

The leaf venation as formed in a tensorial field

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Abstract. The veins of plant leaves exhibit a large variety of morphologies. They are often thought to result from their growth in a concentration scalar field. It is shown here that the topology of these patterns rather corresponds to what is expected from growth in a tensorial stress field. This is demonstrated by analogic experiments performed on crack formation in gel films where many characteristic venation patterns, of both dicotyledons and monocotyledons, were reproduced. This suggests, for the origin of the veins formation, a set of hypotheses which is new but supported by known physiological data.

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The spontaneous formation of patterns in nature corresponds to various types of breaking of symmetry of initially homogeneous systems. Very different processes can be reduced to a similar mathematical structure and lead to the formation of similar patterns. A large and widely studied family of patterns results from growth in various Laplacian or diffusive scalar fields [1] in such phenomena as *e.g.* viscous fingering, crystal growth, diffusion limited aggregation or landform erosion. Although the patterns produced have in each case some specificities, they all share the same characteristic topology: they are hierarchised *tree-like branched patterns*. Vein formation in plants is also assumed by the existing models [2–4] to be part of the same family of diffusive processes, (except for a simulation [5] based on a Turing type diffusion-reaction process). In these theories, a hormone is generated, diffuses through the tissues, inducing a local differentiation into veins which progressively canalise the flow [6]. The simulation of these models leads to complex branched patterns. An essential characteristic of these patterns is that the extremities of the branches are free: they never reconnect to form closed loops [7].

However, in reality, the leaf venations [8–10], in spite of the variety of their patterns, always present such reconnections as observed in the three examples shown in Figure 1. They are thus different from tree-like branched patterns and can be seen as variants of a different morphology, the *net-like structures* which are dominated by the systematic reconnections to form a reticulum. It can

be noted that in mature leaves this morphology leads to a redundancy in the flow paths which is physiologically beneficial. There exists a physical archetype of patterns with a net-like structure: the 2D cracks patterns. Beautiful structures of this type can, for instance, be observed in the glazes of ceramics. In cracks, the origin of the formation of a reticulum is directly related to the tensorial nature of the stress field and can be easily explained. In a homogeneously 2D stretched medium (Fig. 2), the stress field is a tensor of rank 2. A first crack, propagating along the x -direction, relaxes the stress components σ_{yy} and σ_{xy} . But the stress parallel to the crack direction, σ_{xx} , is only weakly affected. Later, if a second crack grows in the vicinity of the first one, it will propagate so as to relax σ_{xx} and will thus collide at a right angle with the first fracture.

The first aim of the present letter is to show that the main morphologies of the leaf venation can be obtained [11] in crack growth experiments. We use variants of experiments (Allain *et al.* [12,13]) performed with concentrated colloidal suspensions of latex particles of diameter 0.1 μm in water (with volume fraction 0.50 and 0.25). These suspensions are deposited on a glass plate or on a silicon wafer and left to desiccate by evaporation, a process which is limited by diffusion of water into air [14]. The suspension first becomes a gel which then tends to shrink as it dries. It is prevented from doing so by the adhesive forces on the substrate. This growing mismatch results in stresses which are at the origin of the crack formation. For the sake of comparison with botanical patterns we explore the morphologies of these cracks with various boundaries and growth conditions.

The arrays of smaller veins of dicotyledons (Fig. 1a) form at a late stage when the leaf growth has become

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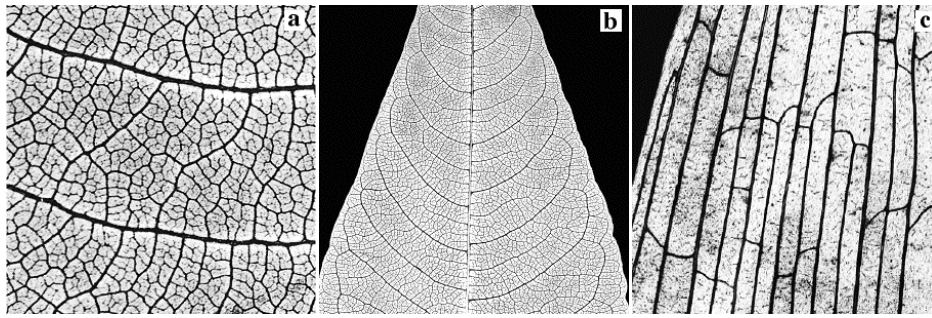


Fig. 1. Three examples of venation patterns. (a) The polygonal net-like structure of the small veins of a leaf of *Polygonum Polystachium*. (b) The secondary veins of *Polygonum Polystachium* are all connected to each other by loops located near the leaf margin. This is the ‘brochidodromous’ organisation [10]. (c) A detail of the venation of Lily of the valley, *Convallaria Maialis*, a monocotyledon.

