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► **To cite this version:**

Vincent Hakim. From growing bubbles and dendrites to biological forms. *Comptes Rendus. Mécanique*, 2020, 348 (6-7), pp.627-636. 10.5802/crmeca.23 . hal-03028988

HAL Id: hal-03028988

<https://hal.science/hal-03028988v1>

Submitted on 23 Aug 2024

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INSTITUT DE FRANCE
Académie des sciences

Comptes Rendus

Mécanique

Vincent Hakim

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Volume 348, issue 6-7 (2020), p. 627-636

Published online: 16 November 2020

Issue date: 16 November 2020

<https://doi.org/10.5802/crmeca.23>

Part of Special Issue: Tribute to an exemplary man: Yves Couder

Guest editors: Martine Ben Amar (Paris Sciences & Lettres, LPENS, Paris, France),
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Les Comptes Rendus. Mécanique sont membres du
Centre Mersenne pour l'édition scientifique ouverte
www.centre-mersenne.org
e-ISSN : 1873-7234



Tribute to an exemplary man: Yves Couder

Morphogenesis, elasticity

From growing bubbles and dendrites to biological forms

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Abstract. We first describe how some ingenious experiments performed by Yves Couder illuminated the physics of viscous fingering and dendritic growth in solidification. We then recall the analogy he stressed between leaf venation and fractures in drying gels and how this and other results obtained by Yves, greatly contributed to highlight the role of mechanical forces in biological development. Finally, we briefly describe the recently appreciated role of phase separation, a topic with many important contributions of Yves, for the description of membraneless intracellular organelles.

Résumé. Ce court texte est dédié à la mémoire d'Yves Couder. Nous commençons par décrire brièvement comment quelques expériences qu'il a menées ont mis en évidence des mécanismes fondamentaux à l'oeuvre dans la croissance de digitations visqueuses en mécanique des fluides et, de dendrites cristallines en solidification. Nous rappelons ensuite l'analogie qu'il a soulignée entre les formes des veines sur les feuilles végétales et celles des fractures apparaissant à la surface de gels se desséchant, et comment ces expériences, et d'autres qu'il a conduites, ont souligné le rôle important des forces mécaniques dans le développement biologique. Nous concluons sur l'importance, récemment appréciée, du phénomène de séparation de phase, que les contributions d'Yves ont permis de mieux comprendre, pour l'existence d'organelles intracellulaires sans membrane.

Keywords. Diffusion-controlled growth, Viscous fingering, Solidification, Phase condensation, Synapses.

1. Introduction

It is with sadness and the feeling of a deep loss that I am contributing to this memorial volume for Yves Couder. Yves was a very talented and inventive experimental physicist. He admired the works of G. I. Taylor [1] and took great inspiration from them with an unusual ability to devise “simple” experiments that produced wholly surprising results. I take the opportunity of this article to recall a few of these that he obtained in the 80's at ENS when I had the chance to get to know Yves and to collaborate with him.

A main achievement of statistical physics in the 70s was the understanding of scaling and of the appearance of non-trivial exponents at phase transition points in systems at thermodynamics equilibrium [2]. Turbulence in fluid dynamics and its well-known scaling laws, appeared as one

central phenomenon that remained to be precisely understood (and still is today, in spite of much progress). Nonlinear dynamics and chaos in systems with few degrees of freedom attracted a renewed attention in the physics community. The theoretical discovery of scaling in the routes to chaos [3–6], as well as its observation in experiments [7] seemed to many as an encouraging promise. Yves Couder watched from close these developments as he was pursuing his research at ENS in solid state physics [8]. Taking the opportunity of an experimental class he was teaching, Yves changed his research field to fluid dynamics and turbulence, a subject that always remained dear to his heart (see e.g. [9, 10]). Yves's ingenuity became immediately apparent with his entry in the subject. He introduced soap films [11] to study with Marc Rabaud, his first PhD student [12] and others [13, 14], two dimensional phenomena in fluid mechanics, like vortex formation, shear instabilities, instabilities of von Kármán wakes and of course two dimensional turbulence [15] (by towing a comb in the soap film).

