

Fibonacci's flowers

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The spiral arrangements of leaves on a stem, and the number of petals, sepals and spirals in flower heads during the development of most plants, represent successive numbers in the famous series discovered in the thirteenth century by the Italian mathematician Fibonacci, in which each number is the sum of the previous two (1, 1, 2, 3, 5, 8, 13, 21, 34, 55...). Seeds on the heads of sunflowers, for example, are arranged in two sets of spiral rows, one curving to the left and the other to the right. Thus, if 34 seed rows curve clockwise, there will be either 21 or 55 anticlockwise spirals on a sunflower head. Pine cones (see picture) are found both in the 'dexter' (righty) form, in which most spirals run clockwise, and in the 'sinister' (lefty) form, in which anticlockwise spirals predominate.

This set of phenomena is called phyllotaxis, from the Greek (*phylon*—leaf; *taxis*—order). Phyllotactic patterns have been described for centuries, but the mechanisms that initiate these patterns remain undefined. The geometric arrangement follows from the regular packing of leaf primordia on a stem as the diameter of the stem slowly increases. But how does this pattern of growth conform to the numbers in Fibonacci's series?

The meristematic tissue, an undifferentiated mass of cells at the tip of a plant shoot, has near its boundary a region called the apical ring, where new plant organs are formed through extensive cell division in a structure called the primordium. Thus, phyllotactic patterns are thought to result from regulated differentiation of the primordia from cells originally derived from the meristematic

tissue of the vegetative or floral shoot. So in flower development, it seems that the floral tip produces seeds in spiral arrays as a result of spiral growth combined with primordia moving radially away from the centre of the apex.

Two main hypotheses have been proposed to explain the generation and maintenance of phyllotactic patterns. In the famous 'field' model, the position of the primordium is determined by undulating inhibitory fields, presumably composed of biochemicals, that emanate from the existing primordium and the apical meristem. The second model suggests that tissue mechanics and biophysical forces combine to promote morphogenesis in predictable ways. Yet neither of these models produces testable predictions, and they both lack convincing experimental support. Furthermore, they explain only the propagation of established patterns, not how phyllotaxy actually originates.

The connection between mathematical number series and pattern development remains to be described in biological terms. I would like to propose another, simpler theoretical model, based on cellular differentiation, to explain the *de novo* generation of phyllotaxy. Imagine an asymmetric cell division that gives rise to a mature cell that is competent to divide, as well as a juvenile cell that must first grow for one more length of the cell cycle to mature before it begins its division cycle. Remarkably, such an asymmetric cell division will indeed produce cell numbers in each generation that match the Fibonacci series.

This outcome is analogous to the original mathematical challenge posed by Fibonacci for his high-school students, to calculate the numbers of breeding rabbits when the

Plant mathematics

Asymmetric cell division offers a possible explanation of the spiral patterns seen in many plants.

newborns have to grow before they can begin breeding. Another striking analogy concerns stem cells—undifferentiated cells that divide to renew themselves as well as to give rise to more specialized cell types. Many cases exist in biology in which one daughter cell maintains the stem-cell characteristic while the other daughter is differentiated. For example, in early divisions of embryos of the nematode *Caenorhabditis elegans*, the times taken by different daughter cells to divide are very different. I suspect that a similar cell-division pattern may underlie the development of mathematical patterns in plants.

Intuitively, the stem-cell proposal predicts that floral meristems growing spirally and dividing asymmetrically will produce dexter and sinister arrangements in equal proportion, an outcome that is not predicted in such a straightforward way by the other models discussed above. Of 37 cones picked from a pine tree, I found that 20 cones were dexter and 17 were sinister, which is consistent with the idea that the direction of asymmetry is random. Likewise, six other trees all produced both kinds of cone. Randomness is expected in binary systems in which no bias exists, such as the tossing of a coin or the development of a crusher or clipper claw on the left or right side in lobsters. The currently prevailing models are unsatisfactory for answering such a fundamental question in biology.

At the very least, the stem-cell model is attractive in its simplicity compared with other models, and may provide a new framework for explaining existing results as well as becoming a concept that will guide research. At present, the challenge is to correlate asymmetric patterns of cell division with the generation of Fibonacci patterns, and to design tests to distinguish between these models. Perhaps the most useful approach may be to study mutants with altered developmental patterns. ■

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FURTHER READING

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Something sinister: the pine cone on the left is in the 'lefty' form; that on the right is dexter, or 'righty'.