



Mini Review

# Three ways to confirm the correctness of the biomechanical model of the morphogenesis of spiral phyllotaxis

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## Abstract

The mystery of the phyllotaxis phenomenon has been inspiring inquiry among generations of botanists and mathematicians. Of particular interest is the fact that the number of visible spirals is equal to the numbers from the Fibonacci series. The article proposes three methods to prove the adequacy of the biomechanical model of the morphogenesis of spiral phyllotaxis: mathematical, simulation software, and experimental. Evidence of the biomechanical model leads to a critical rethinking of the understanding of plant morphogenesis.

## Introduction and terminology

Phyllotaxis (from the Greek *phýllon* — leaf and *táxis* — arrangement): Covers a very wide range of botanical objects, in the structure of which orderliness, helicity, periodicity, or symmetry are observed. These structures, which are often surprisingly beautiful, are usually called *phyllotactic patterns*.

Primordium (plural primordia): A discrete element (seed germ, seed, leaf, flower petal, new shoot) of a phyllotactic pattern.

Parastichy (plural parastichies): Visually distinguishable right- or left-handed spiral formed by primordia.

The parastichy index: The number of parastichies with the same twist.

Fibonacci phyllotaxis: A pattern of spiral phyllotaxis in which parastichies indexes are equal to the Fibonacci numbers (Figure 1).

Genetic spiral: An imaginary spiral that sequentially passes through all primordia.

Divergence angle: The smaller angle between two rays starting at the center of the inflorescence and passing through

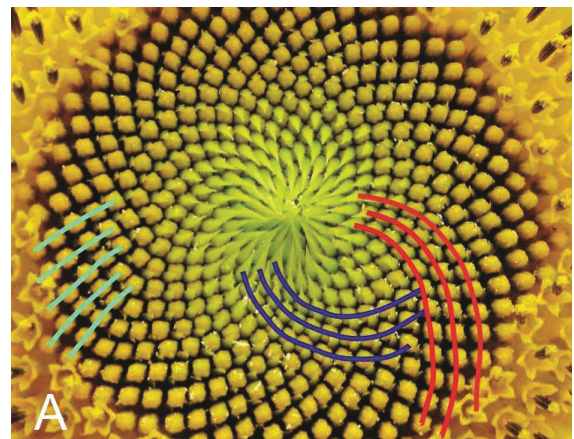


Figure 1: Planar spiral phyllotaxis in sunflower at inflorescence with a visible parastichy index of (21, 34, 55).

a pair of successive primordia, respectively. For Fibonacci phyllotaxis, this is the golden angle  $\frac{2\pi}{\tau}$ .

Planar spiral phyllotaxis: Observed on a planar or convex inflorescence in which a person sees the right- and left-handed spirals. The most striking example of such a phyllotaxis is the sunflower inflorescence, on which up to four different families of spirals can be distinguished (Figure 1).



Element of a phyllotactic pattern (EPP, plural EPPs, EPP(*i*) - EPP number *i*): Mathematical abstraction of the primordium.

Rise of phyllotaxis: Visual transition from a pair of parastichies with index  $(F_{i-1}, F_i)$  to  $(F_i, F_{i+1})$  is the most important feature of spiral phyllotaxis.

The most famous and undeniable manifestation of Fibonacci numbers in living nature is spiral phyllotaxis - a phenomenon that combines beauty and mathematics [1,2]. Therefore, the process of the emergence of Fibonacci spirals is of particular interest to both mathematicians and naturalists. Thousands of measurements have been carried out, hundreds of articles have been written, and dozens of books have been published, but there has not yet been a full-fledged theory explaining the morphogenesis of this phenomenon.

What is remarkable is that we find patterns of spiral phyllotaxis in plants from different kingdoms. This suggests that different plants with spiral phyllotaxis have a universal mechanism for the morphogenesis of these patterns.

The range of hypotheses attempting to explain the morphogenesis of spiral phyllotaxis patterns is quite wide, but not all of them can be considered scientifically acceptable. Four directions can be roughly distinguished: biochemical, biomechanical, bioinformational, and "biomagical".

**Biochemical:** Modern botany considers plants as objects consisting of a large number of cells, between which and within which various physical and chemical processes occur. These processes are adequately described by statistical and differential-integral mathematical tools. Therefore, a significant part of researchers tried to build a model of the morphogenesis of Fibonacci phyllotaxis, relying on mathematical methods well-tested in biology [3].

