Phyllotaxis: Its geometry and dynamics

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We have found a relation between the irrational divergence angles and the number of spirals based on the properties of the generalized Fibonacci numbers. Our numerical simulation shows that the patterns of the spiral phyllotaxis depend mainly on the initial growing speed of the primordia. [S1063-651X(98)04504-8]

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I. INTRODUCTION

Phyllotaxis has been known for a long time, and is of interest to botanists and mathematicians as well as physicists (See Ref. [1] for an updated review). It deals with arrangements of plant organs such as leaves, bracts, branches, petals, and florets, called *primordia* in their young stages. Among all the phyllotactic patterns, the most common one is the spiral pattern. The primordium appears one at a time near the growing center (*apex*), and grows outward. One can trace the primordia according to their order of appearance with a spiral called *genetic spiral*. However, a human's eye is attracted to the conspicuous spirals that link each primordium to each nearest spatial neighbor. Two sets of conspicuous spirals (called *parastichies*) run in opposite directions and cross one another. The most striking feature is that the numbers of parastichies in the opposed set are nearly always two consecutive numbers of the Fibonacci series. Furthermore, the angles relative to the apex between two successive primordia on the genetic spiral, called the divergence angles, are all close to the golden angle, $\Phi=(1-\tau)\times 360°\approx 137.5°$, where $\tau=(\sqrt{5}-1)/2$ is the golden mean.

In Fig. 1 we show a picture of a sunflower. Two sets of parastichies are clearly seen. There are 34 clockwise spirals and 21 counterclockwise spirals. The primordia can be labeled by its order of appearance on the genetic spiral. Primordia labeled 189 and 190 are indicated by small dots in Fig. 1. The divergence angle of these two primordia is very close to the golden angle Φ.

There have been many works on reconstructing the spiral pattern based on the observed facts [2]. Most of them focus on the Fibonacci series and the golden angle. However, spiral patterns with numbers of parastichies different from the Fibonacci numbers are also observed in plants (see text below). In this paper we address two questions: First, is there a definite relation between the divergence angles and the parastichy numbers? Second, what is the origin of these patterns? In particular, why is a particular pattern preferred over the others? The first question was investigated rigorously by Jean [3]. In this paper we derive an alternative formula that relates the divergence angle to the numbers of parastichies based on the properties of the generalized Fibonacci numbers (defined below). For the second question, we adopt the model of Douady and Couder [4]. They introduced a dimensionless parameter g, which is equivalent to the logarithm of the *plastochrone ratio* [5], to describe the successive appearance of new primordia. The position of a new primordium is determined by the requirement that the total energy of the system is the lowest. They found that an explicit form of the energy law is not necessary as long as it is repulsive. The requirement is a realization of the inhibitor mechanism suggested by Schoute [6], and discussed in detail by Mitchison [7]. We perform a numerical simulation, and show that it is the initial value of g that determines the number of parastichies. Under the assumption that all initial values of g are equally favored, the relative frequencies of patterns observed in plants can also be explained by the results of our simulation.

We will first prove a simple theorem in Sec. II, and then use the theorem in Sec. III to determine the divergence angle of any pattern with a parastichy pair. The dynamics of the formation of the parastichies is described in Sec. IV. Section V is the conclusion.

II. A MATHEMATICAL THEOREM

The Fibonacci numbers [8] F_n

$$1,1,2,3,5,8,13,21,34,55,\ldots \tag{1}$$

are defined by the relation

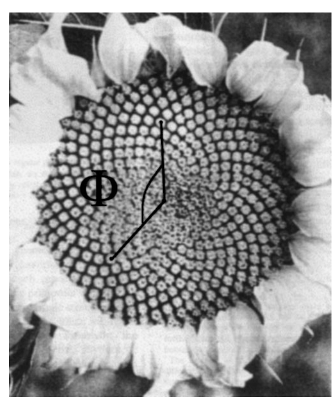

FIG. 1. The sunflower has two sets of conspicuous parastichies. The numbers of parastichies are 21 and 34, which are two consecutive numbers in the Fibonacci series. The divergence angle of two consecutive primordia on the genetic spiral is close to the golden angle.

