Phyllotaxis as a Physical Self-Organized Growth Process

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A specific crystalline order, involving the Fibonacci series, had until now only been observed in plants (phyllotaxis). Here, these patterns are obtained both in a physics laboratory experiment and in a numerical simulation. They arise from self-organization in an iterative process. They are selected depending on only one parameter describing the successive appearance of new elements, and on initial conditions. The ordering is explained as due to the system's trend to avoid rational (periodic) organization, thus leading to a convergence towards the golden mean.

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The elements of a plant (leaves, sepals, florets, etc.) form very regular lattices, with a crystallinelike order. In the most common arrangement (e.g., on a sunflower head or a pinecone), the eye is attracted to conspicuous spirals (*the parastichies*) linking each element to its nearest neighbors. The whole surface is covered with a number i of parallel spirals running in one direction, and j in the other. The most striking feature is that (i,j) are nearly always two consecutive numbers of the Fibonacci series, $\{F_k\}=\{1,1,2,3,5,8,13,21,34,\ldots\}$ where each new term is the sum of the two preceding ones. Early works [1-3] showed that such patterns resulted from the successive appearance of the elements on a uniquely tightly wound spiral, called *the generative spiral*. The basic quantity is then *the divergence* φ which is the angle between the radial directions of two consecutive elements. Measurements [3] of divergences on mature plants showed that they were surprisingly close to the golden section: $\Phi=2\pi(1-\tau)\approx 137.5°$, where $\tau=(-1+\sqrt{5})/2$ is the golden mean.

A basic hypothesis is that these phyllotactic patterns result from the conditions of appearance of the primordia near the tip of the growing shoots (for reviews see Refs. [4] and [5]). The stem tips (the apical meristems) have axisymmetric profiles [Fig. 1(a)]. The summit is occupied by a stable region: the apex. The primordia (which will evolve into leaves, petals, stamens, florets, etc.) are first visible as small protrusions at the periphery of the apex. In the reference frame of the tip, due to the growth, the existing primordia are advected away from the apex while new ones continue to be formed [6]. In botany, it was suggested [7] that a new primordium appears with a periodicity T near the tip in the largest gap left between the previous primordia and the apex.

Altogether this forms an iterative process which we wish to investigate as a dynamical system. To implement a laboratory experiment and a numerical simulation, we retained from botany the following characteristics: Identical elements are generated with a periodicity T at a given radius R_0 from a center in a plane surface [8]. They are radially advected at velocity V_0, and there is a repulsive interaction between them (so that the new element will appear as far as possible from the preceding ones, i.e., in the largest available place). The results can be interpreted using only one adimensional parameter $G=V_0T/R_0$.

The experimental system [Fig. 1(b)] consists of a horizontal dish filled with silicone oil and placed in a vertical magnetic field $H(r)$ created by two coils near the Helmholtz position. Drops of ferrofluid of equal volume ($v\approx 10$ mm^3) fall with a tunable periodicity T at the center of the cell. The drops are polarized by the field and form small magnetic dipoles, which repel each other with a force proportional to d^{-4} (where d is their distance). These dipoles are advected by a radial gradient of the magnetic field (from 2.4×10^4 A/m at the center to 2.48×10^4 A/m at the border of the dish), their velocity $V(r)$ being limited by the viscous friction of the oil. In order to model the apex, the dish has a small truncated cone at its center, so that the drop introduced at its tip quickly falls to its periphery. G can be tuned by changing either the periodicity T or the gradient of H (controlling

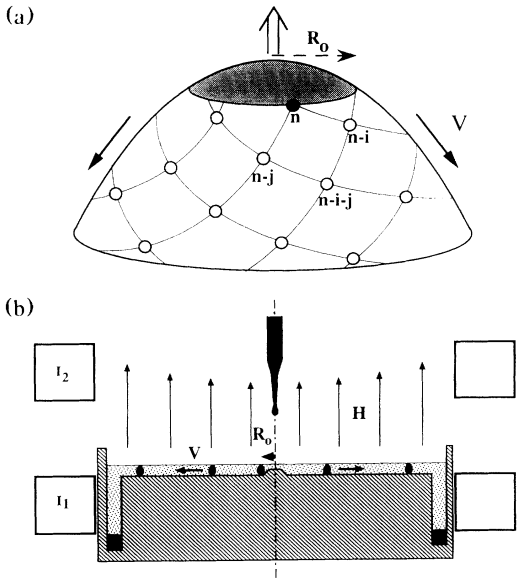

FIG. 1. (a) Sketch of the growth in plants. (b) Sketch of the experimental apparatus.