In 1981, a different display of ingenuity came from a different place and would attract the attention of Yves for some years. Tom Witten and Len Sander invented Diffusion-Limited-Aggregation (DLA) [16]. In the so-called off-lattice version of this simple model, brownian hard disks are successively released randomly away from a preexisting cluster, attach to it upon encounter and make the cluster grow. The striking observation is that computer simulation of these simple rules creates a growing cluster which is a random fractal, of dimension $d \simeq 1.7$ in a two dimensional setting. Understanding this phenomenon appeared to many more important than the initial motivation of DLA as a model of soot formation or of coagulated aerosols. Mathematically, the probability field of the brownian disks in DLA controls the growth of the random cluster. It was immediately realized that deterministic analogs of DLA were to be found in dendritic growth in an undercooled melt or in a supersaturated solution. Heat or concentration replaces in these settings the brownian disks and their diffusion controls the motion of the solid-liquid interface. The diffusion field can even be approximated by a solution of the Laplace equation in the regime when the growth velocity is slow enough for the diffusion length $l_d = D/v$ to be much longer than the aggregate, with D the diffusion constant of heat or solute and v the interface velocity.

Dendritic growth is a prominent feature of solidification and plays an important role in metallurgical processes which provides sufficient motivation in itself to try and understand it [17]. Related phenomena involving the motion of an interface controlled by a Laplacian field also arise in fluid mechanics. When gas is blown into oil between two thinly spaced horizontal glass plates, a so-called Hele-Shaw cell, a gas bubble grows. The dynamics of the gas/oil interface is governed by the pressure field in the oil which can be assumed constant in the transverse/vertical direction. In this setting, the pressure is a two-dimensional field that obeys Laplace's equation. It is a real life counterpart of the probability field in DLA [18]. In this somewhat specialized corner of fluid mechanics, there remained a small puzzle at the beginning of the 80's. GI Taylor and his then student Phil Saffman had carried the experiment in the 50's, motivated by the analogy with the technique of oil extraction which consists of pumping water into an oil-containing porous medium. They had observed that when carried out in a long channel the gas bubble occupied only half of the channel width [19]. Saffman and Taylor had also obtained an analytic description of the advancing bubble shape, the "Saffman-Taylor finger", by assuming a constant pressure drop between the gas and the oil at the gas/oil interface. This reasonable approximation follows from Laplace's law for the pressure difference due to capillary effects, by assuming that the varying curvature of the finger in the horizontal plane could be neglected as compared to its much higher and approximately constant curvature in the vertical direction between the closely-spaced glass plates. The puzzle was that Saffman and Taylor had obtained a continuous family of finger shapes occupying different fraction λ of the channel but that only the $\lambda = 1/2$ shape corresponded to their experimental finding. They had found no good theoretical reason to select this particular shape. An analogous difficulty also existed for dendritic growth. Ivantsov had found in the 40's that a para-

bolic shape was a solution for a growing dendrite growing in an undercooled medium when the solid interface was supposed to be at the thermodynamic liquid/solid melting temperature [20]. But there, as for the Saffman–Taylor finger, it only determined the product ρV of ρ , the radius curvature of the parabola tip, times V , the dendrite growing velocity, as a function of the undercooling. In this case, the source of the problem was clear on dimensional ground alone, since the diffusion constant was the only dimensional constant available to scale length in Ivantsov's treatment. Introducing another dimensional quantity was required to determine separately ρ and V . Taking into account the small melting temperature change due interface curvature, the Gibbs–Thomson effect, could improve the situation but it was not clear how to properly do it, in spite of some efforts, particularly by Jim Langer [17] and his collaborators.

