The unified rule of phyllotaxis explaining both spiral and non-spiral arrangements

Supplemental Materials

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Supplementary Text

According to observations, the main sequence patterns of an elongated shoot (1/3, 2/5, 3/8, etc.) originate from the 137.5° arrangement at the shoot tip, depending on the vascular connections (fig. S1). The present model considers what longitudinal arrangements originate from a general angle.

Three patterns for 360α=78.0, 99.5, and 137.5 degrees are shown in fig. S2*a-c*, where each arrow indicates the tendency to the nearest vertical arrangement. The first two angles

are of anomalous spiral phyllotaxis, which are rarely found in place of the third angle of normal spiral phyllotaxis. When α is close to these angles, fitness f is given by

$f_a=-w_2(\alpha-1/2)^2-w_3(\alpha-1/3)^2-w_4(\alpha-1/4)-w_5(\alpha-1/5)^2$,

$f_b=-w_2(\alpha-1/2)^2-w_3(\alpha-1/3)^2-w_4(\alpha-1/4)-w_5(\alpha-1/4)^2$,

and

$f_c=-w_2(\alpha-1/2)^2-w_3(\alpha-1/3)^2-w_4(\alpha-2/5)^2-w_5(\alpha-2/5)^2$,

respectively. Frequencies w_i (i=2~5) are non-negative parameters satisfying $w_2+w_3+w_4+w_5=1$. Since higher-order patterns are neglected for simplicity, no other case than the above three cases need be considered.

For $w_2=w_3=w_4=w_5=1/4$, the three functions are plotted in fig. S2*d*. Fitness f for general values of α and w_m is given by the maximum (most fitted) among the three cases,

$$f=\max[f_a,f_b,f_c].$$

To put it explicitly, $f=f_a$ for $0<\alpha<0.225$, $f=f_b$ for $0.225<\alpha<0.325$, and $f=f_c$ for $0.325<\alpha<1/2$. Two peaks in Fig. 2d-f are due to f_b and f_c. In general, f_c is larger than f_a and f_b, while f_b can be as large as f_c if $w_2=w_3=0$, $w_4+w_5=1$.

The peak of f_c lies at

$$\alpha=w_2/2+w_3/3+2(w_4+w_5)/5,$$

Where $\partial f_c/\partial\alpha=0$. Thus, this optimal angle α is an weighted average of Schimper-Braun fractions 1/2, 1/3 and 2/5, which occur with relative frequencies w_2, w_3, and w_4+w_5,

respectively.

In principle, it is possible to evaluate the parameters w_i from the frequencies of occurrence of various patterns. In practice, however, no data has been published except in the original work of Bonnet [1]. Figure S3 shows irregular variations of the cycle 5 of a 2/5 phyllotaxis observed on branches of various plants. According to the top of the the fourth column, three 3-cycles and six 5-cycles were observed on a peach tree, indicating that 1/3 and 2/5 occur with a relative frequency of three times 3 to six times 5, or w_3:w_4+w_5=9:30 . Therefore, w_3=3/130.23 and w_4=w_5=5/130.39 . These are used as representative values in Fig. 2*f* and Fig. 3*d* of the main text. The present model is so skeletal that high accuracy is not claimed for the 137.5° angle value. If the model is properly generalized to take account of higher-order patterns (like 3/8 and 5/13), optimal angle approaches to the ideal value 137.5° [2].

To visualize evolutionary trajectories, a further parameter has to be introduced. In terms of the ratio *c* of evolutionary rates of α and w_2, (α, w_2) evolves in the direction of $(\partial f/\partial \alpha, c\,\partial f/\partial w_2)$. In Fig. 3*b*, *c*=10.

1. Bonnet, C. 1754 *Recherches sur l'usage des feuilles dans les plantes*. Elie Luzac, fils.
2. Okabe, T. 2015 Biophysical optimality of the golden angle in phyllotaxis. *Scientific Reports* **5**, 15358.