The most prominent representative of the biochemical direction was the outstanding mathematician of our time Alan Turing. In the early 50s, Turing published a fundamental article "The Chemical Basis of Morphogenesis" [4], dedicated to the self-organization of matter and self-oscillating chemical reactions, which are described by second-order differential equations. At the same time, Turing was keenly interested in the phenomenon of phyllotaxis and tried to model its morphogenesis using the same mathematical apparatus. Only in 1992, Turing's unfinished article "Morphogen theory of phyllotaxis" [5] was published, in which he tried to explain the appearance of Fibonacci phyllotaxis patterns by the self-oscillating nature of chemical reactions in plants.

However, Fibonacci numbers do not appear in solving equations describing self-oscillating processes. The Fibonacci numbers also do not appear as basic constants in statistics or in differential-integral calculus, such as the constant  $\pi$  arises in trigonometry or  $e$  in differential-integral calculus. This allows us to assume that a certain recursive process underlies the morphogenesis of spiral phyllotaxis [1].

**Biomechanical:** The foundations of the biomechanical approach to modeling morphogenesis of phyllotaxis were laid

back in the 19th century by Bravais-Bravais [6], and continued by Church [7], Jean [8], Mitchinson [9], Barabe and Lacroix [10], and Levitov [11]. It is especially necessary to note the importance of the research of Adler [12], who formulated "A model of contact pressure", which is the foundation of the recursive dynamic model of the morphogenesis of spiral phyllotaxis put forward in [1]. According to this model, each "newborn" primordium appears in the center of the inflorescence, then increases in size and, under the pressure of other primordia, moves from the center of the inflorescence to the periphery.

**Biomagical:** Hofmeister [13], based on visual observations of very early stages of inflorescence development (Figure 2), postulated that the new primordium is formed furthest from the existing primordia, with the pattern being filled from the edge to the center and the divergence angle is being kept with high precision. This postulate is called the "Hofmeister rule". It follows from this rule that each new primordium, under the influence of certain "magical forces," is formed exactly in the place in which it should be formed. It's like the old joke: "the bomb always hits the center of its funnel."

Attempts to explain the "Hofmeister rule" have given rise to many hypotheses based on various "magic" forces, for example, standing waves, or interactions that contradict classical physics (Hertel [14], Bainbridge [15], Deb [16], Godin [17]), and sometimes common sense (Bakker [18], Walch [19]).

In [1,2], an explanation of the "Hofmeister rule" was proposed as a visual phenomenon caused by the fact that each primordium passes through invisible and then visible stages of development **Video 1** <https://youtu.be/sJFrB7TnqPc> from [2].

**Bioinformational:** The mainstream of modern hypotheses trying to explain the emergence of Fibonacci patterns is the attribution to auxin (growth hormone) transferring information about the place of formation of a new primordium (Reinhardt [20], Jönsson [21]) according to the "Hofmeister rule".

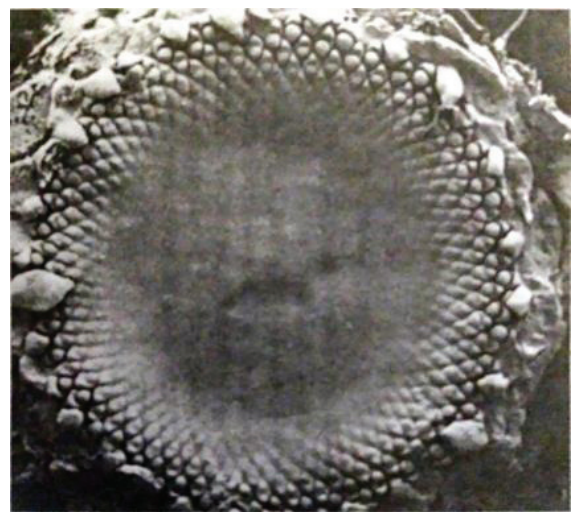


Figure 2: Micrograph taken by J. H. Palmer with a scanning electron microscope from Jean[8]. Reproduced with permission of The Licensor through PLSclear.



## Static model of spiral phyllotaxis

The foundations of the classical static model of spiral phyllotaxis were laid back in the 19th century. Broun [22] and Schimper [23] proposed that one (genetic) helix can be drawn through all discrete Elements of a phyllotactic pattern (EPPs) and these EPPs can be numbered starting from the center of the helix. Rozin [1] proposed the development of this model, suggesting that the centers of EPPs are located at the intersection of two oppositely twisted helices so this model was called the Double Helix (DH-Model).

The Double Helix Model, combined with the hypothesis that human visual perception combines EPPs located at a minimum distance from each other into parastichy, allowed Rozin [1] to obtain new mathematical results. Some of them:

The most important characteristic of the phyllotaxis pattern is the dependence of the EPP diameter on its number  $d_i = f(i)$ , and the divergence angle does not depend on  $i$  and is constant.