2. Diffusion-controlled growth at ENS in the 80's

In part motivated by DLA, different labs repeated the Saffman and Taylor's experiment in the mid 80's. In particular, Patrick Tabeling investigated the phenomenon during his stay in the then newly founded Libchaber's lab at Chicago [21] and continued to do it when he created his own lab at ENS, next door from Yves'. Yves proposed to his students to perform the experiment in a radial setting and to revisit previous results by Paterson [18], again as an experimental project in the class he was teaching. When gas is blown in the center of a Hele-Shaw cell, the growing bubble is initially circular but it soon becomes unstable. It develops a convoluted shape with several arms, perhaps evolving toward the fractal shape of a DLA cluster. In this simple setting, typically for Yves, he and his students soon noted [22] a startling phenomenon that has escaped the attention of others. A few small air bubbles remained in their set-up after they had filled it with oil. When one arm of the growing bubble hit one of these small bubbles, its shape was completely transformed: it started to resemble a growing dendrite, as shown in Figure 1 (reproduced from [22]). Back in his own lab, Yves and his collaborators carefully introduced a small bubble in the Saffman–Taylor experiment in a channel and produced the whole series of finger shapes of any width λ [23], by varying the gas flux injection rate. Similar results were obtained by putting a thin thread or by carving a thin groove in the center of the channel [24]. These results showed that the growing shape was extremely sensitive to perturbations at its tip.

These discovery by Yves and his collaborators strongly resonated with theoretically findings obtained at about the same time (see [25] for a review and reprints of some articles). With the advent of computers, Phil Saffman came back, 20 years later, to the unsolved selection question for Saffman–Taylor fingers. With his student John McLean, they numerically solved the equation for the interface profile and showed that only the $\lambda = 1/2$ solution was obtained, as in the experiment, when taking into account the pressure variation due to capillary effects [26]. The role of the tip boundary condition was nicely exemplified in a following numerical work [27] where it was shown that in presence of capillarity effects a whole discrete family of solutions existed, $\lambda = 1/2$ being the lowest and presumably only stable member. The theoretical explanation of this results was obtained concomitantly to the beautiful experimental work of Yves. Different theoretical groups at U.C. Santa Barbara around Jim Langer, at Schlumberger-Doll Research, at Chicago U. and at ENS around Y Pomeau showed that capillary effects even though formally small, were a crucial singular perturbation of the zero surface-tension case. It was shown that capillary effects produced exponentially small effects, of the form $\exp(-C/\epsilon)$ with ϵ the small parameter, responsible for selecting the growing form, which explained previous unsuccessful perturbative attempts. For Saffman–Taylor fingers this provided a quantitative explanation of the numerical results. Perhaps, more importantly, it showed that, similarly to threads and grooved plates in Yves' experiments, anisotropy in the surface tension of crystals was necessary for the existence of dendrites and was responsible for the selection of the growth velocity (see [25, 28]).