Supplementary Figures S1-3

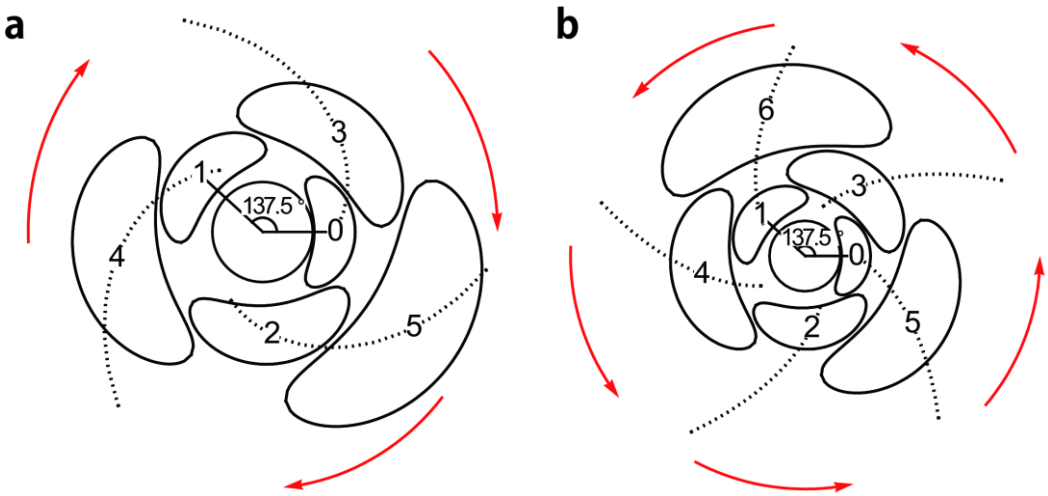

Figure S1: The 137.5° arrangement at the shoot tip gives rise to (*a*) 1/3 and (*b*) 2/5 phyllotaxis as the vascular bundles (dotted curves) are strengthened whereby the stem is twisted (arrows).

