

Principle of Minimax and Rise Phyllotaxis (Mechanistic Phyllotaxis Model)

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Introduction

Pattern formation in organisms is one of the commonest phenomena observed in nature. The arrangement of repeated units such as leaves around a stem, florets in the head of a daisy, scales on a pine cone or on a pineapple, and seeds in a sunflower is known as **phyllotaxis**. These repeated units are called in their young stages **primordia**.

History

The study of phyllotaxis is traced from the first primitive observations in ancient times to sophisticated studies of today.

Little is known about the Ancient Period which goes back at least to Theophrastus (370 B.C.-285 B.C.) and Pliny (23 A.D.-79 A.D.). Theophrastus, in his Enquiry into Plants, says about plants that 'those that have flat leaves have them in a regular series'. Pliny, in his Natural History, gives more detail. In his description of oparine he says that it 'is a ramose, hairy plant with five or six leaves at regular intervals, arranged circularly around the branches'.

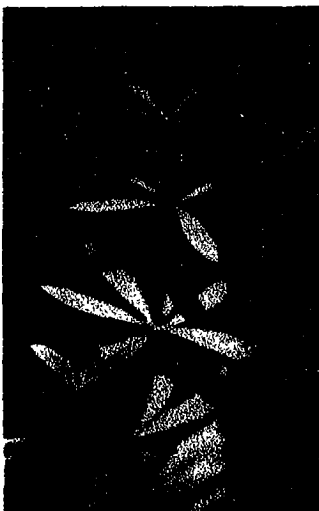
The Modern Period (from the fifteenth century to 1970) is marked by the observations of Leonardo da Vinci (1452-1519), Kepler (1571-1630), by the works of Bonnet (1754), Schimper (1830), Braun (1831, 1835), the Bravais brothers (1837), Lestiboudois (1848), Hofmeister (1868), Schwendener (1878), A. H. Church (1904), D'Arcy W. Thompson (1917), Snow and Snow, (1962).

The Contemporary Period (from 1970 onwards): there were studies of H.S.M. Coxeter (1972), Adler (1974), L. V. Belousoff (1976), G. W. Ryan, J. L. Rouse and L. A. Bursill, Douady and Couder (1992), Meinhardt (1984), R. V. Jean.

The list of these scientists is not complete.

Patterns

Regardless of the overwhelming multiformity of plants structure, there are common patterns that link a wide range of species. There are two large categories of patterns can be recognized, the **spiral** and the **whorled patterns**.



Whorled pattern

In a number of common species the leaves are arranged in whorls at the level of the stem. The number n of leaves in a whorl varies from species to species, in the same species, and can even vary in the same specimen. In the whorled patterns the leaves at any one node are generally inserted above the gaps of the preceding ones.

Spiral pattern

The most common pattern, the spiral pattern, involves an insertion of a single primordium at each node. In this case it is possible to trace the spirals which in the botanical literature are called **parastichies**.



The primordia in parastichy can be or can not be in contact. Those segments of parastichies which are obvious to the eye, thanks to the contacts, are termed **contact parastichies**.

The parastichies running in the same direction with respect to the axis of the plant with the same pitch constitute a **family of parastichies**, and two obvious families winding in opposite directions are called a **parastichy pair**.

Direction and numbers are characteristic of a parastichies family

We can characterize the patterns, first, by determining the direction of a parastichies winding, and, second, by counting the number of the parastichies in the family.

Spirals winding direction

Spirals winding doesn't have a strictly determined direction. The shoots of plants can be both left-handed and right-handed enantiomorphs.