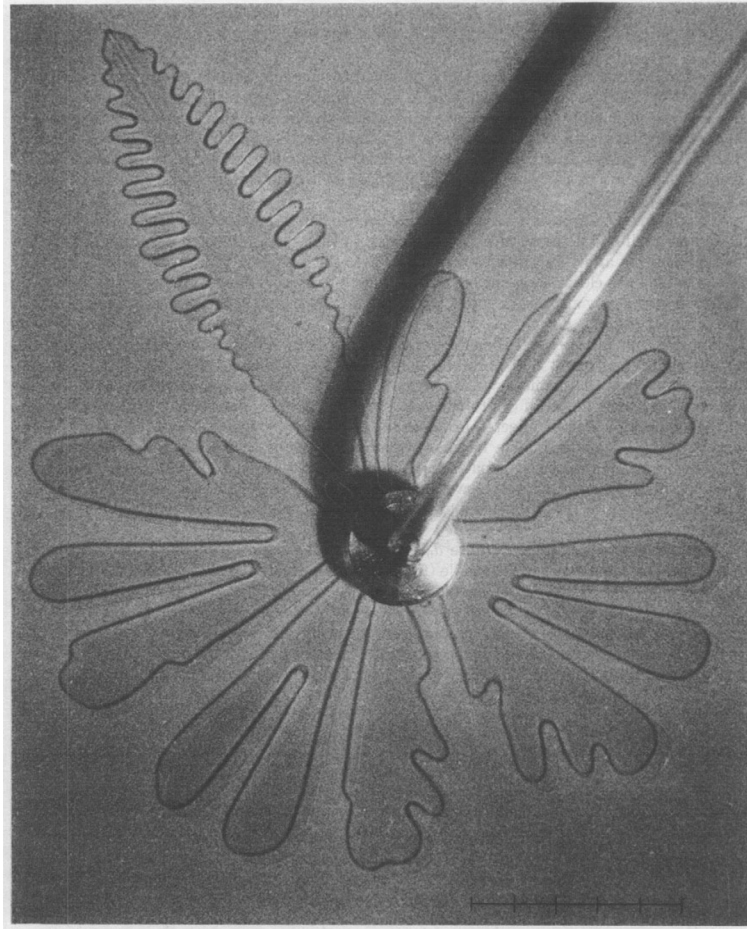


Figure 1. Pattern obtained by blowing nitrogen into oil in a Hele-Shaw cell with plate spacing $b = 0.04$ cm. The scale at the bottom of the picture is graduated in cm. The velocity of growth of the dendritic finger is 1.8 times the velocity of the other fingers. This particular dendrite is due to a pulsating tip created by a very small gas bubble trapped at its extremity. (Reproduced with permission from [22].)

For the next further few years, experiments and theory went hand-in-hand with Yves' insightful experiments continuing to play a key role. Metal disks were drawn in front of growing bubbles to create control singularities in the complex plane and dramatically change the bubble shape [29], knots were added to threads to measure the bubble response to perturbations [24] and air was blown into wedge shape cells to uncover bubbles growing self-similarly [30] as well as unexpected twists on their selection mechanism [31, 32]. Air sucked into oil between two rotating cylinders was shown to be an analog of the liquid solid interface of directional solidification, where a melted alloy solidifies by being drawn into a cold region. This “printer instability” [33, 34] allowed Yves and his collaborators to show the existence various possible interface instabilities, and also of sustained spatio-temporal chaos [35], as shown in Figure 2.

All these contributions by Yves played a key role in the elucidation of the fundamental mechanisms of diffusion-limited growth. This helped in particular to clarify basic mechanisms in solidification and analyze its myriad of phenomena from fundamental principles, an approach that has, by now, grown into a fully mature science [36].

