Physical Phenomenology of Phyllotaxis

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From a physical and phenomenological standpoint, we provide a model description of phyllotaxis by investigating conditions to realize an arbitrary phyllotactic fraction, emphasizing the importance of insensitivity to initial conditions and model parameters, especially, a finite range of repulsive interaction.

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Phyllotaxis, the regular arrangement of leaves on a plant stem, has since long attracted the minds of botanists, mathematicians and physicists[1–3]. Most commonly, alternate leaves along a twig execute a spiral with an angle of 1/2, 1/3, 2/5, 3/8 of a full rotation one after another, while other fractions are also observed though less prevalently or quite rarely. Hence phyllotaxis is regarded not as a universal *law* but only as a fascinatingly prevalent *tendency*[4]. Mathematically, number theoretical properties elucidated for decades have deepened our understanding of the subject significantly[5–12]. Nevertheless, there still remains the fundamental problem of why some fractions are observed prevalently while others are only rarely and how the difference in frequency of occurrence between sequences of fractions is brought about. We address this issue from a physical and phenomenological viewpoint. Motivated by the important findings that similar phenomena are realized in physical models[13–15], we attempt to find a simple model description of phyllotaxis with a rich mathematical structure by investigating conditions to realize an arbitrary phyllotactic fraction in a comprehensive manner.

The nth object (primordium) is represented by a positive integer n, vertical coordinate, and an angular coordinate θ_n measured from $\theta_0 = 0$ at $n = 0$. We assume a regular spiral with an offset angle $2\pi\alpha$, i.e.,

$$\theta_n = 2\pi n\alpha, \tag{1}$$

where α is a real number. Denoting interaction energy of the nth object with the mth object as $V_n(\theta_m - \theta_n, m-n)$, we obtain the total interaction energy

$$\begin{aligned} E &= \sum_{n=0}^{\infty}\sum_{m>n} V_n(\theta_m - \theta_n, m-n) &(2)\\ &= \sum_{n=0}^{\infty}\sum_{m=1}^{\infty} V_n(2\pi m\alpha, m). &(3)\end{aligned}$$

For the sake of simplicity, let us assume to write

$$V_n(2\pi x, m) = u_n V(2\pi x, m) = u_n v_m V(x), \tag{4}$$

then we obtain

$$E = v(\alpha)\sum_{n=0}^{\infty} u_n, \quad v(\alpha) \equiv \sum_{m=1}^{\infty} v_m V(m\alpha). \tag{5}$$

We investigate conditions to realize a local minimum of $v(\alpha)$. Specifically, a minimum is reached according to a relaxation equation like

$$\frac{d\alpha}{dt} = -\frac{dE}{d\alpha}, \tag{6}$$

from an initial condition,

$$\alpha(0) = \alpha_{\mathrm{ini}}. \tag{7}$$

We study $v(\alpha)$ within $0 < \alpha \le 1/2$, for $v(1-\alpha) = v(-\alpha)$.

In Eq. (4), $V(x)$ is a periodic function with period 1 and has a repulsive peak $V(0) = 1$ at $x = 0$. Beside α_{ini} in Eq. (7), we introduce two model parameters to characterize the finite range interaction $V_n(\theta, m)$. One is a half-width X of $V(x)$, i.e., $V(x) \simeq 0$ for $X < x (< 1/2)$. For example, we may assume

$$V(x) = e^{-\left(\frac{2x}{X}\right)^2}. \tag{8}$$

Then, the angular width of the original interaction $V_n(\theta, m)$ is given by

$$\Delta\theta \simeq 4\pi X. \tag{9}$$

The other is a vertical range of influence $n_{\max}$, i.e., $V_n(\theta, n_{\max}) \simeq 0$, or $v_n > 0$ for $0 < n \le n_{\max}$ while $v_n \simeq 0$ for $n > n_{\max}$. In what follows, the parameter $n_{\max}$ is particularly important, as the effect of finite interaction range seem to have never been systematically investigated.