The direct and converse statement is true: if we observe a Fibonacci phyllotaxis pattern, then the divergence angle is equal to  $\frac{2\pi}{\tau^2}$ .

There is a one-to-one relationship between the shape of the genetic spiral and the dependence of the EPP diameter on its number. If the genetic spiral is  $\rho(\theta) = \theta^\nu$  in polar coordinates, then  $d_i = \sqrt{2\pi\nu} i^{\nu-0.5}$ . Video 2; <https://youtu.be/9H7Nf6BjDaA> shows how the pattern changes when the parameter  $\nu = 0.5 \div 3$  changes but the divergence angle remains unchanged.

Accordingly, if the genetic spiral is an Archimedean spiral  $\rho(\theta) = \theta^\nu$ , then  $d_i = \sqrt{2\pi i}$ .

A genetic spiral cannot be a logarithmic spiral  $\rho(\theta) = w^\theta$ , because it does not generate a pattern with the rise of phyllotaxis.

## Biomechanical model of morphogenesis of spiral phyllotaxis

The biomechanical model consists of two processes, discrete and continuous [1,2]:

Discrete - The appearance of a new EPP in the center of the inflorescence at regular intervals.

Continuous - Each EPP grows uniformly and increases in volume or area.

Increasing the volume or area of each EPP creates pressure on surrounding EPPs, which also grow. According to the laws of classical physics, all EPPs will exert pressure on each other. In [1], it was proven that the resulting pressure vector of all EPPs on each individual EPP lies on a ray starting at the center of the inflorescence and passing through the EPP (i.e., directed from the center of the inflorescence toward its periphery). The result of the pressure created by the growth of all EPPs is the movement of each EPP away from the center of the inflorescence.

In the classical static model of phyllotaxis, EPPs were numbered from the center of the inflorescence, and “de facto” was its “EPP age.” In the biomechanical model, which is a dynamic model, EPPs will be numbered as they are added. Then at the periphery of the inflorescence, there will be EPPs with lower numbers, and the “newborn” EPP will have the highest number. Video 3 <https://youtu.be/nqOuWhGp82w> explains the work of the biomechanical model of spiral phyllotaxis morphogenesis. The creation of this video is explained in [24].

The morphogenesis of the spiral phyllotaxis pattern, according to this model, occurs as a recursive repetition of the transition from a phyllotaxis pattern with  $N$  EPPs to a pattern with  $N+1$  EPPs, whereas:

- At regular intervals ( $T_c$  - cycle time) a new EPP is added to the center of the inflorescence;
- Each EPP continuously grows (increases in size) and creates pressure on surrounding EPPs;
- Under the pressure of surrounding EPPs, each EPP continuously moves away from the center of the inflorescence;
- The phyllotaxis pattern maintains a genetic helix and a constant angle of divergence.

Here we need to clarify the term “inflorescence center,” for which we will consider the first cycles of the model. At the beginning of the first cycle of operation of the biomechanical model, EPP(1) appears and starts to grow. The second cycle begins after “cycle time” with the appearance of EPP(2), which appears touching EPP(1). The third loop adds EPP(3) which will touch EPP(1) and EPP(2). The fourth cycle adds EPP(4) which is placed in the space between EPP(1), EPP(2), and EPP(3). Thus, the “inflorescence center” will be the space between EPP( $i-3$ ), EPP( $i-2$ ), and EPP( $i-1$ ) in the  $i$ -th cycle of the biomechanical model.

Every scientific hypothesis needs analytical proof or experimental verification. The author sees three methods (or ways) to prove that the Biomechanical model adequately describes the morphogenesis of spiral phyllotaxis patterns: mathematical, simulation software, and experimental. Due to the different nature of these methods, they have different veracity criteria.

## Mathematical method

The mathematical method involves the analytical calculation of the movement locus of each EPP according to the Model. The criterion for proving the veracity of the Biomechanical model will be that the divergence angle between EPP( $j-1$ ) and EPP( $j$ )

(Figure 3) will be constant and equal  $\frac{2\pi}{\tau^2}$ .

$$\lim_{N \rightarrow \infty} \angle C_{j-1} O C_j = \frac{2\pi}{\tau^2}$$

Were  $C_j$  the center of EPP( $j$ ),  $O$  the center of the inflorescence,  $N$  number of EPPs, and  $N > j \gg 0$ .