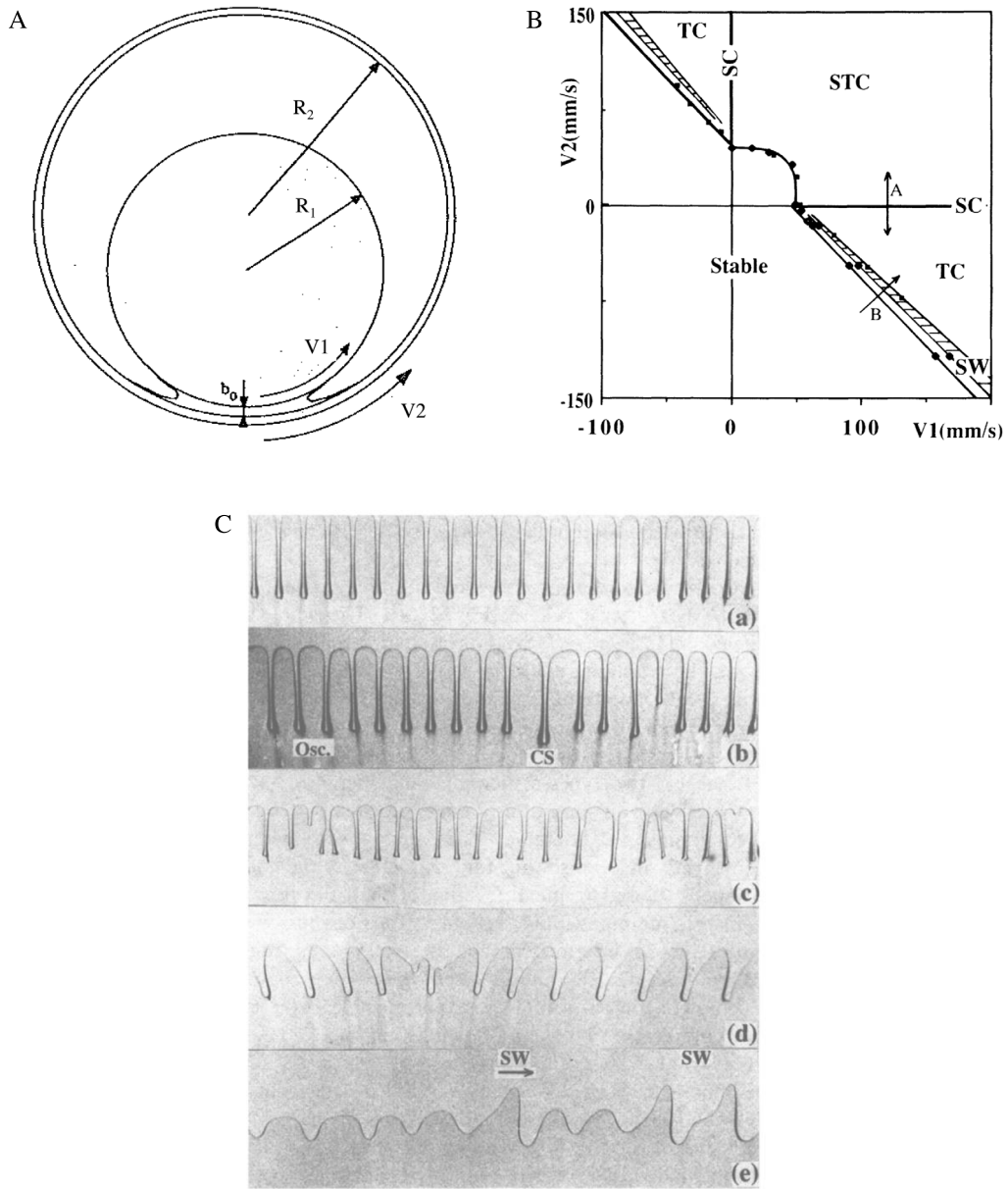


Figure 2. (A) Sketch of the experimental apparatus showing the two rotating cylinders coated by oil and the two menisci limiting the gap region. (B) Stability diagram of one meniscus in the plane (V_1, V_2) in a cell of minimum thickness $b_0 = 0.37$ mm, with cylinders radii $R_1 = 71$ mm, $R_2 = 49$ mm. One observes stationary periodic cells (SC on the two axes), spatiotemporal chaos (STC), traveling cells (TC), and solitary waves (SW) moving on a stationary sinusoidal front (hatched region). (C) Photographs of a part of the front in the cases of (a) a stable pattern of stationary cells; (b) a pattern with weak spatiotemporal chaos showing a coherent structure (CS) and cells oscillating in time (Osc); (c) a pattern with strong spatiotemporal chaos; (d) a pattern of traveling cells (TC), showing a source and a sink; and (e) solitary waves (SW) propagating on a stationary sinusoid. (Reproduced with permission from [35].)

3. From physics to biology

The development of biological organisms displays fascinating examples of pattern formation and morphogenesis. At the beginning of the 90's, it appeared to many people that advances in the understanding of physical patterns as well as in biology, made it possible to try and analyze the basic underlying mechanisms. This was certainly the feeling of a number of physicists that had studied dendrites or viscous fingering, Yves being one prominent example. Yves got particularly interested in plants, motivated by the diversity of their forms as well as the ease of collecting, keeping and examining diverse specimen. Yves' beautiful work with Stephane Douady on pyllotaxis is well known [37]. I would like to recall here, other contributions of Yves, more related to his work on dendrites and that, I believe, have deeply influenced our current view of morphogenesis.