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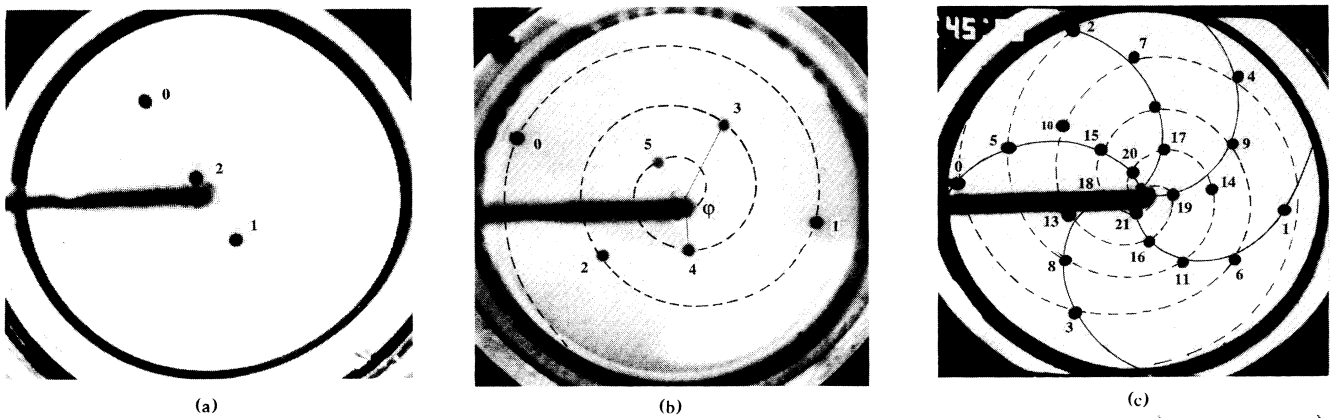

FIG. 2. Three photographs of experimental patterns. The numbers show the order of deposition of the drops (arbitrary origin). (a) $G \approx 1, \varphi = 180°$. (b) $G \approx 0.7, \varphi = 150°$ with $(i=1, j=2)$. (c) $G \approx 0.15, \varphi \approx 139°$ with $(i=3, j=5)$.

V_0). The drops ultimately fall into a ditch at the periphery. We used an ionic ferrofluid in nitric acid [9] with a volumic concentration of 8%. The magnetization was $M = \chi H$ with $\chi = 0.493$.

The experiment shows that the final steady pattern depends crucially on G. For a strong advection [Fig. 2(a), $G = 1$], each new drop is repelled only by the previous one so that successive drops move away in opposite directions (this mode with $\varphi = 180°$ is called the alternate or distichous mode in botany). Below a threshold $G_{1,1}$ each new drop is repelled by the two previous ones and cannot remain in line with them. When the third drop slides to one of either side of this line there is a symmetry breaking into a chiral mode which selects once and for all the direction of rotation of the generative spiral. A steady regime is reached with a constant divergence φ [in Fig. 2(b), $\varphi = 150°$ and $i=1$, $j=2$]. For smaller G the new drop becomes sensitive to the interaction of three or more previous ones, and the divergence gets nearer to Φ. In Fig. 2(c) for $G = 0.15$, $\varphi = 139°$ and the spiral Fibonacci mode is $i=3$, $j=5$.

Our numerical simulations are based on similar physical hypotheses. In a plane, the locus of appearance of elements is a circle C of radius R_0 centered at the origin. These elements are punctual particles, each generating a repulsive energy $E(d)$, where d is the distance to the particle. Several energy laws were used, $1/d$, $1/d^3$ (case of the ferrofluid drops), and $\exp(-d/l)$: the results were qualitatively the same. To decide the place of birth of a particle, we compute in each point of the circle C the value of the total energy due to all the previous particles, and place the new element at the point of minimum energy. All particles after their appearance are given the same radial motion with a velocity $V(r)$, thus neglecting any later reorganization due to the interaction of particles [10]. In this case the results are qualitatively independent of the chosen radial motion. In order to remain close to botany [4,5] we chose an exponential growth $[V(r) = V_0 r / R_0]$.