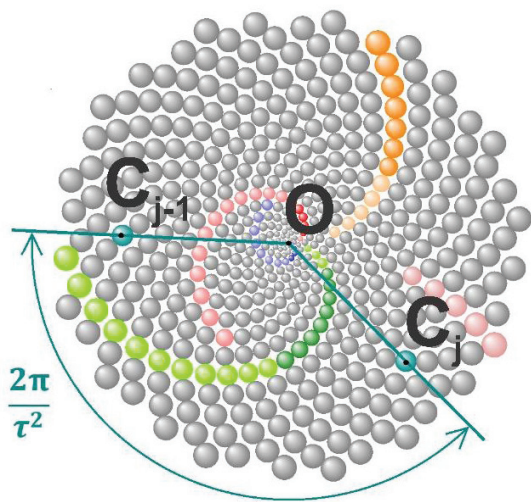


Figure 3: The divergence angle between EPP( $j-1$ ) and EPP( $j$ ).

Due to the recursive nature of the Model, one possible method for calculating locus is mathematical induction. Thus, in [1], it was proven that during the transition from a state with  $N$  EPPs to a state with  $N+1$  EPPs, the divergence angle between any EPP( $j-1$ ) and EPP( $j$ ) does not change. However, it has not been proven that the divergence angle is constant and equal to  $\frac{2\pi}{\tau^2}$ .

As mentioned above, from the analysis of the static model [1,2] it follows that the divergence angle does not depend on the EPP diameter growth function:

$$d_i = \sqrt{2\pi v} (N - i)^{v-0.5}$$

where  $i$  is the EPP number in the dynamic model and  $N$  is the iteration number. This allows you to first carry out analytical calculations for the special cases  $v=1$  and/or  $v=1.5$ , and then move on to the general case.

### Simulation-software method

This method involves writing a program that numerically calculates the motion locus of each EPP. To do this, the time between the appearance of new primordial  $T_c$  is divided into time quantum (for example, 100), and the relative position of EPPs is calculated through each time quantum. The diameter EPP( $i$ ), at time  $t$ , can be calculated as:

$$d_i(t) = \sqrt{2\pi v} \left( \frac{t}{T_N} - i \right)^{v-0.5}$$

Just as in the mathematical method, the criterion for proving the reliability of the Biomechanical model will be that the divergence angle between EPP( $j-1$ ) and EPP( $j$ ) will be constant and equal to  $\frac{2\pi}{\tau^2}$ . Calculating the divergence angle at  $j=100$  and  $t=150T_c$  can be considered sufficient. It is also possible at the first stage to carry out calculations for the special cases  $v=1$  and/or  $v=1.5$ , and then move on to the general case.

### Experimental method

For experimental confirmation, it is necessary to find or create a physical object that replaces the EPP. The main property of such an object should be an increase in volume (or area) starting from a given point in time.

The reliability criterion will be the visual observation of parastichy with indices 8 and 13. As calculated in [1], parastichy with index 13 is reliably visible in the range  $EPP(37) \div EPP(97)$  for the static model. That is, at least 100 EPPs are needed for the experiment. In this case, the EPP must increase its diameter by 10 times:

$$\frac{d_{100}}{d_1} = \frac{\sqrt{2\pi \cdot 100}}{\sqrt{2\pi \cdot 1}} = 10$$

Discrete objects that can increase their diameter by 10 times from a given point in time have not yet been found. The closest "candidates" for replacing EPP in this experiment are a water superabsorbent polymer (other names: hydrated water gel or water beads), but the available samples increase the diameter by a maximum of 6 - 7 times.

### The perspectives

A remarkable feature of the phenomenon of spiral phyllotaxis is its accessibility for observation without any special equipment. So, anyone interested, and not just a professional researcher only, can see various manifestations of this phenomenon in any flower shop or botanical garden. Likewise, the three methods proposed in this article for proving the reliability of a biomechanical model do not require special expensive equipment but allow any researcher to show their resourcefulness. Each naturalist can choose a method, a method close to him, in order to solve a problem that the outstanding mathematician of our time, Turing, could not solve.

Proving the reliability of the biomechanical model will allow us to take a different look at the reproductive process of plants and the role of auxin in it. This will allow us to find new non-chemical and non-GMO methods for increasing plant productivity. An interested reader will be able to draw conclusions about the emerging biotechnological prospects and their ethical purity.

### Conclusion

Confirmation of the biomechanical model of the morphogenesis of spiral phyllotaxis will allow us to state that the morphogenesis of spiral phyllotaxis is a biomechanical process. Auxin is not the driving force for the morphogenesis of phyllotaxis patterns, since there is no need for any signaling systems for the morphogenesis of spiral Fibonacci patterns.

Processes in a living plant can be described by integer mathematics, particularly by recurrent sequences, but not by statistical and differential-integral mathematical tools only, and the presence of Fibonacci numbers is due to the recursive process of pattern morphogenesis.



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