Yves noted and stressed the analogy between the venation pattern of leaves and those of fractures in drying gels [38]. A scalar diffusing field is screened by existing structures. For instance in DLA diffusing particles do not reach the interior of an existing aggregate and different growing branches appear to avoid each other. This is not the case for fractures, the growth of which is controlled by a stress field. A fracture only releases the stress normal to it but leaves residual parallel stress which allows another fracture to join it in a perpendicular direction. Yves and his collaborators noted that leaf veins, similarly to fracture, appeared to join at right angles, as shown in Figure 3. They thus proposed that leaf venation was controlled by a tensorial field [39]. More generally, it suggested and led Yves to think that mechanical constraints played an important role in morphogenesis and cell differentiation, an idea that was also supported by other works [40, 41] but that was not widely accepted at the time. This motivated Yves to try and directly apply forces on growing plants. In a collaborative work between his lab and plant development experts, he showed that applying force to a growing meristem changed its shape and reoriented microtubules in meristem cells towards maximal stress orientations. This very influential work [42] has certainly played a significant role in the now widely shared view that mechanics is a key actor in development of both plants and animals [43, 44].

4. Phase condensation and diffusion-controlled interfaces in biology?

As recalled above, Yves contributed very much to the present understanding of viscous fingering and dendrites formation in solidification [45]. These structures rely on phase separation between a solution and a solid phase, or between gas and oil. More recently, the importance of phase separation for cellular biology has become recognized [46–48]. This promises further developments of this classic subject. While organelles like the Golgi apparatus or the endoplasmic reticulum are separated by a membrane from the rest of the cell, other organelles are membraneless. One prominent example is the nucleolus, the largest organelle inside the nucleus of eukaryotic cells, which is the site of ribosome biogenesis and which also sequesters many proteins. Less familiar examples include Cajal bodies, PML bodies or cleavage bodies in the nucleus and stress granules and processing bodies in the cytoplasm [47]. Some behave like liquids droplets and can fused or be fissioned by shear, while other, like stress granules behave in a more solid-like manner. In recent years, it has been proposed with much success that these membraneless organelles are the result of phase separation [46–48].

Phase separation can also be at work to create structures of lower dimensionality. For instance, it has been suggested to produce lipid rafts [49] in membrane, or clusters of proteins in the membrane or close to it, like E-cadherin clusters [50], or postsynaptic domains [51–53] to which we will return below. Phase separation can also be at play, in one dimension along the DNA, to create structures like heterochromatin domains (see [54] and references therein) or transcriptional enhancers (see [55] and references therein).