$$F_n = F_{n-1} + F_{n-2}, \tag{2}$$

and the beginning two numbers $F_1 = 1$ and $F_2 = 1$. Two identities we need below for F_n, which can be easily proved by induction, are

$$F_{n-1}F_{n+1} - F_n^2 = (-1)^n, \tag{3}$$

$$F_{n+1}F_{n-2} - F_nF_{n-1} = (-1)^{n+1}. \tag{4}$$

Using the properties of Farey numbers [7] [the Farey series of order N, $\mathcal{F}(N)$, is the ascending series of irreducible fractions between 0 and 1 whose denominators do not exceed N. The basic property of Farey series is that if h/k and h'/k' are consecutive terms in $\mathcal{F}(N)$, then $|kh' - k'h| = 1$), identities (2) and (3) are equivalent to the following statement:

$$\frac{F_{n-2}}{F_{n-1}}, \quad \frac{F_n}{F_{n+1}}, \quad \frac{F_{n-1}}{F_n}$$

are consecutive terms of $\mathcal{F}(n+1)$.

One can define the generalized Fibonacci numbers $G(p,q,n)$, by Eq. (2), with the beginning two numbers being p and q:

$$G(p,q,n) = G(p,q,n-1) + G(p,q,n-2),$$

$$G(p,q,1) = p, \tag{5}$$

$$G(p,q,2) = q.$$

Obviously, $F_n = G(1,1,n)$ and $G(1,3,n)$ are known to be a Lucas series. Equation (5) can be solved to give an explicit expression for $G(p,q,n)$:

$$G(p,q,n) = \frac{1}{\sqrt{5}}\left\{\left[\left(\frac{\sqrt{5}+1}{2}\right)^n - \left(\frac{1-\sqrt{5}}{2}\right)^n\right]p + \left[\left(\frac{\sqrt{5}+1}{2}\right)^{n-1} - \left(\frac{1-\sqrt{5}}{2}\right)^{n-1}\right](q-p)\right\}, \tag{6}$$

$G(p,q,n)$ can be related to F_n by

$$G(p,q,n) = pF_n + (q-p)F_{n-1} = pF_{n-2} + qF_{n-1}. \tag{7}$$

Using Eqs. (3), (4), and (5), one can prove the following theorem.

Theorem

$[G(a,a+b,n-1)/G(p,q,n)]$ and $[G(a,a+b,n)/G(p,q,n+1)]$ are two consecutive Farey numbers in $\mathcal{F}(N)$ for $G(p,q,n+1) \leqslant N < G(p,q,n+2)$ if and only if p/q and b/a are consecutive in $\mathcal{F}(M)$ for $\max(q,a) \leqslant M < q+a$.

Proof: Based on the basic property of Farey series, we need only to show

$$|G(p,q,n+1)G(a,a+b,n-1) - G(p,q,n)G(a,a+b,n)| = 1. \tag{8}$$

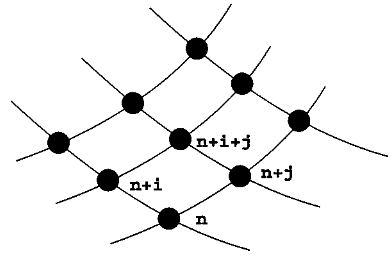

FIG. 2. The conspicuous parastichy pair for a given plastochrone ratio. The closest neighbors of the primordium $n+i+j$ are $n+i$ and $n+j$.

Using Eqs. (7), (3), and (4), we have

$$|G(p,q,n+1)G(a,a+b,n-1) - G(p,q,n)G(a,a+b,n)| = (-1)^n(pa-qb).$$

Thus Eq. (8) is satisfied if and only if

$$|pa - qb| = 1, \tag{9}$$

Q.E.D.

III. RELATION BETWEEN THE DIVERGENCE ANGLES AND THE PARASTICHY NUMBERS

As a plant grows, the plastochrone ratio decreases [7]. The conspicuous parastichy numbers follow the Fibonacci rule [7], namely, the numbers of parastichy pair (i,j) (assuming $i<j$) make a transition to numbers $(j,i+j)$. This can be seen from Figs. 2 and 3. We use a black dot to represent a primordium, and label it by a number showing its order of appearance. Assume the number of clockwise parastichies is i, and the number of counterclockwise parastichies is j. We can assume $i<j$ without loss of generality. It is obvious that along each one of the clockwise (counterclockwise) parastichies, the labels of primordia differ by $i(j)$. When the parastichy numbers are (i,j), the primordium $n+i+j$ is closest to $n+i$ and $n+j$ (Fig. 2). When g decreases, the distance between $n+i+j$ and n is shortened by a large amount, so that the primordium $n+i+j$ is now closest to n and $n+j$ instead (Fig. 3). Thus the conspicuous parastichy number i changes to $i+j$.