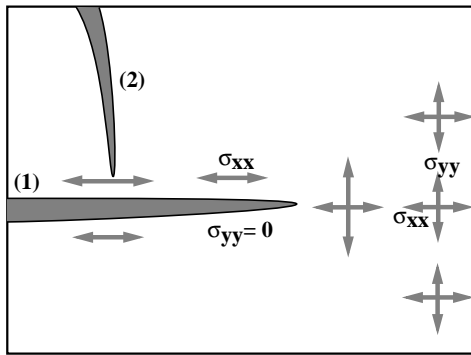


Fig. 2. Sketch of the growth of fractures in an initially homogeneously stretched medium. The reverse situation, of a compressed cellular medium, leads to the crushing of strips of material. The situation then corresponds to this sketch with all the stresses having the opposite directions.

homogeneous and isotropic [8,9,15]. They should thus be compared to crack patterns grown in homogeneous and isotropic conditions. Such patterns are obtained (Fig. 3a) in the drying of large and thin layers (of thickness $e \sim 10 - 100 \mu\text{m}$) far from the boundaries. Dynamically, the order of formation of the successive cracks is responsible for a hierarchy of structures, the first cracks to form being the longer. As new cracks keep forming, their length is limited because they grow in a domain limited by the older ones. They collide with them at right angle, forming an increasingly complex polygonal pattern with a typical spacing between cracks approximately equal to $4e$. Both this hierarchical dynamics and the resulting topology of the patterns are the same for cracks and veins (see Fig. 3a and Fig. 1a). The only difference between the two patterns lies in the number of successive orders. During its growth a leaf expands by several order of magnitudes (*e.g.* from 0.1 mm to 100 mm) so that a much larger range of veins of successive order is generated than for a gel which shrinks only by approximately 10%. In the case of thin gel layers ($\leq 10 \mu\text{m}$), at the end of the pattern formation, when little elastic energy is left, the last cracks stop growing. Thus they fail to cross the polygons formed by their older

neighbours and remain open ended (Fig. 3a). This is observed in leaves where the last veinlets remain open ended in the smallest areoles [8,9].

We can now focus on the organisation of the main veins (Fig. 1b). They are the first to form: the central (primary) vein when the leaf is still a peg-like shaped primordium, the secondary veins when the blade starts growing. In the most common organisation of dicotyledons, the main vein is axial and the secondary ones are pinnately organised. The main two archetypes are related to the morphology of the secondary veins. In the ‘brochidodromous’ organisation they form loops near the border (Fig. 1b) while in the ‘craspedodromous’ organisation they go straight to it.

These structures form in a tightly confined medium where the role of the boundaries is essential. We thus investigate the behaviour of cracks in confined media where they interact with boundaries. Our samples are now long and narrowing bands of suspension deposited on the glass plate. During drying, the meniscus bordering the deposited fluid is strongly pinned onto the substrate. The first fracture, longitudinal and centred, releases the transverse stress. Due to the remaining stress, transverse secondary cracks then form which can exhibit two behaviours. When the contact angle of the solution with the substrate is low ($\sim 25^\circ$) the cracks which grow towards the border, rotate away from it. The resulting pattern is then formed of a series of loops due to the collision of each secondary crack with its neighbour. Comparison of Figure 3b with Figure 1b shows that we have thus obtained the brochidodromous organisation. The contact angle of our latex suspension can be modified by adding salt to the solution. Values up to $\sim 45^\circ$ are thus obtained. In this case, the layer is thick near the meniscus and the fractures move straight to it, simulating the craspedodromous organisation.

These behaviours can be modelled by a simple 2D elastostatic model where the stresses in the strip, averaged throughout the thickness, are induced by the inhomogeneity of the concentration field. The differences between the small and large contact angles can be embedded in the boundary conditions. For small contact angles, the volume effect of the pinning is strong and induces a zero

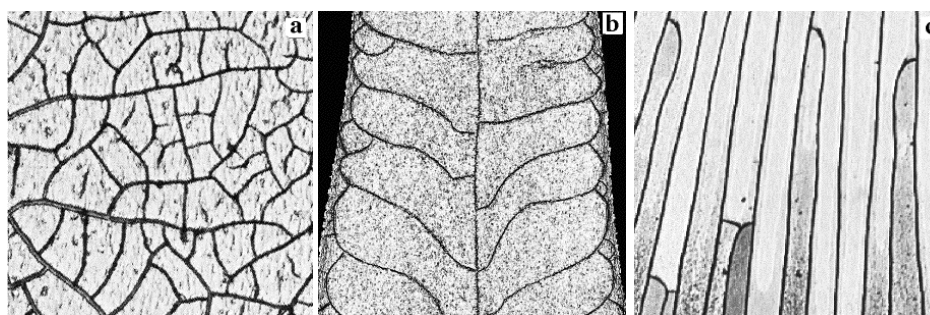


Fig. 3. (a) A pattern of cracks formed in a thin layer of gel, about $20\ \mu\text{m}$ thick in which the drying is spatially homogeneous. The typical spacing of the cracks is $80\ \mu\text{m}$. (b) The cracks resulting from the drying of a wedge shaped strip of gel deposited on a silicon wafer. (c) A pattern of cracks obtained in a gel layer having a constant thickness gradient. The drying of the gel proceeds from the thin region (at the bottom) to the thick one. When a crack stops growing it connects perpendicularly, first to one of its neighbour (top of the photograph), then to the other (bottom).

displacement in the direction perpendicular to the border. One can easily show that in this case the stress component normal to the border increases in its vicinity. The criterion due to Cotterell and Rice [16] states that the crack propagation becomes unstable when the stress parallel to the crack exceeds the opening stress. This argument explains that the crack, when approaching the border, rotates in order to keep releasing the main stress. In contrast, when the contact angle is large, the volume effect of the pinning is weak so that the boundaries of the strip can be considered as traction free. Thus the stress component parallel to the crack decreases when approaching the border. This explains the stable propagation of the crack in this region.