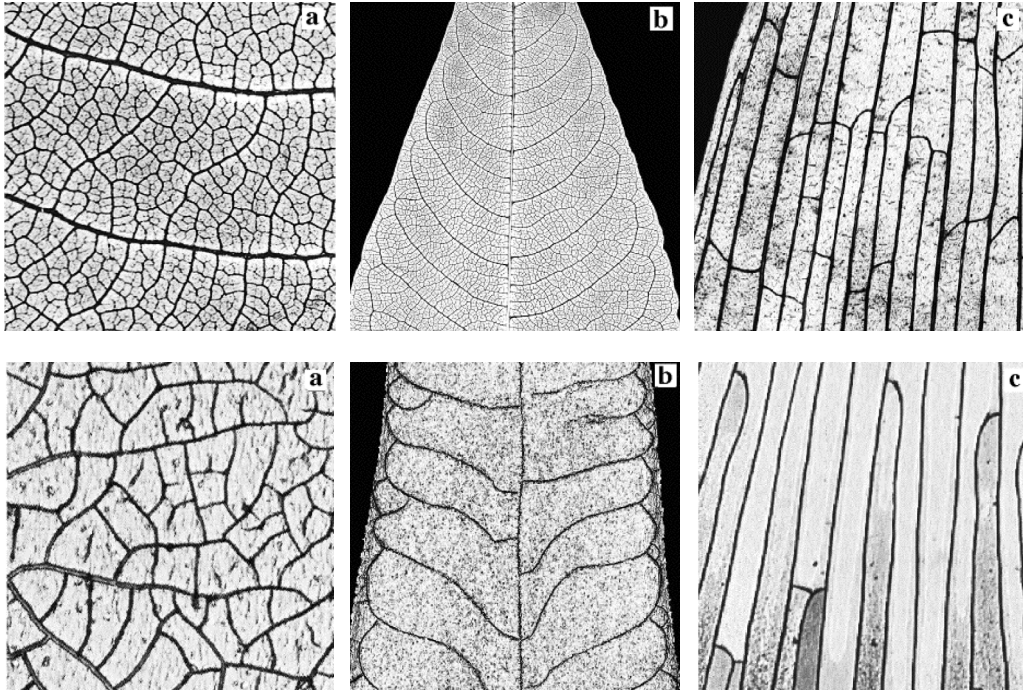


Figure 3. Top: three examples of leaf venation patterns. (a) The polygonal net-like structure of the small veins of a leaf of *Polygonum Polystachium*. (b) The secondary veins of *Polygonum Polystachium* are all connected to each other by loops located near the leaf margin. (c) A detail of the venation of Lily of the valley, *Convallaria Maialis*, a monocotyledon. Bottom : three examples of crack patterns. (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. (Reproduced with permission from [39].)

One general question that needs to be addressed in these phase separation scenarii is the formation of structures of finite size [46–48]. As is well-known [56], the appearance of the favored phase in the less favored ones depends on the creation of nuclei larger than a critical size. These nuclei then grow and invade the less favored ones, like for instance crytalline dendrites in a supersaturated solution. This leads to a decrease in the difference of free energy between the two phases e.g. supersaturation decreases and to a late coarsening regime. This ultimately produces a single structure, the size of which is only limited by the available material. Moderate-size structures can be created by different mechanisms, the structure material can be in limited amount, phase separation can take place in a subcellular compartment (e.g. a spine for excitatory synapses [52]) or in the presence of further stabilizing components. Activity i.e. spending energy to maintain the structure is an alternative strategy that we now discuss on the example of synapses.

Synapses are particular interesting since these chemical junctions are the site of information transmission between two neurons and are also believed to be the substrate of memory. In spite of this latest function, synapses are very dynamic structures [57]. Neurotransmitter receptors continuously go in and out synapses and even structural scaffolding proteins, like gephyrin

for inhibitory synapses, have a residence time at synapses shorter than the hour. Building on available data, it has been proposed in [53] that post-synaptic domains are diffusion-controlled structures. In this proposed picture, gephyrin molecules are brought to the synapse attached to receptors that diffuse laterally in the membrane. This leads to growth of the post-synaptic domain similarly to the growth of a two-dimensional crystal in a supersaturated solution. However, this growth is proposed to be counterbalanced by the turnover of gephyrin molecule into the cytoplasm. This leads to the formation and maintenance of a long-lived structure of finite size [58]. Analogous turnover mechanisms have been proposed in the context of lipid rafts [49] and the arrest of coarsening by chemical reactions has also been studied theoretically [59].

Rearrangement after aggregation appears sufficiently fast in the case of post-synaptic domains and obviously for liquid ones, so that the structure is not ramified like a snowflake, a DLA cluster or a growing bubble in radial viscous fingering. However, it cannot be excluded that biological structures with more complex shapes remain to be discovered. I cannot resist but think that this would have picked Yves' curiosity and that he would have conceived and performed a simple illuminating experiment to try and see which complex shapes could be produced by diffusion and turnover.

Acknowledgements

I wish to thank Marc Rabaud for his critical reading of the present manuscript and for useful comments, and him and Ludovic Pauchard for their help in reproducing figures from their works with Yves.

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