On the other hand, the parastichy numbers can also be contracted when g increases using the reverse rule: $(j,i+j) \to (i,j)$, or equivalently, $(i,j) \to (j-i,j)$. Thus the numbers of the right and left spirals are in general two consecutive numbers in the generalized Fibonacci series $G(p,q,n)$.

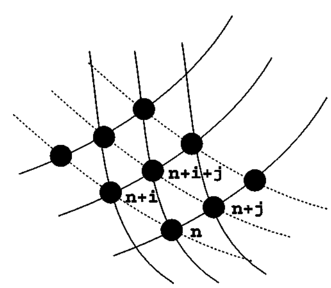

FIG. 3. The conspicuous parastichy pair for a smaller plastochrone ratio than that in Fig. 2. The closest neighbors of the primordium $n+i+j$ are n and $n+j$.

TABLE I. Divergence angles of some common parastichies.

Parastichies $[p,q]$	Divergence angle (degrees) ϕ
[1,1]	137.508
[1,2]	137.508
[1,3]	99.502
[1,4]	77.955
[2,5]	151.136
[3,8]	132.178

With two opposed spirals, the angle of the primordium $n+i+j$ has to be between the angles of primordia $n+i$ and $n+j$. Assume the divergence angle of parastichies is ϕ, then the condition

$$[i\phi]<0<[j\phi] \tag{10a}$$

or

$$[j\phi]<0<[i\phi] \tag{10b}$$

has to be satisfied, where $[s\phi]$ is defined as the difference between $s\phi$ and its closest integer $(s\phi)$:

$$[s\phi]=s\phi-(s\phi). \tag{11}$$

Now i and j are in general two consecutive generalized Fibonacci numbers, say $i=G(p,q,n)$ and $j=G(p,q,n+1)$. When g decreases, relation (9) has to be satisfied, while i and j make a transition to a larger n.

Define the angle ϕ_n as

$$\phi_n=\frac{G(a,a+b,n)}{G(p,q,n+1)}+(-1)^n\varepsilon_n, \tag{12}$$

with ε_n a very small positive number, $\varepsilon_n<1/G(p,q,2n+2)$, and converges to 0 as $n\rightarrow\infty$. a and b are determined by Eq. (9). Use the theorem, in particular Eq. (8), we have

$$[i\phi_n]=\frac{(-1)^{n+1}}{G(p,q,n+1)}+(-1)^n\varepsilon_n G(p,q,n), \tag{13}$$

$$[j\phi_n]=(-1)^n\varepsilon_n G(p,q,n+1) \tag{14}$$

satisfying Eq. (10). Take the limit $n\rightarrow\infty$, we obtain the divergence angle ϕ,

$$\phi=\lim_{n\rightarrow\infty}\phi_n=\lim_{n\rightarrow\infty}\frac{G(a,a+b,n)}{G(p,q,n+1)}$$
$$=\lim_{n\rightarrow\infty}\frac{aF_{n-2}+(a+b)F_{n-1}}{pF_{n-1}+qF_n}=\frac{(a+b)+a\tau}{p+q/\tau}=\frac{a+b\tau}{q+p\tau}. \tag{15}$$

Note that for a given p and q, if a and b satisfy Eq. (9), then $kq\pm a$ and $kp\pm b$, $k\in I$, also satisfy Eq. (9) and produce the same divergence angle ϕ (except the sign.)

In Table I we list the divergence angles of some common

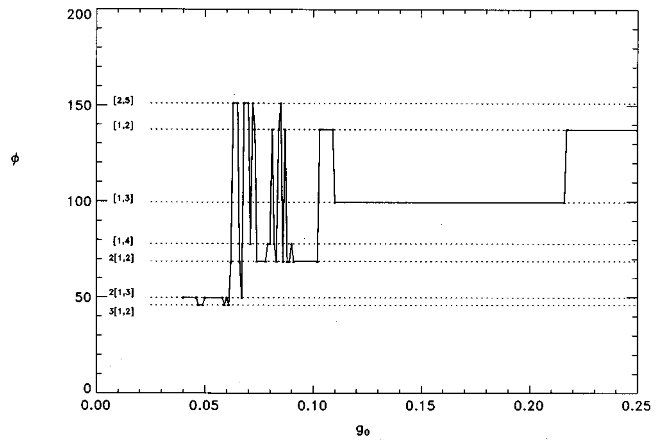

FIG. 4. The divergence angles (in degrees) of different initial g with a decreasing rate 0.000 25 per primordium.

