Phyllotactic Patterns on Plants

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Recommended and with a Commentary by Wim van Saarloos, Lorentz Institute, University of Leiden.

Anyone who has ever looked carefully at plants will have been struck by the intriguing regularity of the patterns that one can often observe in the placement of the seeds or the leaves. A well-known example of a regular spiral pattern is the placements of the seeds in the head of a sunflower. You may also be intrigued by the placement of stickers on a cactus or the fractal-like appearance of your cauliflower and broccoli. The study of geometric and numerical patterns in plants is known as "phyllotaxis"; it is a huge field with a long history [1]. If one analyzes some of the patterns, one can find all kinds of interesting regularities in them, e.g. the placement of leaves on the stem of a plant is found to be governed by the Fibonacci numbers.

If so many of these patterns have an underlying mathematical structure, where does this structure come from? Can we understand them starting from our understanding of the growth dynamics of the plants? Surprisingly little is known about this, but Shipman and Newell take, in my view, an important step in the right direction by their analysis of an elastic model for the growth region of a plant shoot.

A few years ago, Douady and Couder invented a mechanical analog of flower patterns [2]. These authors released little magnetic dipoles in the center of a flat surface one by one. The magnetic repulsion drives each of the dipoles outward from the center, along the minima of some complicated energy landscape determined by the interaction of all the particles. The reason that this work got so much attention [1] is that snapshots of the particle positions reproduced some of the geometric patterns found in phyllotaxis. However, this is just a mechanical analog which shows how patterns with intriguing geometric features can result from simple rules and interactions; it does not give any insight into the physical mechanism underlying the patterns in a growing plant.

Shipman and Newell do start from a true physical picture of the growth process of the tip of a plant shoot. Since the outer skin of the tip is normally one or two cells thick, they model the skin of the shoot as a thin shell which experiences compressive stresses due to a combination of growth stresses and the hardening processes. The interior region of the shoot is modeled as a simple elastic medium coupled to the compressed shell. The dynamical model of Shipman and Newell then essentially becomes a relaxational model in which the driving force is the total elastic energy. The relaxational dynamics thus drives the shell surface to the minima of this free energy. In order to analyze these and the type of patterns this model gives rise to, the authors expand the elastic energy in terms of the amplitudes A of modes with different wavenumbers. A key observation of the paper is that for such a model of an elastic shell coupled on one side to an elastic medium, the asymmetry of the model results in the presence of cubic symmetry-breaking terms in the amplitude expansion of the free energy. In the presence of such cubic terms, transitions are always subcritical (first-order-like) [3]. Moreover, as is well known, these cubic couplings describe the interaction of three modes, and the authors show that Fibonacci-like sequences, and whorl, spiral and hexagonal configurations can be recovered ("postdict", the authors write quite frankly) from the minimization of the free energy and understood in terms of the mode selection rules imposed by the cubic terms. This scenario is self-consistent if the cubic terms are dominant. From this perspective, the fact that Fibonacci-type sequences are usually not observed for less curved or flattish-topped plants, also comes out naturally from the model. So, even though the paper is not easy reading for the uninitiated, there are lots of amusing results coming out from such a simple idea.

[1] For a popular introduction, see e.g the chapter "Flowers for Fibonacci" in the book Life's other Secret by I. Stewart (Wiley, New York, 1998).

[2] S. Douady and Y. Couder, Phyllotaxis as a Physical Self-Organized Growth Process, Phys. Rev. Lett. 68, 2098 (1992).

[3] Some readers may be familiar with fluctuation-induced first order transitions in the transitions in diblock-copolymers (the "Brazovsky mechanism") or in superconductors (the "Halperin-Lubensky-Ma effect"), where in both cases cubic terms in the free energy are generated by integrating out fluctuations.