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Repulsion pressure model and numerical simulation for spiral phyllotactic patterns of plants

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ABSTRACT

We present biologically motivated simple models to study phyllotaxis patterns. A simplified MaxMin-principle is applied for determining new-born primordium appearance. We propose a new repulsion pressure model to interpret the angle movement of each primordium influenced by the repulsion from all other primordia or from the nearest left and right neighbors. For a large range of growing velocities, both mechanisms can generate uniformly packed patterns under suitable settings of repulsion parameters. Measurement of the pattern uniformity and demonstration of robustness are also provided.

1. Introduction

The study of geometric and numerical patterns in plants is known as "phyllotaxis". It is a central subject in plant morphogenesis which deals with the arrangements of plant organs such as leaves, bracts, branches, petals, florets, scales, etc. One can observe phyllotactic patterns macroscopically when viewing shoot tips. The center of the tip is occupied by a stable circular region, called apex. Around the apex, one by one, tiny lumps called primordia are formed. Each primordium migrates away from the apex where new ones continue to form. Eventually, the lump develops into a leaf, a petal, etc. [4,9,20].

There are two main phyllotactic patterns: the spiral patterns with one primordium per node and the whorled patterns with two or more primordia per node. In most of the flowering plants and conifers, secondary spirals are observed: one winding clockwise, the other counterclockwise, and appearing to interpenetrate each other. The numbers of these two families of spirals (the parastichy numbers) are usually two successive numbers from the Fibonacci sequence (1,1,2,3,5,8,13,21,34,55,...) [18]. Other parastichy numbers are from the Lucas Series (1,3,4,7,11,...). In rare cases, series such as (1,4,5,9,14,...) or (1,2,5,7,12,...) are also observed [6]. The divergence angle is the angle between two successive primordia, as seen from the center of the apex. The most efficient packing that makes the most solid and robust seed head occurs when the divergence angle is equal to the golden angle, $\theta_G = 2\pi/(1+\omega) \approx 137.5^\circ$, where ω is the golden ratio $\frac{\sqrt{5}+1}{2} = 1 + \frac{1}{1+\frac{1}{1+\frac{1}{1+\ddots}}}$ [21]. In particular, the Fibonacci numbers arise when the divergence angle is near the golden angle.

Phyllotactic patterns are widely studied by botanists, physicists and mathematicians. In 1868, based on microscopic observations, Hofmeister established a hypothesis on the appearance of the new primordium [7]. It suggests the new-born primordium should be placed at the position with the largest minimum distance with other pre-existing primordia. This is called the MaxMin-principle [2]. This hypothesis was supported by many experiments done by Snow and Snow [18] and others. It was also extended by Snow and Snow to the space-filling theory [19], which proposes that the new primordium appears when and where there is a large enough space at the periphery of the apex. It is first mathematically investigated by Adler [1].

Hofmeister's hypothesis was also used in Douady and Counder's famous experiment [5], which used drops of magnetic ferrofluids to simulate the repulsion forces in the primordia. The drops were polarized by the magnetic field, and they repelled each other; they were given a boost in the radial direction by making the magnetic field stronger at the edge of the dish than in the middle. The patterns that appeared depends on how large the intervals between drops were. A very prevalent pattern had the divergence angle very close to 137.5°.

Regarding the location of the appearing of new primordia, recently there are fruitful research results showing that auxin, a mobile hormone in plants, regulates the initiation and location of

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newly born primordia in some plants [14]. On the other hand, it is observed that primordia position is frequently adjusted postmeristematically [15]. Hence the "correct" location of the newborn primordia alone may not be the sole factor that contributes to the the extremely regular phyllotactic patterns in plants. Accordingly, two biological processes must be involved: the mechanism determining the location where the new-born primordium appears, and the interaction among the primordia during the growth process. A number of methods have described these processes to a certain extent [6]. Based on Douady and Counder's experiment, Atela, Golé and Hotton provided a Max–Min dynamical model to study 3D phyllotaxis pattern formation [3]. They choose the position on the apex circle where the minimum distance with all existing primordia is maximized as the birth place of the new primordium. Furthermore, they suggest that one only needs to consider some primordia "before" the new born one instead of all pre-existing ones. Later, they study 2D pattern formation problem under the MaxMin-principle, where they consider the influence of all pre-existing primordia [8].

Inspired by the early work in [5] and the dynamical system model [3,8], we implement the MaxMin-principle to study 2D phyllotaxis problem. Our model further simplifies Atela et al.'s work by considering only the influence on the new born primordium from its two predecessors.