parastichy numbers which are two consecutive terms of the generalized Fibonacci series $G(p,q,n)$. In Table I and what follows, the series $G(p,q,n)$ is simply denoted by $[p,q]$. $2[p,q]$, $3[p,q]$ denote cases in which there are two and three sets of parastichy pairs, respectively.

Multiplying the divergence angle ϕ by p and q, respectively, using Eq. (9), we have

$$p\phi=\frac{pa+pb\tau}{q+p\tau}=\frac{(qb\pm1)+pb\tau}{q+p\tau}=b\pm\frac{1}{q+p\tau}, \tag{16}$$

$$q\phi=\frac{qa+qb\tau}{q+p\tau}=\frac{qa+(pa\pm1)\tau}{q+p\tau}=a\pm\frac{\tau}{q+p\tau}. \tag{17}$$

Thus a and b are the closest integers of $p\phi$ and $q\phi$, namely, $a=(p\phi)$ and $b=(q\phi)$. We obtain the alternative formula of Eq. (15) for ϕ given by Jean [3]:

$$\phi=\frac{(p\phi)+(q\phi)\tau}{q+p\tau}. \tag{18}$$

Jean's formula [Eq. (18)] is neat because it determines the divergence angle ϕ using the parastichy numbers only, without introducing other integers such as a and b in Eq. (15). But, in practice, it is not clear how one can calculate ϕ from

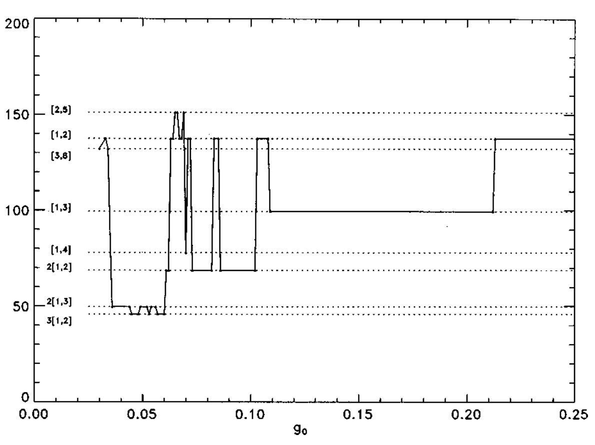

FIG. 5. The divergence angles (in degrees) of different initial g with a decreasing rate 0.000 10 per primordium.

Eq. (18), since ϕ also appears in a very particular form on the right-hand side of the formula. Jean [3] introduced an algorithm to calculate ϕ based on Eq. (18). In our formula [Eq. (15)], the auxiliary integers a and b introduced through Eq. (9) are easily determined, since the numbers p and q are normally small integers. One can therefore calculate the divergence angle based on Eq. (15) very easily.

IV. ROLE OF THE PLASTOCHRONE RATIO

We have shown that once the pattern of an opposed parastichies appears, the divergence angle is uniquely determined by a self-organized manner. The next question is how does a plant choose its parastichy numbers. Have they been set in the genetic code? Or do they form according to the environmental situation? Douady and Couder [4] introduced a model in which a single parameter g, which might be due to genetics or environment, determines the parastichy numbers by a dynamical process. We follow this point of view.

When a plant grows, g decreases and eventually goes to zero. There are in fact two factors to be considered. One is the initial value of g and the other the decreasing rate of g. The former might be inherited from the gene, while the latter could be mostly due to environmental effects. We find that the initial value of g is crucial in determining the parastichy numbers and hence the divergence angle.

Our simulation is based on the model of Douady and Couder [4]. Each primordium appears initially on a small circle centered at the origin. After its appearance, it is given a radial motion with a velocity proportional to its distance to the center. The place of birth of a primordium is determined by the condition of lowest total energy. We take the energy law to be $1/d^3$, where d is the distance between two primordia. The results are qualitatively the same for several other repulsive energy laws. For a given decreasing rate of g, we scan the initial g from 0 to 1 with step 0.001, and record its final parastichy numbers as $g \rightarrow 0$. (We have also recorded the divergence angles to make sure that the parastichy numbers and the divergence angles are consistent according to Table I.)

