powers photosynthesis; (iii) it is the reception center for raw products (minerals and water) necessary for the manufacture of complex molecules; (IV) is the distribution center of these molecules throughout the plant structure.

To fulfill its function as a receptor for solar energy, the shape of the leaf has evolved to improve its capacity for exposure to direct solar radiation. To fulfill the functions of receiving nutrients and distributing the products of photosynthesis, the leaf has evolutionarily developed a channel structure that can fulfill these objectives increasingly efficiently, within the framework of environmental restrictions.

The first stage of evolution consists of developing a channel structure where mineral salts and water can circulate. Nature's "intelligence" lies in its ability to develop structures that perform in the vicinity of the optimum point of operation [2]

Constructal theory has proven that such basic point-to-area structures are flow trees. Dichotomous branching flow trees have been shown to provide the best flow access to the fluids circulating in them [5].

In Fig. 1 (a), in fact, we can observe that this was the solution adopted by nature. Chloroplasts, i.e. the cells where photosynthesis takes place, cover the outside of the channels that transport mineral salts and water in a layer with the maximum thickness δ that allows the transmission of sunlight. The next stage of evolution (Fig. 1(b)) corresponds to the widening of the tree to maximize exposure to sunlight.

Fluids circulate in the leaf structure in bundles of microchannels driven by forces other than pressure gradients. Therefore, the total current is proportional to the cross-sectional area (d^2) of the bundle (leaf vein) of diameter *d*. Then, in this case, the general form of the flow resistance at the level *n* of a dichotomous branching tree of channel bundles of length l_n reads: $r_n = k2^{-n}d_n^{-2}l_n$ (where *k* is a constant) which gives rise to the following structural rule of the flow tree $(d_{n+1}/d_n) = 2^{-3/4}$ (see [5]). A general rule of symmetric trees is that the resistance is the same at all branching levels, i.e. $r_n = r_0, \forall n$ [5]. Therefore $r_n = kd_0^{-2}l_0$ and, $l_{n+1}/l_n = 2^{-1/2}$. Hence, the additional resistance R_N that comes from adding a *N*th branching level is $R_N = kd_0^{-2}l_0$. The *N*th branching level will accommodate a number of cells equal to $2^N\sigma\pi d_N l_N\delta$ where σ stands for cell density.

Therefore, the total resistance per unit cell reads:

$$(\rho_N)_{microphyll} = k\,2^{N/4}/(\sigma\pi d_0^3\,\delta). \tag{1}$$

3. **FLOW ACCESS IN A LEAF**

Microphylls evolved into megaphylls and present-day leaves, representing a new concept for organizing the distribution of fluids that enter and leave the chloroplasts. From a central vein (bundle of microchannels) lateral veins develop from each side that feed chloroplasts distributed in a layer of thickness δ (Fig. 2).

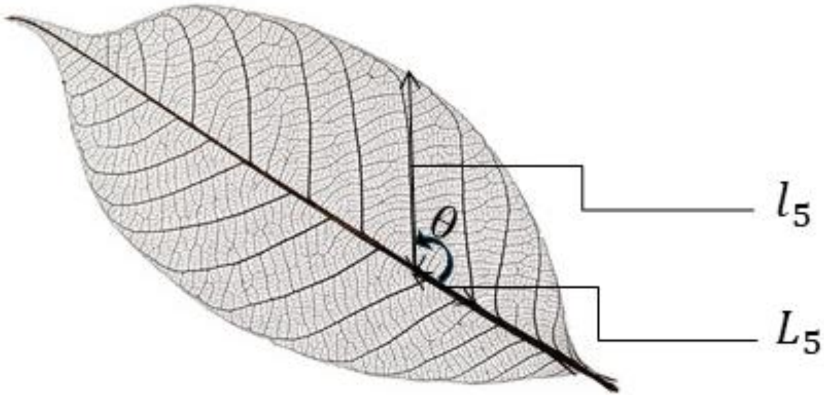

Fig. 2 – Present-day leaf, with a central vein and lateral second-order veins.

Let l_n be the length of the n^{th} lateral vein and L_n be the length of the adjacent segment of the central vein. So, the area served by these veins is $A_n = L_n l_n \sin\theta$. The total resistance to flow that fluids face to serve this area is made up of the resistance to moving fluids along the entire length of the microchannels that serve that area (proportional to total length $(\sum_{i=1}^{n} L_i + l_n)$ plus the resistance to delivering fluids to A_n from the adjacent veins (inversely proportional to the number of third-order veins and, therefore, to the length of the origin veins).

Therefore, it reads $R_{n(leaf)} = \alpha_n(\sum_{i=1}^{n} L_i + l_n) + \frac{\beta_n}{(L_n+l_n)}$, then the flow resistance per cell served in that area is:

$$(\rho_n)_{leaf} = (1/L_n^3)(\emptyset_n + \gamma_n)(\sigma\delta\sin\theta)^{-1}, \quad (2)$$

where $\emptyset_n = \alpha_n L_0^2 \lambda_n^2 \left[\psi_n^{-1} \sum_{i=1}^{n} \left(\frac{L_i}{L_n}\right) + 1\right]$, and $\gamma_n = \frac{\beta_n}{(\psi_n+\psi_n^2)}$, with $\lambda_n = \frac{L_n}{L_0}$ and $\psi_n = \frac{l_n}{L_n}$.

4. MICROPHYLL EVOLUTION INTO LEAF

As microphylls are free to morph, according to Constructal Law they will evolve to gain greater and greater access to flows. Therefore, microphylls would have evolved into leaves when $(\rho_n)_{leaf} < (\rho_N)_{microphyll}$, *i.e.*, in view of eqs. (1) and (2) once the following condition was verified:

$$2^{N/4} > (d_0/L_N)^3(\emptyset_n + \gamma_n)(\pi/(k\sin\theta)). \quad (3)$$

This condition is easily satisfied by the present-day leaves because $d_0/L_N \ll 1$ while microphyll resistance per cell grows with $2^{N/4}$, which constitutes a limiting factor for microphyll development.

Additionally, planar leaves offer better access to sunlight, which is essential to power photosynthesis. In this way, the evolutionary transition between microphylls and present-day leaves is explained based on Constructal Law.

5. CONCLUSIONS

The Constructal Law provides the theoretical framework for understanding the evolution of plant leaves from microphylls to present-day leaves. In this context, it is possible to perceive that the planar leaf structure provides access to water and mineral salts and removes photosynthesis products from each chloroplast with lower resistance than that provided by microphylls, in addition to better access to sunlight. Evolution towards better design through easier and easier access to flows are the drivers of evolution (Constructal Law) [1].

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