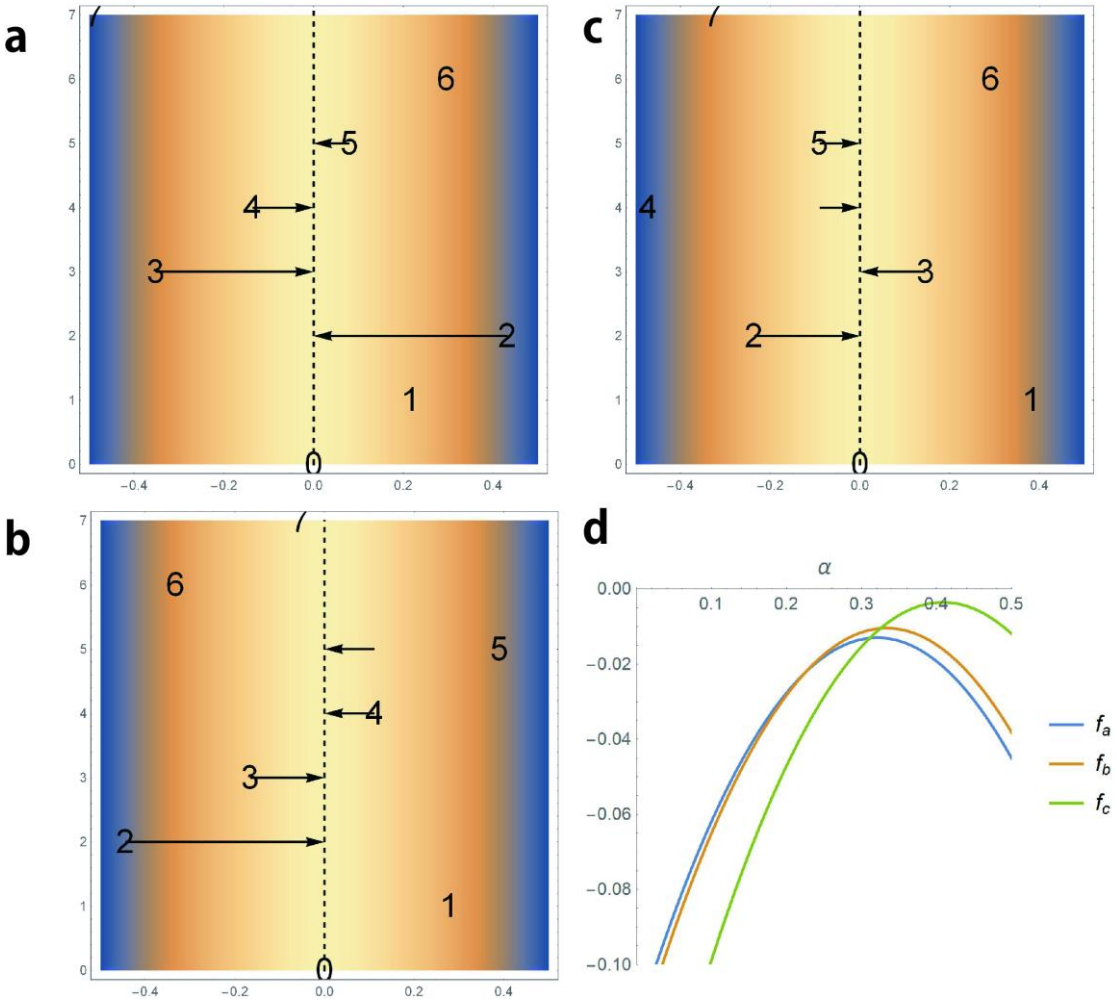

Figure S2: An arrow indicates tendency of leaves to a longitudinal arrangement (*a*) 360α=78.0 (α=0.216). (*b*) 360α=99.5 (α=0.276). (*c*) 360α=137.5 (α=0.382). (*d*) f_a, f_b and f_c as a function of α for w_2=w_3=w_4=w_5=1/4.

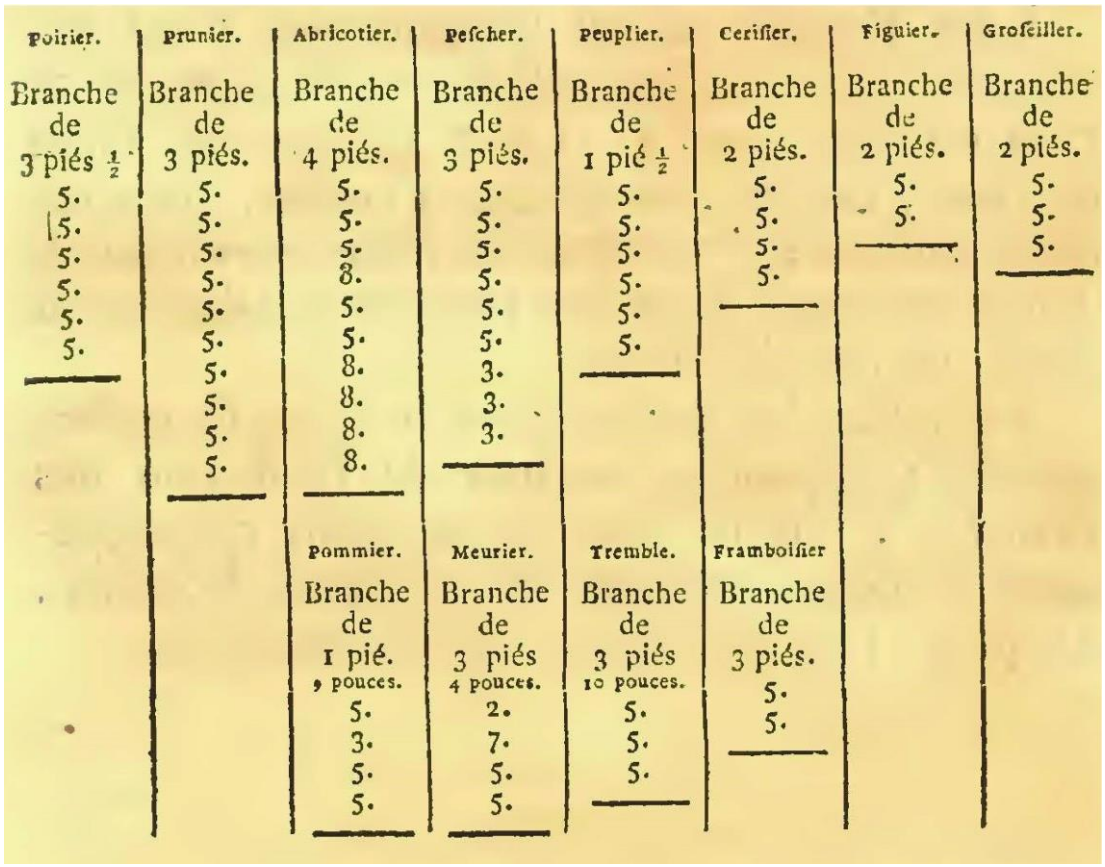

Figure S3: Irregular variations of the cycle 5 of a 2/5 phyllotaxis on individual branches of various plants [1] (not in copyright).