A brutal way to start the simulation is, at a fixed value of G, to begin without any previous particles and to see which pattern is spontaneously obtained. For large G (> 0.4) the divergence angles are the same as in the experiment. But for small G, the system undergoes long transients, and either converges on various steady regimes (with several possible values of φ) or stabilizes on more or less complicated periodic regimes. We will focus on the steady regimes [11]. The possible values of φ plotted versus G form several curves (Fig. 3). In order to investigate the limits of existence of each curve, we also initially forced an artificial pattern and observed whether it could keep growing. We find all the curves in Fig. 3 to be interrupted above a limiting value of G, except for the main one. All the obtained patterns present spirals with a given set of parastichies numbers (i,j) (Fig. 4). Along a

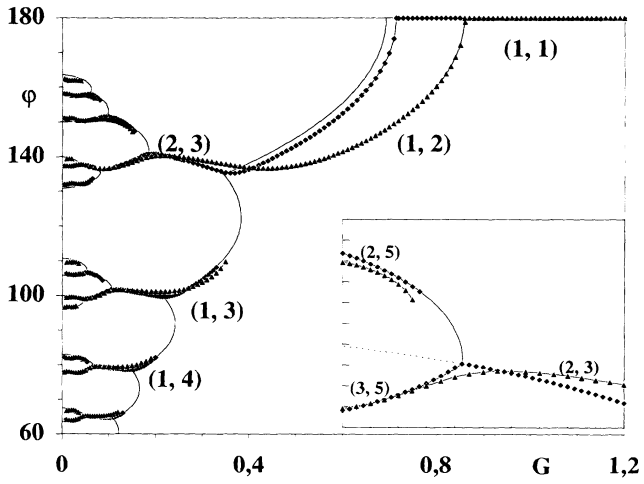

FIG. 3. Diagram of the steady divergences φ ($\varphi > 0$) obtained as a function of G for two energy profiles $1/d^3$ (triangles) and $\exp(-d/l)$ with $l = 0.1$ (squares). The solid line shows a diagram obtained using the geometrical condition. Inset: Detail of a transition.

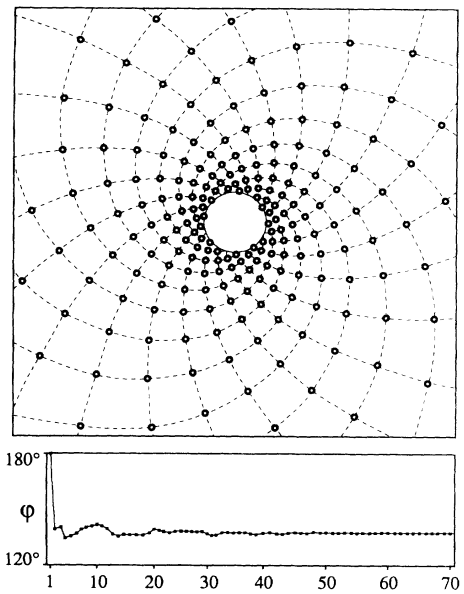

FIG. 4. A pattern $i=13$, $j=21$ obtained after a transient from $G=1$ to $G=0.01$ which lasted $6T$. At the bottom the convergence of φ from 180° to 137.47° is shown.

curve, when G is decreased the pattern undergoes a transition, at $G_{i,j}$, from parastichies numbers (i,j) to $(j,i+j)$. This corresponds to the change of sign of the slope in the curve $\varphi(G)$. A remarkable asset of the diagram (Fig. 3) is that near each $G_{i,j}$ a new curve with parastichies numbers $(i,i+j)$ also appears with a different φ and thus disconnected. Following a given curve $\varphi(G)$, a Fibonacci type of series builds up because of the transition rule $(i,j)\rightarrow(j,i+j)$. Each of the curves $\varphi(G)$ corresponds to a different pair of initial terms for the series and converges for $G=0$, towards the related irrational angle. The main curve goes to 137.508°, the others to 99.502°, 77.955°, 151.135°, etc. [3].