Fibonacci numbers

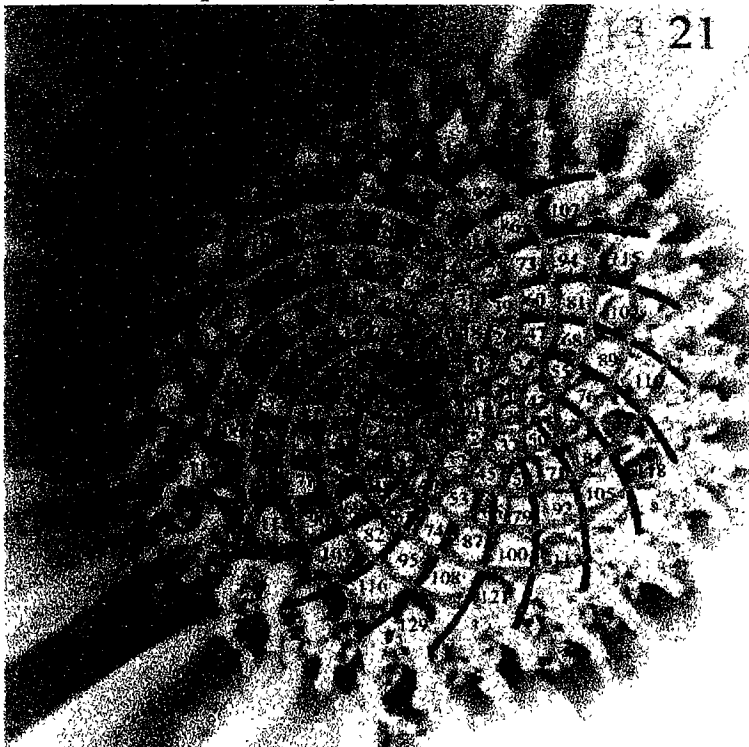
A parastichy pair formed by a family of m spirals in one direction and n spirals in the opposite direction is denoted (m, n) .

The numbers m and n in the parastichy pair on pineapples, cones, and sunflowers are consecutive Fibonacci numbers. The first few Fibonacci numbers are 1, 1, 2, 3, 5, 8, 13, ... , where the sum of two consecutive numbers is the next number.

Fibonacci-type sequences

When visible opposed parastichy pairs do not contain numbers that are consecutive values in the Fibonacci sequence, they often contain those from another sequence, derived in the same manner as the

Fibonacci sequence, but with other initial terms for instance 1 and 3 (the Lucas sequence).

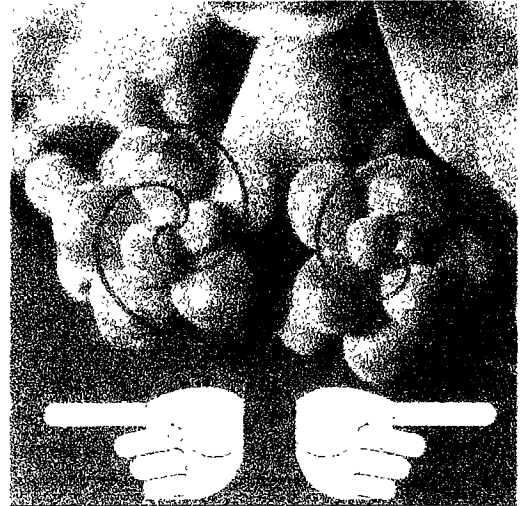


Rising Phyllotaxis

The numbers of visible opposed parastichies rise along the Fibonacci sequence. In the inner part we have few visible opposed parastichies, and in the outer part more visible opposed parastichies. With an increase of the shoot radius a change of parastichy pair takes place, for example, from (8, 13) to (21, 13), from (21, 13) to (21, 34) et cetera.

An explanation of this phenomena called **rising phyllotaxis** is the key element in the understanding of origin of patterns on plants.

The prevalence of the Fibonacci sequence in phyllotactic patterns is often referred to as "the mystery of phyllotaxis," and "the bugbear of botanists."



Model

The spherical soap-bubble-like primordia arise from a liquid at the center of the cylinder top, one by one, according to the rule: every primordium moves in the largest available space. (This rule reminds of Hofmeister's rule (1868): every primordium arises in the largest available space. The primordia move radially and simultaneously, with the equal rate, and grow in diameter until they experience contact pressure.

By the way, the paths of horizontal motion of primordia are not rectilinear.

Increasing amounts of contact parastichy pairs realize due to the rearrangement of primordia, during their movement from center towards rim. Parastichy becomes contact and visible to the naked eye when primordia touch one other.

The model is formulated in **centric representation**, where each family of parastichies is a set of identical **Archimedean spirals**.

We have centric vector spiral lattice in nodes which primordia stand.

The primordia are numbered according to their age, that is according to the order in which they arise on the plant apex, with 0 being the youngest.

