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A Review of Vogel's Planar Model for Study of Phyllotaxis in Plants

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Abstract
An important aspect of plant form, in botany, is phyllotaxis or phyllotaxy which is the arrangement of leaves on a plant stem (from Ancient Greek phýllon "leaf" and táxis "arrangement") or scales on a cone axis, florets in a composite flower head etc. Phyllotactic spirals form a distinctive class of patterns in nature. The basic phyllotactic patterns are opposite, or alternate spiral with an opposite leaf arrangement, two leaves arise from the stem at the same level (at the same node), on opposite sides of the stem. An opposite leaf pair can be thought of as a whorl of two leaves. In This Paper, a useful model suitable for the synthesis of realistic images of flowers and fruits that exhibit spiral phyllotactic patterns has been reviewed .This model relate phyllotaxis to packing problems. This model operates in a plane and was originally proposed by Vogel to describe the structure of a sunflower head. This model correctly describes the arrangement of florets visible in actual capitula. In this model, the most prominent feature is two sets of spirals or parastichies, Parastichies one turning clockwise, the other counterclockwise, which are composed of nearest neighboring florets.

Keywords
Phyllotaxis, Planar Model , Realistic Images, Parastichies

I. Introduction

Phyllotaxis, a subdivision of plant morphology, is the study of the arrangement of repeated units such as leaves around a stem, scales on a pine cone or on a pineapple, florets in the head of a daisy, and seeds in a sunflower. Remarkably these units often form systems of spirals or helices.

Ancient Egyptians probably observed and knew about some regular patterns in plants.

Ancient Greek scholars wrote about regular leaf and plant patterns. In 1400's: Leonardo da Vinci wrote in a notebook about parastichy patterns in plants. In 1700's: Charles Bonnet and G.L. Calandrini studied parastichies of fir cones. In 1830's: Alexander Braun observed that pairs of parastichies numbers for pine cones are usually consecutive Fibonacci numbers.

The study of phyllotaxis has now matured as a science. The area of phyllotaxis is dominated by intriguing mathematical relationships. Mathematics has now entered into the study of phyllotaxis in a variety of ways. Many branches of mathematics have been used, including statistics, calculus, differential equations, analytic geometry, linear algebra, number theory, and even hyperbolic geometry. The observed organizations are classified in only two categories. In the first, formed of the distichous and spiral modes, the leaves appear one at a time along the stem. The striking peculiarity of this family is that it is directly related to the Fibonacci series and the golden mean. In the second, constituted of whorled modes, a constant number of leaves appear simultaneously at the same height on the stem and form successive whorls. The sequence

$\langle 1, 1, 2, 3, 5, 8, 13, 21, \ldots, F_k, F_k+1, \ldots \rangle$,

where each term after the second is the sum of the two that precede it, and Fk is the kth term of the sequence. These numbers are now called Fibonacci numbers, and the sequence is called the Fibonacci sequence. This sequence was to become of first importance in phyllotaxis. It is possible to generate other sequences similar to the Fibonacci sequence by starting with any two numbers and then using the same addition rule to generate the rest. Among them, the sequences

$\langle 1, 3, 4, 7, 11, \ldots \rangle$ and $\langle 2, 5, 7, 12, \ldots \rangle$

also play a role in phyllotaxis.

The golden number

$\tau = (\sqrt{5}+1)/2$,

which is also important in phyllotaxis study, is mathematically related to the Fibonacci sequence by the formula

$\lim F_k/F_{k+1} = \tau$.

The observation of this sequence in botany constituted a mystery which served as a main spur to the development of the subject. We can express this mystery by saying that the numbers of spirals in observed systems of opposed families of spirals (as seen in daisies and sunflowers for example) are generally consecutive terms of the Fibonacci sequence. Also, the angle of divergence between two similar units along the so-called genetic spiral (one of the numerous spirals observed in buds and on mature plants) is 137.5°, a value closely related to the sequence by the formula 360° limFk/Fk+1, and to the golden number by the formula $360°/\tau^2$, the two expressions being equal.

Fermat's spiral (also known as a parabolic spiral) follows the equation

$$r = \pm\theta^{1/2}$$

in polar coordinates . It is a type of Archimedean spiral.[7]

In mature -discphyllotaxis, when all the elements are the same size, the shape of the spirals is that of Fermat spirals—ideally. That is because Fermat's spiral traverses equal annuli in equal turns.