In terms of iterative dynamical systems, these transitions are bifurcations. We find that near $G_{1,1}$, the threshold of the first bifurcation, the divergence φ varies as $180°-\varphi\propto(G_{1,1}-G)^{1/2}$, and the number of iterations (i.e., of particles) necessary to reach a steady regime diverges. These are the characteristics of a direct symmetry-breaking bifurcation. Here it leads from an alternate pattern to a chiral spiral pattern. All the other bifurcations, because the symmetry is already broken, are imperfect (see below): at each of them only one curve is continuous and a new curve appears disconnected (Fig. 3).

This is the key point of our result, and the main difference with previous works [12–14] obtaining a type of diagram first derived by Van Iterson [12]. He reproduced the phyllotactic arrangements by looking to the regular patterns formed by hard disks paving a cylinder (or a cone) and found a relation between φ and the ratio of the radius of the disks to that of the cylinder. In our case, a diagram of this type can also be obtained by stating that a new particle appears exactly equidistant from $n-i$ and $n-j$ [cf. Fig. 1(a)]. This approximation transforms our dynamical problem into a geometrical one. If a geometrical constant H of the assumed regular spiral [15] is set equivalent to G, it is possible to compare the geometrical relation between φ and H [for each (i,j)] and our simulations results (Fig. 3). As in all geometrical models [12–14], the curve corresponding to parastichies (i,j) (with $j>i$) is connected at G_{ij} with the two curves $(j,i+j)$ and $(i,i+j)$. The geometrical models fail to obtain the selection because they do not take into account the fact that the condition on the new element is not only to be located between two previous ones, but also that its place should be the best (e.g., the largest space). To our knowledge only one previous work [16] has used such a criterion in the simulation of the diffusion of an inhibitor in a cylindrical geometry. A convergence of φ towards Φ had been obtained though the overall structure of the bifurcations diagram was not described.

All the bifurcations and their imperfections can be simply interpreted. For parastichies numbers (i,j), the new particle n is repelled essentially by the j previous ones, and is precisely between $n-i$ and $n-j$ [17]. If G was decreased and no other particles other than the latest j are taken into account, the divergence would tend toward a rational: n would appear at the same angular position as a previous particle, which, from the regularity of the pattern, is $n-(i+j)$. But near G_{ij}, the repulsion due to $n-(i+j)$ becomes no longer negligible and n slides to avoid the proximity of this particle. As $n-j$ is older than $n-i$, the situation is not symmetrical and n is always angularly between $n-(i+j)$ and $n-j$ [Fig. 1(a)]. Below G_{ij}, n thus slides between $n-j$ and $n-(i+j)$ selecting the transition with the Fibonacci rule. When G is decreased, the system thus avoids all the successive possible periodic arrangements and φ converges towards the simplest irrational numbers. Figure 4 shows a pattern obtained after a short transition (lasting $6T$) in which G has decreased from 1 to 0.01. In the resulting steady regime $i=13$, $j=21$ and $\varphi=137.47°$.

Our results can be compared to those of Levitov [18] published during the course of our work. In a cylindrical geometry he assumed a regular helical lattice with repelling elements, and sought the lattice slope for which the interaction energy is minimum. He showed that the compression of the whole lattice produces a similar diagram of imperfect bifurcations. This theoretical work appears far from the problem of botanical growth. The relation to our work, however, is similar to that between the investigation of the energy of periodic lattices and the search for the growth mechanism of crystals. The convergence of both results shows that the dynamics of appearance of the new primordia at the place of lowest repulsive energy creates a final structure of minimum glo-

bal interaction energy.

Examining finally the relevance of our results to botany we can note that the process we described is robust relative to the law of interaction. A hypothesis for the physiological process of the primordia's interaction was thus not necessary. Our model is also robust relative to

[9] R. Massart, IEEE Trans. Magn. **17**, 1247 (1981).
[10] Note that the repulsion of the particles is only important initially. We checked this in the experiment: The trajectories of the drops are radial except very near the center. This is also coherent with the botanical observations, in which no primordia motions were ever reported.
[11] The regime in which φ oscillates in time corresponds ei-