Contact-pressure models have been applied to study the interaction of primordia in the growth process [2,16]. It is expected that if the primordia touch each other (close to each other within a given distance) at some phase of their growth process, the contact-pressure makes the primordia move to the largest possible distance to each other. An important work of the investigation and simulation of contact-pressure models was given by Ridley in 1982 [16]. Based on this idea, extended work has been conducted by Hellwig [6] and many others. In 1991, Levitov proposed that the spirals of phyllotactic patterns are reproduced based on the lowest energy configurations of repulsive particles in the apex [10,11]. Levitov's idea was supported both experimentally and numerically by Nisoli et al. in 2009, who constructed a magnetic cactus made of magnetic dipoles mounted on bearings stacked along a 3D stem [12,13]. We remark here that Nisoli et al.'s work can be mapped and applied to 2D phyllotactic patterns.

In the contact pressure model, one has to determine the distance range within which the contact pressure exists. The patterns obtained may vary if the distance range to contact pressure differs. We hereby introduce the idea that primordia behave like magnetic ferrofluid drops in Douady and Counder's experiment. Thus any two primordia have repulsion pressure to each other no matter they are close to each other or not. Again, this can also be simplified by considering only the repulsion pressure from the nearest left and nearest right neighbors. For the adjustment of the primordia's position, only angular movement is allowed. We used the above mechanism to study the interaction of primordia during the growing process and obtained very robust simulation results. Both the repulsion interactions from all others and from only the nearest left and right neighbors are considered. For a large range of growing velocities, one can always find suitable parameter settings to generate uniformly packed patterns under both repulsion mechanisms.

The remainder of this paper is structured as follows. In Section 2, a simplified MaxMin-principle model is introduced to determine the location of the new-born primordium. In Section 3, our repulsion pressure model is introduced to study the interaction among primordia during the growth process. Two repulsion mechanisms are proposed, repulsion from all other primordia and repulsion from only the nearest left and nearest right neighbors. In Section 4, we provide an indicator for pattern uniformity measurement. Numerical simulation results are provided for each section. In Section 5, robustness of both repulsion mechanisms is examined. Finally, concluding remarks are given in Section 5 to address further research issues.

2. A simplified Max–Min model

In this section, we introduce our simplified Max–Min model for the development of 2D phyllotactic patterns. Based on Hofmeister hypothesis [2], the MaxMin-principle suggests the new-born primordium should be placed at the position with the largest minimum distance with other pre-existing primordia. Details of Hofmeister's hypothesis are as follows:

(i) The stem apex is axisymmetrically represented by a circle of given radius R_0 from the center in a plane surface;
(ii) Primordia are generated with a periodicity T at the periphery of the apex;
(iii) Due to the shoot's growth, primordia move away from the center. The distance between the origin and the primordium at time length t from birth equals to

$$R_0 + vt^s,$$

where v is the growing velocity, and t is the time length of the primordium's existence.

We assume that plants provide a constant supply of substance for growth, and this results in the area of the circle between the primordium and the origin growing at a certain speed. Here we set $s = 0.5$. This particular value of s will give the result that, when each of the primordia is given a suitable angle, the primordia can spread out very evenly across a circular region, so that they will cluster with the same density no matter they are near the center or near the perimeter of the region. In Fig. 1, we show the patterns formed with different values of s but with the same value of velocity $v = 1.805$, which gives the golden divergence angle $\alpha = \theta_G$ under our simplified Max–Min model. One can observe that when $s < 0.5$, the primordia are packed more densely near the perimeter, and when $s > 0.5$, the primordia are packed more densely near the center. Actually, one can always apply a nonlinear mapping to transform patterns generated by $s = 0.5$ to those with different s values but the same other parameter settings.

We start by assuming that there is no further reorganization leading to changes of angular position of the primordia outside the region of the apex R_0. In Section 3, we apply our repulsion pressure mechanisms to simulate the interaction in the primordia during the growth process.

To facilitate our discussion, we label the primordia according to their emerging sequence. We define θ_i to be the angle between the positive x axis and the straight line joining the origin and the ith primordium. Then at time t_k, the birth time of the kth primordium ($k > i$), the orthogonal coordinates of the ith primordium are

$$((R_0 + v\sqrt{t_k - t_i})\cos\theta_i, (R_0 + v\sqrt{t_k - t_i})\sin\theta_i).$$

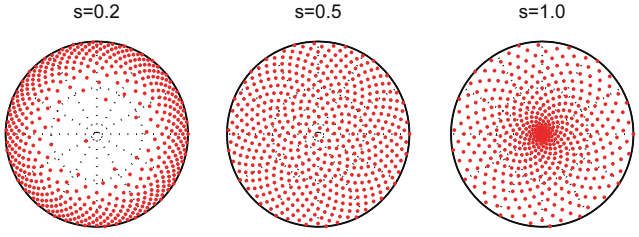

Fig. 1. Comparison of patterns with the same growing velocity and the same divergence angle but different values of s.