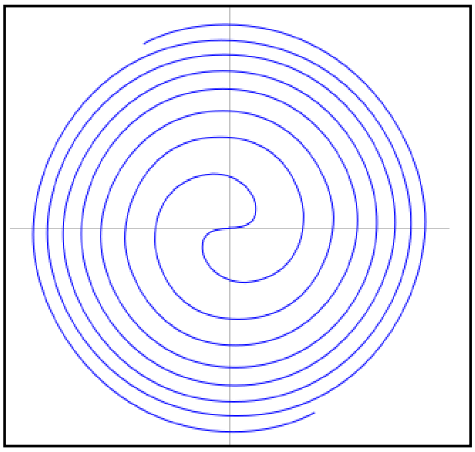

Fig. 1: Assumptions of the Planar Model

One of the best known models of sunflower phyllotaxis was proposed by Vogel (1979) in response to an early work by Mathai and Davis (1974). The elements in Vogel's model are arranged on a Fermat's (parabolic) spiral which has a general form r2 = a2θ. Every turn of spiral in the model contains on average φ+1 elements. Since Fermat's spiral crosses the annuli of equal areas in equal number of turns, equal number of head contain on average equal number of elements. The irrational angle between successive elements ensures that no two elements are located at the same angle. These two properties alone do not guarantee efficient packing of elements as locally the element packing density may differ significantly and large areas of unused space can be present. The planar model was given by Vogel [1] to describe the structure of a sunflower head. Vogel [1] derives it using two assumptions.

- Each new floret is issued at a fixed angle α with respect to the preceding floret.
- The position vector of each new floret fits into the largest existing gap between the position vectors of the older florets.

The Planar model operates in a plane. One of them is the "remarkable fact that the numbers of spirals which can be traced through a phyllotactic pattern are predominantly integers of the Fibonacci sequence" . For example, Coxeter [2] notes that the pineapple displays eight rows of scales sloping to the left and thirteen rows sloping to the right. Furthermore, it is known that the ratios of consecutive Fibonacci numbers Fk+1/Fk converge towards the golden mean $\tau = (\sqrt{5} + 1)/2$. The Fibonacci angle 3600τ−2, approximately equal to 137.5^0, is the key to the this model discussed.

In order to describe the pattern of florets (or seeds) in a sunflower head,

Vogel [1] proposed the $\varphi = n * 137.5^0$, $r= c\sqrt{n}$ (1)

where:

- n is the ordering number of a floret, counting outward from the center. This is the reverse of floret age in a real plant.
- φ is the angle between a reference direction and the position vector of the nth floret in a polar coordinate system originating at the center of the capitulum. It follows that the divergence angle between the position vectors of any two successive florets is constant, α = 137.5°.
- r is the distance between the center of the capitulum and the center of the nth floret, given a constant scaling parameter c.

The distribution of florets described by formula (i) is shown in fig. 1

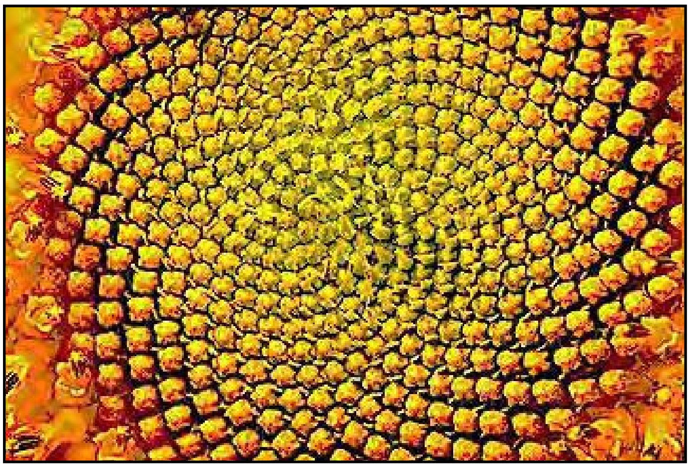

Fig. 2:

The ratio f_{k+1} / f_k as k becomes bigger and bigger, approaches a particular value

2/1 = 2.0	34/21 = 1.619047...
3/2 = 1.5	55/34 = 1.6176470...
5/3 = 1.6666…	89/55 = 1.6181818...
8/5 = 1.6	144/89 = 1.6179775...
13/8 = 1.625	233/144 = 1.61805555...
21/13 = 1.615384…	…...

which is called the Golden ratio.