A third experiment is meant to simulate the most usual type of venation of monocotyledons where the main veins are parallel to each other (Fig. 1c). In order to obtain an anisotropic growth we performed directional drying of the gel layer. This is obtained with a large layer having a thickness gradient. The initial cracks form in the thinner region and propagate in the gradient direction [12], forming an array of parallel and equidistant fractures. After the propagation of these cracks, there remains a mismatch between the shrunken gel and the substrate, resulting in a longitudinal stress. A series of secondary fractures, perpendicular to the initial ones, will form and the final pattern will be similar to monocotyledons veins. Another detail of this type of venation can be reproduced. In *e.g.* bread wheat [17], or lily of the valley (Fig. 1c) the number of longitudinal veins reduces as the leaf becomes narrower near its tip. A stopped vein is connected with both its two neighbours. This situation can be simulated by giving a narrowing width to the sample. The cracks, as they grow, are forced to be nearer to each other than needed to release the stress. When a crack stops growing it connects perpendicularly with one of its neighbours, then with the other (Fig. 3c). The pattern is identical to that of leaves (Fig. 1c).

The fact that a large variety of venation patterns can be obtained with cracks suggests that the vein formation occurs in a tensorial field. In order to seek the possible origin of this field we must now recall some facts about plant physiology. A cross section of a leaf is characterised

by two epidermal layers separated by an inner tissue, the mesophyll. The veins are located in the mesophyll region. In their mature state they are complex bundles associating xylem and phloem which transport sieve and sap respectively. But what must be examined here is the period of formation. At the initial stage, the precursor of a future vein appears in the central region of the mesophyll when some cells differentiate into a specific tissue: the procambium. This procambium [8,9] is only weakly differentiated from the surrounding mesophyll and is characterised by strands of elongated cells with specific cell divisions. At this point it does not have transport properties. It is only later that procambium will differentiate into xylem and phloem and acquire them. Since the procambium forms the draft of the vascular system, the problem is that of its genesis.

From the previous study, a natural idea is that the mechanical stresses play a role in the differentiation of procambium. The mechanical stresses in botanical tissues have been shown to be very large and they have already been considered by botanists as being important in other morphogenetic problems such as phyllotaxis [18]. Several works [19,20] on growing organs, stems or hypocotyls, have shown that the parallel growth of the epidermis and of the inner tissues, generates growing stresses of opposite signs in these tissues. The stress is tensile in the epidermis and compressive in the inner tissues. The situation is similar in leaves where the mesophyll is submitted to a compressive stress which increases as the leaf grows in size.

We present the hypothesis that the differentiation into procambium is the response of mesophyll cells submitted to a compressive stress exceeding a threshold value. It is thus somewhat similar to the breakdown of physical cellular solids under compression [21] which is known to form localised squeezed bands of collapsed cells. The difference is that here we rather assume that when the compressive stress becomes large, the cells of band shaped regions react by having specific cell divisions where the newly formed partition is perpendicular to the main stress. This process has already been observed in a different context. Experiments [22,23] performed on botanical tissues have clearly

shown that oriented cell divisions can be forced by an externally applied compressive stress. In these situations, as in our hypothesis, the new wall forms perpendicularly to the direction of main compression, a shear free direction.

Within this model the analogy of the morphology of the veins with the fractures is reduced to a basic origin: both grow in tensorial stress fields. We can add three remarks. (i) Since the increase of the stresses is due to the leaf expansion, the model links directly the formation of veins to the growth. As a result the homogeneity of the venation is guaranteed. (ii) At the leaf edge the two epidermis meet; the stress, which comes from the mismatch between the mesophyll and the two epidermis, vanishes so that the border is analogous to the menisci of our experiments. (iii) While the cracks meet exactly at right angle, other angles are possible for veins because, once formed, they keep a role in the mechanical properties of the tissue, while cracks correspond to a complete disruption of this material. These angles are investigated elsewhere [24].

A large number of works have discussed the roles of biochemical [2,3] and mechanical [18] processes in the morphogenesis of plants. While the former has been demonstrated by many experiments [25], the direct evidence for the latter is scarcer. This is the context which gives its meaning to our results, since they suggest that the mechanical stresses in growing tissues determine the geometry of procambial strands. The reality is certainly complex with an interplay of mechanics and biochemistry since the hormones which have strong morphological effects, auxins or expansins [25], are known to modify the mechanical properties of the cells. More work is needed to characterize this interplay which is certainly essential in the regulation of a coherent tissue growth.

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