By way of illustration, we show $v(\alpha)$ for $n_{\max} = 5, 6$ and 7 in Fig. 1. At $n_{\max} = 5$, there are five minima around $\alpha = 1/6, 2/9, 2/7, 3/8, 3/7$. Among them, two remain almost intact as we increase $n_{\max}$ from 5 to 7, that is, 2/9 and 3/8. The latter has a wider range of α_{ini} allowed for, i.e, $1/3 \lesssim \alpha_{\mathrm{ini}} \lesssim 2/5$, shown as $\Delta\alpha_{\mathrm{ini}}$ in Fig. 1. In other words, 3/8 has a tolerance width $\Delta\alpha_{\mathrm{ini}} \simeq 0.067$ wider than $\Delta\alpha_{\mathrm{ini}} \simeq 0.05$ for 2/9. On the other side, $\alpha = 3/8$ becomes a local *maximum* at $n_{\max} = 8$, where 2/9 still remains intact. In fact, 3/8 remains as a local minimum only for $n_{\max} = 5, 6, 7$, or for

$$n_{\max,0} \le n_{\max} \le n_{\max,0} + \Delta n_{\max}, \tag{10}$$

with $(n_{\max,0}, \Delta n_{\max}) = (5, 2)$. Similarly, we get $(n_{\max,0}, \Delta n_{\max}) = (5, 3)$ for 2/9. The local minimum

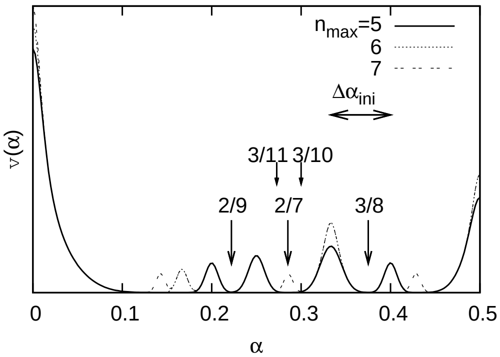

FIG. 1: $v(\alpha)$ for $n_{\max} = 5, 6$ and 7 ($X = 0.1$ and $v_n = 0.8^n$ for $n \le n_{\max}$) .

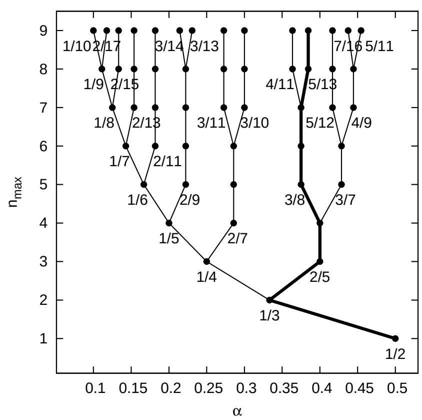

FIG. 2: Positions of local minima of $v(\alpha)$, represented by rational numbers attached to the points. Lines connecting the points represent hierarchical branching structure.

at $\alpha = 2/7$ for $n_{\max} = 5, 6$ ($(n_{\max,0}, \Delta n_{\max}) = (4, 2)$) becomes a local maximum at $n_{\max} = 7$, where the maximum at 2/7 is flanked on both sides by two newborn 'daughter' minima at 3/11 and 3/10, or 2/7 branches into 3/11 and 3/10 at $n_{\max} = 7$.

The positions of the local minima of $v(\alpha)$ and the branching structure are shown in Fig. 2 as a function of $n_{\max}$. There is a vertical segment stretching upward from a point labeled with a fraction, whose length represents $\Delta n_{\max}$ for the fraction. Rational numbers between 0 and 1/2 have their own $\Delta n_{\max}$ and $\Delta\alpha_{\rm ini}$. Thus they are plotted in the $\Delta n_{\max}$-$\Delta\alpha_{\rm ini}$ plane in Fig. 3.

Nature's apparent preference for particular rational numbers may be explained by the following hypotheses.

(i) A fraction is derived from its parent in increasing order of $n_{\max}$.

(ii) Between two fractions which appear at a branch point, the one with larger $\Delta n_{\max}$ is favorably realized.

These are simple enough as a basic mechanism and biologically plausible if we regard $n_{\max}$ as a generation index of a developing tree. The former (i) states continuous

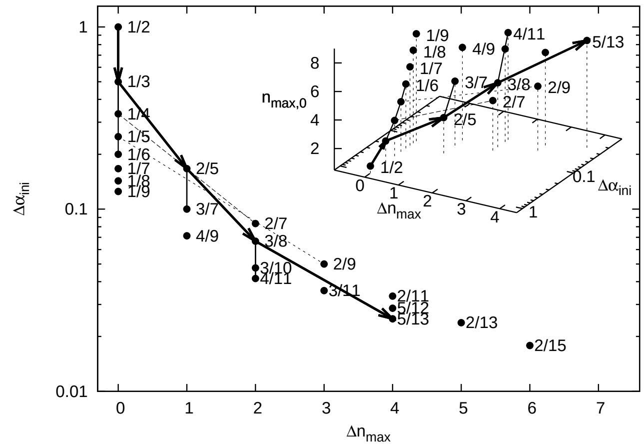

FIG. 3: For the local minima of $v(\alpha)$ labeled by rational numbers, $\Delta\alpha_{\rm ini}$ is plotted against $\Delta n_{\max}$, the length of the vertical segment in Fig. 2. The inset shows a 3D plot of $n_{\max,0}$ against $\Delta n_{\max}$ and $\Delta\alpha_{\rm ini}$.