We plot the divergence angle vs initial g for two decreasing rates, 0.000 25 and 0.000 10, in Figs. 4 and 5, respectively. For $g_0 > 0.21$, the divergence angle is 137.5°, the golden angle, and the corresponding parastichies are consecutive numbers in Fibonacci series [Eq. (1)]. For $0.11 < g_0 < 0.21$, the parastichies are two consecutive numbers in a Lucas series. For g_0 smaller than 0.11, several generalized Fibonacci series appear interwined. In Fig. 4, the region $g_0 < 0.04$ is not shown because with its decreasing rate 0.000 25, the divergence angle does not converge to a particular value. In Fig. 5, where the decreasing rate is 0.000 10, a definite pattern can still be seen for $0.03 < g_0 < 0.04$. In general, more structure can be revealed by using a smaller decreasing rate for g.

For all the values of $g_0 > 0.04$ we scanned, there are no other patterns except [1,2], [1,3], [1,4], [2,5], 2[1,2], 2[1,3], and 3[1,2]. One more pattern, [3,8], appears when the initial g is smaller, $0.03 < g_0 < 0.04$. We expect more patterns than we have plotted in Figs. 4 and 5, such as [1,5], [1,6], 2[1,4], etc., in the region $g_0 < 0.03$.

TABLE II. Data for eight patterns and 12 750 observations on more than 650 species.

Pattern	Frequency	%
[1,2]	11 641	91.3
2[1,2]	666	5.2
[1,3]	190	1.5
[1,4]	17	
[1,5]	38	
[1,6]	32	
[1,7]	25	
[2,5]	22	

The results are consistent with the observation of the frequencies of the spiral patterns in plants. Jean [9] collected 12 750 observations on more than 650 species, as shown in Table II. Our results of numerical simulation indeed show that pattern [1,2] is the most likely to occur if plants choose the initial g randomly. The second and third most possible patterns are [1,3] and 2[1,2], which are consistent with Table II except that the order is reversed. Two patterns [3,8] and 3[1,2] that appear in our simulation are not included in Table II. These patterns have actually been reported [10]. Pattern [3,8] was claimed by Jean to be a problematic pattern based on the model using the principle of minimal entropy production [11]. According to the model of Douady and Couder and the results of our numerical simulation, the pattern has a small probability to appear when the initial growing speed of the primordia is very small.

V. CONCLUSION

In conclusion, we have found a relation between the parastichy numbers and the divergence angles. Once a parastichy pair appears, the number of parastichies changes according to the Fabonnaci rule, thus leading to a definite limiting divergence angle. Based on the model of Douady and Couder, our numerical simulation shows that the appearance of a particular parastichy pair depends strongly on the initial growing speed of the plant characterized by a single parameter g. The relative frequencies of various spiral patterns collected from the observations on many species are roughly consistent with the results of our numerical simulation. Of course, there are other phyllotactic patterns that are needed to be investigated using the still unknown properties of the plants. In particular, there is no convincing explanation for the whorled patterns [12]. Douady and Couder [4] suggested that adding a criterion of minimal total energy as a threshold for giving birth to a new leaf in the numerical simulation would lead to the appearance of whorled patterns. Work along this line is under investigation.

ACKNOWLEDGMENT

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[5] If we number the order of appearance of primordium by n, and denote its distance to the center of apex by r_n. The plastochrone ratio R is defined as the ratio of the distances of two successive primordia on the genetic spiral, namely, $R = r_n / r_{n+1}$. According to the botanical observation, the plastochrone ratio decreases during the development of a plant. The parameter g is defined as $e^g = R$. Geometrically, to construct a pair of opposed spirals of parastichy numbers (i, j), there exists an algebraic relation between ln R, the divergence angle, and the two numbers i and j. Thus $g = \ln R$ is a more convenient parameter for constructing models.

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[11] See *Phyllotaxis: A Systemic Study in Plant Morphogenesis* (Ref. [1]), Chap. 6.

[12] See the discussion in *Phyllotaxis: A Systemic Study in Plant Morphogenesis* (Ref. [1]), Chap. 8.