The numbering of the primordia is in agreement with the Bravais-Bravais theorem: in a family containing n parastichies, on any one parastichy, the numbers of each consecutive primordia differ by n . Numbers on each n -parastichy are congruent mod n , it means, belong to the same

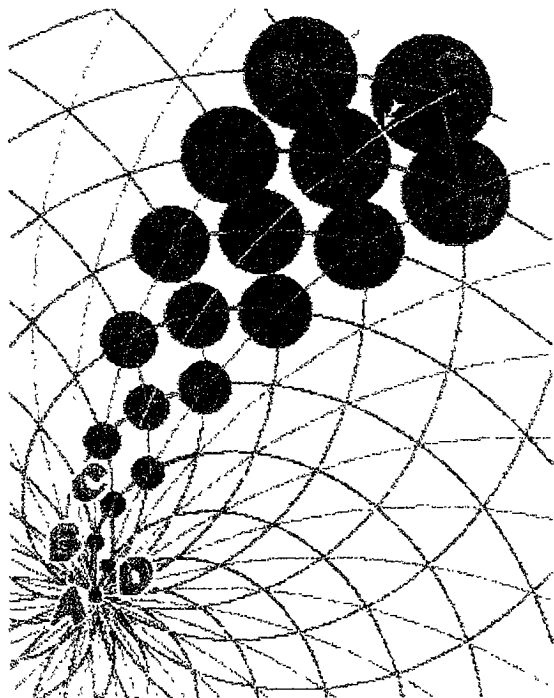
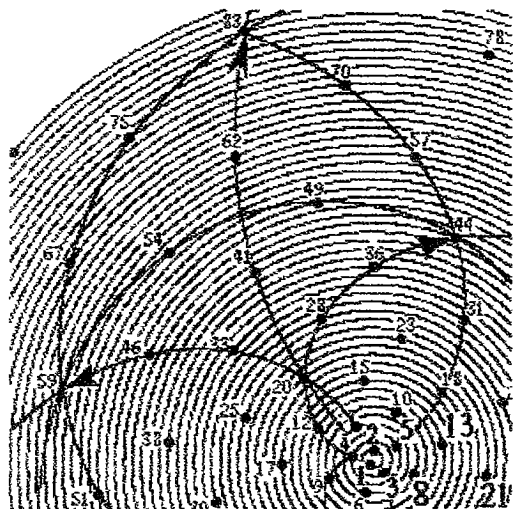
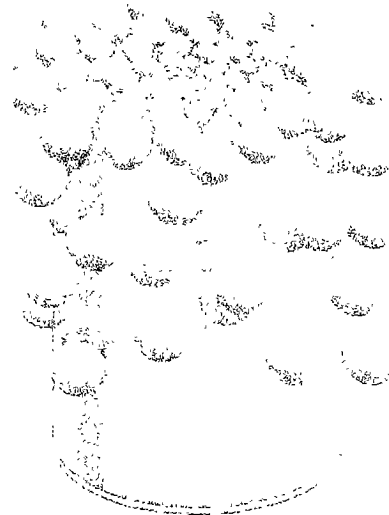
residue class mod n . Any one parastichy is considered as a residue class. Difference of numbers of any primordia is considered, first, as a **lattice vector**, and, second, as a **module** in its residue class.

We can add and subtract integer vectors in agreement with the parallelogram rule.

Origin and replenishment of contact parastichy is described by addition of vectors at a moment of touch of two (younger and older) primordia, moving in the opposite corners of the primitive unit cell.

The appearance of new vectors, or moduli, causes appearance of new residue classes mod m .

It is well known, that there are exactly m distinct residue classes mod m , consequently, after addition of vectors m and n , $(m+n)$ residue classes mod $(m+n)$ will appear, in other words, $(m+n)$ contact parastichies. A contact parastichy pair (m, n) is replaced by contact parastichy pair $(n, m+n)$. Thereby, Fibonacci sequence arises. The rising of spiral phyllotaxis is isomorphic to increasing of Fibonacci sequence. Which was to be proved.