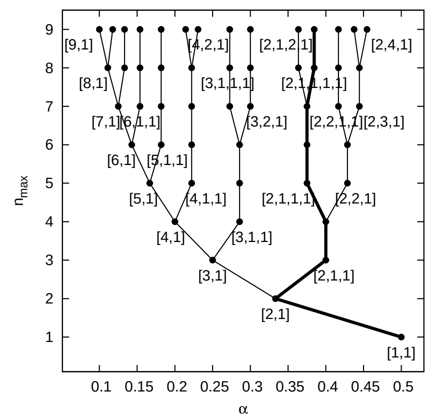

FIG. 4: Positions of local minima of $v(\alpha)$ are represented by continued fractions attached to the points.

fine-tuning of the initial condition $\alpha_{\rm ini}$ in development process. The latter (ii) ensures stability against possible misarrangement (e.g., overshoot) of the interaction range $n_{\max}$. In other words, 2/5 (one of the most common cases) is preferred to 1/4 by redundancy $\Delta n_{\max} = 1$ in the critical dependence on $n_{\max}$. Thus the main sequence $1/2, 1/3, 2/5, 3/8, 5/13, \cdots$, is derived as denoted by the thick line in Figs. 2 and 3, without excluding many other possible ramifications.

It is remarkable that Fig. 2 has the same structure as the Stern-Brocot tree of number theory[16], which contains each rational numbers exactly once. This is important because methodologically we regard rationals, not 'ideal' irrationals[5–11], as fundamental to the phyllotaxis number α[1]. We regard the latter appear only as approximate limits of the former, not vice versa. Thus we consider it more important to have a general basis to deal with all possibly relevant rationals than to study particular numbers favored by specific mechanisms. In general, the parent-child relation between numbers in the tree is concisely represented in terms of *mediants* and *continued fractions*.

For prime numbers m, n, p, q ($0 < n < q, |np - mq| = 1$), the *mediant* $(m+p)/(n+q)$ occurs in between m/n and p/q for $q \le n_{\max} < n+q$, i.e., $(m+p)/(n+q)$ has $(n_{\max,0}, \Delta n_{\max}) = (q, n-1)$ and $\Delta\alpha_{\rm ini} = 1/nq$. Then, in between $(m+p)/(n+q)$ and m/n occurs $(2m+p)/(2n+q)$ with $(n_{\max,0}, \Delta n_{\max}) = (n+q, n-1)$ and $\Delta\alpha_{\rm ini} = 1/n(n+q)$, while $(m+2p)/(n+2q)$ occurs between $(m+p)/(n+q)$ and p/q with $(n_{\max,0}, \Delta n_{\max}) = (n+q, q-1)$ and $\Delta\alpha_{\rm ini} = 1/q(n+q)$. In other words, at $n_{\max} = n+q$, $(m+p)/(n+q)$ becomes unstable to yield two minima at $(2m+p)/(2n+q)$ and $(m+2p)/(n+2q)$. The former has the same value of $\Delta n_{\max} = n-1$ as its parent $(m+p)/(n+q)$, while the latter (with the larger denominator $n+2q$) increases it to $\Delta n_{\max} = q-1 > n-1$. This is read from Fig. 3. At a branching point, one branch grows to the right while the other goes down along the ordinate in the main figure. Those sequences with increasing $\Delta n_{\max}$ comprise the main branch of our tree. The bifurcation rule (ii) may be compared with Levitov's maximal denominator principle on a Farey tree[12].

Numbers are represented as *continued fractions*. A real number α ($0 < \alpha < 1$) is represented as

$$\alpha = \cfrac{1}{a_1 + \cfrac{1}{a_2 + \cfrac{1}{a_3 + \cdots}}} \equiv [a_1, a_2, a_3, \cdots], \tag{11}$$

in terms of positive integers a_i ($i = 1, 2, \cdots$). Every rational fraction has two continued fraction expansions. In one the final term is 1. Hence rational α is represented as $\alpha = [a_1, a_2, \cdots, a_n, 1]$ with a finite number of a_i. According to this notation, Fig. 2 is transcribed to Fig. 4, showing a bifurcation rule

$$[a_1, a_2, \cdots, a_n, 1] \longrightarrow \begin{array}{c} [a_1, a_2, \cdots, a_n, 1, 1] \\ [a_1, a_2, \cdots, a_n + 1, 1]. \end{array} \tag{12}$$

