A physical investigation of the iterative process of botanical growth

S. Douady and Y. Couder
Laboratoire de Physique Statistique,
24 rue Lhomond, 75231 Paris Cedex 05, France.

Two types of organisations are observed for the positions of successive elements (leaves, sepals, petals, stamens...) around the stem of a plant. In the first type of organisation, only one element appears at a time and the successive elements form a regular helix around the stem (spiral modes). In the second, several elements appear simultanuously and form successive whorls along the stem. Of these later modes one is very common in which two opposite leaves are formed simultanuously, successive pairs growing at right angle from each other. It is called the opposite decussate mode by the botanists.

In the first part of the present communication we will show that a physical model[1] based on the simplest iterative rule, gives rise to a self-organization process and produces the specific spiral organisation observed in plants. In the second part of the talk we will present recent results showing that, in a variant of the iterative rule, it is possible to obtain both the whorled organisations and the spiral order. The choice between the two dispositions depends only on the value of the characteristic parameter of growth and on the initial conditions.

First model.

Since the work of A. and L. Bravais[2] more than a century ago, the characteristics of the very specific botanical spiral organisation, has attracted the physicists and the mathematicians interest. The specificity of this organisation is particularly visible on a pine cone or on a sunflower head: the elements are organized in spirals and the numbers of parallel spirals in each directions are two consecutive numbers of the Fibonnaci series (1, 1, 2, 23, 5, 8, 13, 21,...). Similarly in a majority of plants, the leaves along a stem are organized in a spiral, the divergence angle ϕ between the direction of growth of successive leaves being close to $\Phi=2\pi\ (1-\tau)$ where τ is the golden mean. The formation of these spiral structures thus appears as a generic process in the botanical world. This property is linked with the common structure of the growing tips of the stems. Schematically the tip of any vascular plant is formed of a central region (the apical meristem) in the shape of a dome. At the periphery of the meristem protrusions appear, called the primordia. During the growth these primordia are advected away from the tip and grow into e.g. leaves. As their distance to the tip increases, space becomes available around the meristem and new primordia are formed.

The most simple model is due to W. Hofmeister (1868)[3]. He stated that a new primordium forms at regular time intervals at the periphery of the apex in the largest space left available by the previous primordia. Since this time, different hypotheses have been put forward to account for an interaction between the primordia: contact pressure, reaction-diffusion process, diffusion of an inhibitor etc... They create a situation of repulsion or inhibition so that a new primordium will indeed place itself in the largest available space. In all these models the fact that the plant is a living organism accounts for the growth and the biological effects but not directly for the organising process. For this reason we sought to reproduce the dynamics of the system in a physics experiment. We present a laboratory experiment using ferrofluid drops in which the different ingredients of the dynamics of the growth are reproduced. The drops which model the primordia are introduced at regular time intervals at the center of a circular dish. A gradient of magnetic field produces a slow radial advection of the drops. The most recent drop, repelled by the previous ones moves into the largest space left available near the center. In this experiment the drops are seen to organise spontaneously in spiral patterns with Fibonacci order.

This has been completed by a numerical simulation in which repelling elements appear periodically at the periphery of a circle, then move radially. Each new element is placed on a circle at the minimum of the repulsive potential due to all the previous elements. In the numerical simulations, we have also tried various geometry, repulsion forces, with no qualitative difference in the results. Both experiment and numerical simulation demonstrate how these structures result from self-organisation in an iterative process. The observed structure depends only on the initial conditions and on one parameter $G=VT/R_0$ where V is the velocity of advection, T the periodicity of the introduction of the new elements and R_0 the radius of the central circle (A related parameter called the plastochrone ratio was introduced by Richards[4] and is used by the botanists to characterise the growth). In our system when the parameter tends towards zero, the order of Fibonacci spirals increases regularly and the divergence angle tends towards $\Phi=2\pi\ (1-\tau)$ where τ is the golden mean. This particular ordering is explained as due to the system's trend to avoid any rational (periodic) organisation. In non-linear dynamics physicists are used to systems where two independant frequencies[5] tend to lock onto each other leading to the existence around each rational number of a basin of attraction known as an Arnold tongue. We have here the reverse situation where the system avoids successively increasingly complex rationals thus leading to a convergence towards the golden mean. A recent work done on very different basis by L. Levitov[6] shows that under a compression an helical distribution of repulsive points follows the same evolution leading towards an irrational organisation.

Our work can also be compared with the theoretical work of Van Iterson[7], at the begining of the century. On purely geometrical basis, he also found various possible dispositions, including the botanical ones. But he was not able to justify properly why only the dispositions related to the Fibonacci series were observed. In contrast, our results clearly show the selection of this particular familly of arrangements. This difference is only due to the fact we considered a dynamical (iterative) process, instead of a geometrical problem.

Second model.

The next step in this work is the investigation of the relation of the whorled modes to the spiral ones. A natural trend would be to think that the decussate type of growth of certain species is directly determined by genetic factors and has nothing to do with the spiral types of growth (which could also though to be determined genetically). However, in a remarkable experiment, M. and R. Snow[8] have shown that if the tip of a decussate plant was split by a surgical operation breaking its symmetry, the growth continues but now in a spiral mode. This led them to assume that the decussate and spiral growth were related and to put forward[9] a variant of Hofmeister's hypothesis. They removed the condition of periodicity and simply assumed that a new primordium forms whenever and wherever there is a large enough space at the apex periphery. They thus changed the appearance rule fom the largest available space to the first available space.

In order to test this other hypothesis we performed a second type of numerical simulations. As previously, all the deposited elements are advected radially and generate a repulsive potential but the periodicity of introduction of a new element is removed. At each time step the potential is computed in all the points of the perimeter of the central circle. When this potential becomes lower than a chosen threshold E_S in one or several points, one or several elements are added. In the plane radial geometry the spiral modes are recovered, showing that the systems spontaneously prefers a periodic appearance of elements. We can also observe whorled modes, but not as stable as would be expected from the botanical observations. But if the simulation is to be realistic from the botanical point of view, we must also take into account the fact that the region of formation of the primordia is on a paraboloïd, which can be approximated by a cone. The shape of the primordia are also not always circular. These two effects can be both modelized by introducing a polar anisotropy, i.e. a different extension of the repulsion in the azimuthal and radial directions. When this effect is introduced, we obtain in the same system both the periodic spiral organisation and very stable decussate and whorled modes. The occurence of each type of organisation depends on the initial conditions and on the values of the control parameter.

We have thus shown that the hypotheses put forward long ago by the botanists correspond to a physical iterative system in which the position of the new leaf is determined by the previous ones. This system can lead to either the spiral structures or to the whorled ones. Our results are very robust so that they are compatible with several of the hypotheses about the nature of the interaction between the primordia which is not yet known with certainty in the botanical systems. Finally, if one follows the self-organization hypothesis, our work could even been used to give precise predictions for the conditions of appearance of the different regimes of growth, which could be checked in the real botanical world.

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(4) Richards, F.J. (1951) Phil. Trans. Roy. Soc. B 235, 509-564.

(5) For a review see for instance Glazier J.A. and Libchaber A.(1988) IEEE transactions 35, 790-809

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