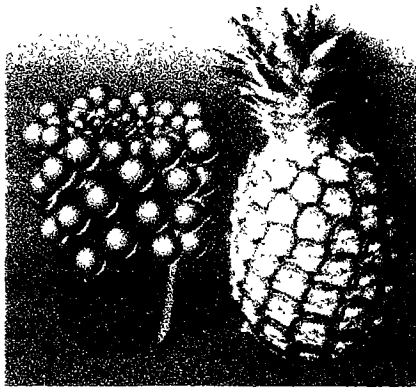
Separation and divergence of primordia result in the disappearance of contact parastichy. In each contact parastichy, addition occurs among the younger primordia nearest to the centre, but subtraction occurs among the older primordia farthest from the centre. The primordia move from the centre to the rim, but location of areas of contact parastichy pairs is not changed.

The appearance of Fibonacci-type sequences is explained by misleading of primordia at initial stages of apex development.

Explanation of chirality

How do the right and left forms appear? Let us examine the initial primordia placement.

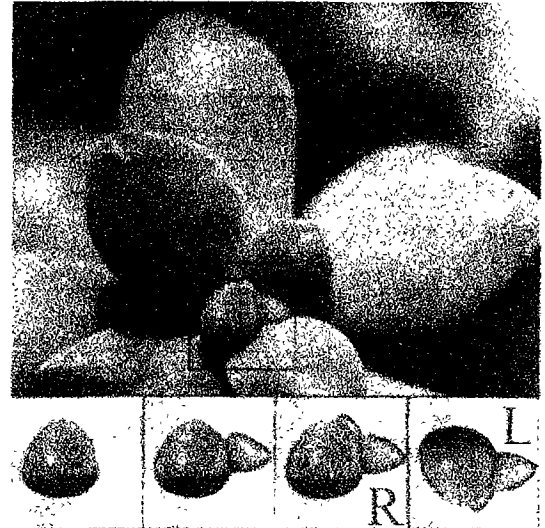
The third primordium can appear both on one, and on the other side from the reflection line which has the first two primordia centers lying on it. Solution of this dilemma will determine hereinafter for each family of spirals its direction. A choice of position for the third primordium, probably, is casual, and depends on external factors, for example, on uneven heating of bud by the sun.



Ornament on the lateral shoot surface

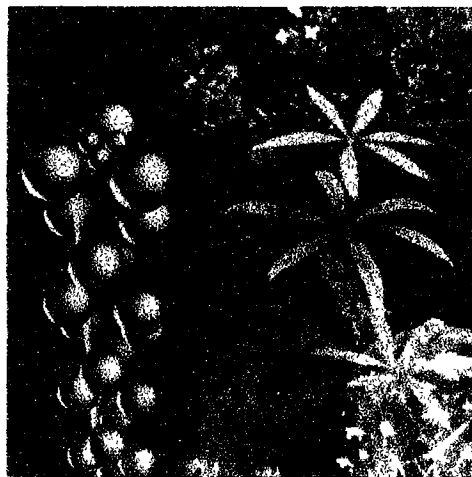
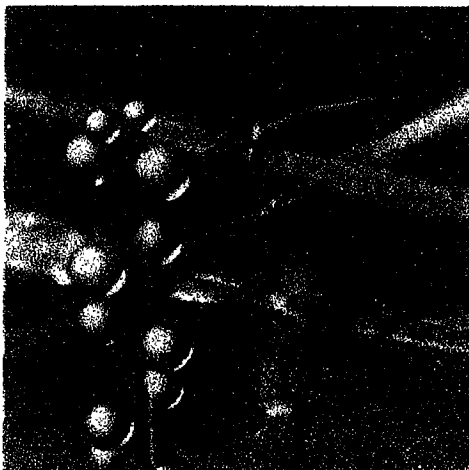
Appearance of the ornament on the lateral cylindrical

surface of shoot is explained by lengthening of internodes along the shoot axis, after primordia had been arranged on discoid, coniform or domed apex of shoot. The sliding of the bubbles on the cylinder wall simulates this lengthening of internodes.



Versatility of model

The model allows to describe a whorled phyllotaxis, as well as the spiral one. If the cylinder is sufficiently narrow, and if the primordia appear as a complex composed of two, three or more bubbles, we have a whorled pattern.



Résumé

The work shows a possibility of complicated accommodation on the basis of simple principle of minimax: "It pops up in the biggest gap".

References

Jean, R. V. Phyllotaxis: A Systematic Study in Plant Morphogenesis. New York: Cambridge University Press, 1994.