The upper one increases $\Delta n_{\max}$, while the lower conserves it. Hence the former may be called a *normal path*[6] or *regular transition*[11]. Therefore, it becomes the most important to study a sequence of rational fractions: $[a_1, a_2, \cdots, a_n, 1]$, $[a_1, a_2, \cdots, a_n, 1, 1]$, $[a_1, a_2, \cdots, a_n, 1, 1, 1]$, $\cdots$, that is, *principal convergents* of a 'noble' (irrational) number[5, 8–10],

$$\alpha = [a_1, a_2, \cdots, a_n, 1, 1, 1, \cdots]. \tag{13}$$

Successive rational approximation

$$\frac{p_n}{q_n} = [a_1, \cdots, a_n] \tag{14}$$

of an irrational number α, Eq. (11), is obtained from relatively prime positive integers p_n and q_n satisfying recursion relations,

$$p_{n+2} = a_{n+2} p_{n+1} + p_n, \quad q_{n+2} = a_{n+2} q_{n+1} + q_n, \tag{15}$$

TABLE I: Principal convergents p_n/q_n of $[2, 1, 1, \cdots]$. The width $\Delta\alpha_{\rm ini}$ allowed for the initial value $\alpha_{\rm ini}$ and $(n_{\max,0}, \Delta n_{\max})$ for (10) to realize $\alpha = p_n/q_n$.

$\frac{p_n}{q_n}$	$\frac{1}{2}$	$\frac{1}{3}$	$\frac{2}{5}$	$\frac{3}{8}$	$\frac{5}{13}$	$\frac{8}{21}$
$\Delta\alpha_{\rm ini}$	1	0.5	0.167	0.067	0.025	0.010
$(n_{\max,0}, \Delta n_{\max})$	$(1, 0)$	$(2, 0)$	$(3, 1)$	$(5, 2)$	$(8, 4)$	$(13, 7)$
$\bar{X}$	0.5	0.333	0.2	0.125	0.077	0.048

TABLE II: For $\alpha = [3, 1, 1, \cdots]$.

$\frac{p_n}{q_n}$	$\frac{1}{3}$	$\frac{1}{4}$	$\frac{2}{7}$	$\frac{3}{11}$	$\frac{5}{18}$	$\frac{8}{29}$
$\Delta\alpha_{\rm ini}$		0.333	0.083	0.036	0.013	0.005
$(n_{\max,0}, \Delta n_{\max})$		$(3, 0)$	$(4, 2)$	$(7, 3)$	$(11, 6)$	$(18, 10)$
$\bar{X}$		0.25	0.143	0.091	0.056	0.034

and

$$p_0 = 0, \; p_1 = 1, \; q_0 = 1, \; q_1 = a_1. \tag{16}$$

The fractions p_n/q_n ($n = 1, 2, \cdots$) are called *principal convergents*. The difference between successive principal convergents satisfies

$$\frac{p_{n+1}}{q_{n+1}} - \frac{p_n}{q_n} = \frac{(-1)^n}{q_n q_{n+1}}. \tag{17}$$

The irrational α is sandwiched between even and odd order convergents,

$$\frac{p_{2k}}{q_{2k}} < \alpha < \frac{p_{2k+1}}{q_{2k+1}}. \tag{18}$$

The main sequence, covering more than 90% of all cases[2], is given by

$$\alpha = \tau^{-2} = [2, 1, 1, 1, \cdots]. \tag{19}$$

where $\tau = (1 + \sqrt{5})/2$. This gives a 'golden' angle $2\pi\alpha \simeq 137.5°$ and the Fibonacci sequence for q_n, as presented in Table I. The principal convergents p_n/q_n approach the limit in Eq. (19) according to (18). The next favored sequences, realized through one unfavorable branch, are $[3, 1, 1, \cdots]$ in Table II, $[2, 2, 1, 1, \cdots]$ in Table III, $[2, 1, 2, 1, 1, \cdots]$ and so on. Then follow $[4, 1, 1, \cdots]$, $[2, 3, 1, \cdots]$, $[3, 2, 1, \cdots]$ and so on. The priority order of observed sequences has been documented by

TABLE III: For $\alpha = [2, 2, 1, 1, 1, \cdots]$.