On question that comes is : What is the mathematical properties of that make φ so special to give the most efficient packing?

φ is irrational, and can be written as a continued fraction:

$$1 + \frac{1}{1},\ 1+ 1/[1 + \frac{1}{1}],\ 1+[1+ 1/[1 + \frac{1}{1}]],\ldots.$$

which are 2/1 ,3/2, 5/3,…….. These are ratios of consecutive pairs of Fibonacci numbers.

Geometric Explanation and Justification of the Planar Model

If all florets have the same size and are densely packed, the total number of florets that fit inside a disc of radius r is proportional to the disk area. Thus, the ordering number n of the most outwardly positioned floret in the capitulum is proportional to r^2, or $r \sim \sqrt{n}$.

When φ=137.50 then one can have most tightly packing as shown below:

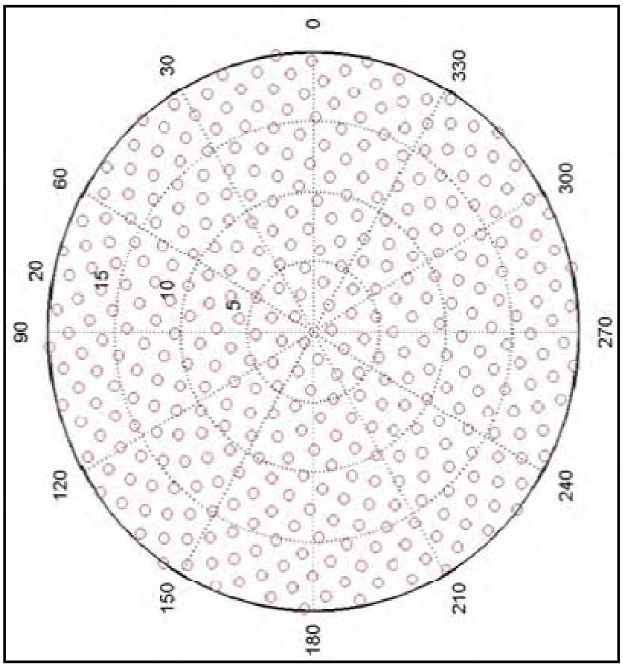

Fig. 3: Limitations of the Planar Model

In the planar model, the divergence angle of 137.50 is much more difficult to explain.

The basic assumptions on which this model is based are insufficient to explain the origin of the Fibonacci angle, and points to several arbitrary steps present in Vogel's derivation.

While it is reasonable to assume that the plant could contain genetic information determining the divergence angle to some extent, it is completely impossible for this alone to fix the divergence angle to the incredible accuracy occurring in nature, since natural variation in biological phenomena is normally rather wide. Although a

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comprehensive justification of Vogel's formula may require further research, the model correctly describes the arrangement of florets visible in actual capitula. The most prominent feature is two sets of spirals or parastichies, which are composed of nearest neighboring florets. The number of spirals in each set is always a member of the Fibonacci sequence; 21 and 34 for a small capitulum, up to 89 and 144 or even 144 and 233 for large ones.
Unfortunately, the assumptions that simplified the mathematical analysis of this model limited the range of its applications. In nature, the individual organs often vary in size, and the surfaces on which they are placed diverge significantly from ideal disks . Spherically shaped cactus bodies provide a striking example, but even elongated structures, such as spruce cones, are not adequately described by this model, which fails to characterize pattern changes observed near the base and the top of a cone.

II. Conclusion

The different models proposed from time to time range widely from purely geometric descriptions to complex physiological hypotheses tested by computer simulations. The two models which we are comparing in this paper relate phyllotaxis to packing problems. In the planar model, the constant divergence angle $\alpha = 137.5^\circ$ is found across a large variety of flower heads. The number of perceived parastichies is determined by the capitulum size, and it changes as the distance from the capitulum center increases. A larger variety of organ sizes and surface shapes can be accommodated using explanatory models, which focus on the dynamic processes controlling the formation of phyllotactic patterns in nature. It is usually postulated that the spirals result from local interactions between developing organs, mechanically pushing each other or communicating through the exchange of chemical substances. Unfortunately, no universally accepted explanatory model has yet emerged from the large number of competing theories [6].

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