$\frac{p_n}{q_n}$	$\frac{1}{2}$	$\frac{2}{5}$	$\frac{3}{7}$	$\frac{5}{12}$	$\frac{8}{19}$	$\frac{13}{31}$
$\Delta\alpha_{\rm ini}$			0.1	0.029	0.012	0.004
$(n_{\max,0}, \Delta n_{\max})$			$(5, 1)$	$(7, 4)$	$(12, 6)$	$(19, 11)$
$\bar{X}$			0.143	0.083	0.053	0.032

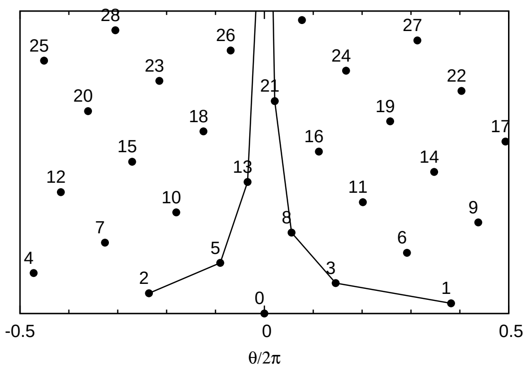

FIG. 5: Lattice points $(n\alpha, n)$ for $\alpha = \tau^{-2}$. The number attached to each point represents n. The principal neighbors are connected with lines.

Jean[2, 17]. Note that we do not exclude any sequence, including such rarely observed cases as the last two.

Let us restate the conditions for the principal convergents of the noble number (13). For $i > n$, p_i/q_i occurs in between p_{i-1}/q_{i-1} and p_{i-2}/q_{i-2} for $q_{i-1} \le n_{\max} < q_i$, i.e., p_i/q_i has

$$(n_{\max,0}, \Delta n_{\max}) = (q_{i-1}, q_{i-2} - 1). \tag{20}$$

And, from Eq. (17),

$$\Delta\alpha_{\rm ini} = \left|\frac{p_{i-1}}{q_{i-1}} - \frac{p_{i-2}}{q_{i-2}}\right| = \frac{1}{q_{i-1}q_{i-2}}. \tag{21}$$

These are presented in the tables numerically.

Lastly, let us examine the width X of $V(x)$ to realize p_n/q_n. In the lattice of points $(n\alpha, n)$, labeled by the non-negative integer n, a set of points $(q_n\alpha - p_n, q_n)$ comprise *principal neighbors* of the origin $n = 0$[5]. In Fig. 5, the points connected with lines represent the principal neighbors. Therefore we may write $v(\alpha)$ as

$$v(\alpha) \simeq \sum_n v_{q_n} V(q_n\alpha - p_n). \tag{22}$$

(We neglect *intermediate convergents* as they are irrelevant here.) For instance, to derive 3/8=[2,1,1,1] from within the region

$$1/3 = [2,1] < \alpha_{\rm ini} < 2/5 = [2,1,1], \tag{23}$$

consider $\alpha_{\rm ini} = [2,1,1+y]$ $(0 < y \le 1)$ and $\alpha_{\rm ini} = [2,1,n]$ $(n = 2,3,\cdots)$. For $5 \le n_{\max} < 8$, we obtain

$$\begin{aligned} v(\alpha) \ &\simeq \ v_1V(\alpha) + v_2V(2\alpha - 1) \\ &\quad + v_3V(3\alpha - 1) + v_5V(5\alpha - 2). \end{aligned} \tag{24}$$

The first two terms in Eq. (24) are neglected when $V(1/5) \simeq 0$, or for $X < 1/5$. Then $v(\alpha)$ is determined by the last two terms. In effect, this is a minimal model to derive a local minimum. As $V(3\alpha-1)$ and $V(5\alpha-2)$ are peaked at $\alpha = 1/3$ and $2/5$ with the half-width of $X/3$ and $X/5$, respectively, an optimal width $\bar{X}$ is estimated by $\bar{X}/3 + \bar{X}/5 = 2/5 - 1/3 = \Delta\alpha_{\rm ini}$, or $\bar{X} = 1/8$. In other words, according to Eq. (9), the optimal angular width of interaction is $\Delta\theta \simeq 90°$ for 3/8. Hence, for $X \simeq \bar{X}$, we obtain $\alpha \simeq 3/8$ from within (23) properly with good accuracy, as expected. For $X \lesssim \bar{X}$, stiffness $v''(\alpha)$ at the minimum, driving force in the right-hand side of Eq. (6), will be reduced, without affecting the minimum position appreciably. The minimum can disappear if X becomes large enough, $X \gtrsim \bar{X}$. In general, p_i/q_i $(i > n)$ of the noble number (13) has

$$\bar{X} = 1/q_i. \tag{25}$$

This is also shown in Tables I, II and III.

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