

Symmetry of STRUCTURE

an interdisciplinary Symposium

Abstracts

I.



Edited by Gy. Darvas and D. Nagy

Buda
Budapest

August 13-19, 1989

Hungary

A MATHEMATICAL STUDY
OF SYMMETRIES ON PLANTS

Roger V. JEAN

Department of Mathematics and Computer Sciences
University of Québec
Rimouski, Québec, G5L 3A1

1. INTRODUCTION

Primordia, the rudiments of leaves on stems, of florets on daisies, of scales on cones, etc, arise on the plant apex in a definite and precise pattern, i.e. with phyllotaxis. A leafy stem may show whorled symmetry, the leaves arising in bunches of $n = 2, 3, 4, \dots$ at the same level of the stem, with consecutive whorls either alternating of superposed. The majority of plants exhibits spiral symmetry, and wherever spiral phyllotaxis is evident in leaf production, it is also found in floral development. In the capitulum of the chrysanthemum two families of n and m spirals can be observed winding around a common pole or center of symmetry. In the plant kingdom, n and m are generally two consecutive terms of the Fibonacci series $\langle 1, 1, 2, 3, 5, 8, 13, \dots \rangle$, corresponding to a divergence angle between consecutively born primordia of about 137.51° or ϕ^{-2} where ϕ is the golden ratio. This constitutes the problem of phyllotaxis (study of patterns of plant organs).

This paper does not deal first with pattern generation, but with pattern recognition. It exhibits symmetry properties inherent to one of the author's mathematical model meant to describe the patterns on plants, so as to be useful to botanists involved in practical pattern assessment. The model is expressed by the formula $r = p(r) (m+n)^{-2}$, the exponent representing the fractal dimension of the set of phyllotactic patterns. One of the properties presented here, involving crucial phyllotactic ratios coined into the single formula $5^{1/2} \log \phi$, recently served to define a minimality criterion and a new predictive model for pattern generation where the possible divergence angles are ordered according, apparently, to their relative frequencies. The heuristic role played by symmetry and the interdisciplinary potential of the methods in phyllotaxis will be briefly discussed.

2. HEURISTIC AND INTERDISCIPLINARITY

The symmetries on plants considered in this paper are easily observable at the surface of the especially beautiful and colorful spiral arrangement of the florets in the capitulum of the sunflower, or of the daisy, and in the cross-sections of buds or shoots (see 1984). The aesthetic aspect of these regular, rhythmic, and ordered arrangements or patterns, together with the astonishment created by the overwhelming presence of the Fibonacci sequence and of the golden number in these patterns, generated a strong desire to look into the depths of the phenomenon. Astonishment, enhanced by the richness of the presence of beauty, is at the beginning of

creative thinking, and is certainly the best incentive the scientific mind can have.

This intellectual and emotional stimulant acted as an heuristic, considered here as something that helps to discover. It is based on the metaphysical faith in regularities. From the heuristic, a first model emerged, able to generate spiral symmetries; it was later on refined (1988a), and soon extended (1988b), given the unavoidable presence of asymmetrical patterns and the belief that the exceptional cases are not bits of sand in a mechanism but rather the hiding place for deeper secrets.

Then one comes to realize that other fields of research (e.g. the study of micro-organisms, proteins (1985), medusae and even quasi-crystals) show the same kind of symmetries. Meaningful conclusions can then be drawn (1989a). Also, the methods of analysis which proved to be fruitful in one case, are seen to be applicable to the analysis of the symmetries in these latter cases. In phylotaxis the central concern is believed to be the building of models that can make predictions (e.g. 1988a), that can be concretely used by biologists (e.g. 1987, 1988b) and that can be taught in classrooms (e.g. 1989b). Finally, the treatment of mathematical notions brought forward by a specific biological problem, is bound to produce new mathematical results (e.g. 1988c).

3. A MATHEMATICAL MODEL FOR BIO-SYMMETRIES

It has been shown that

$$\ln R = 2\pi p(\tau) (m+n)^{-2} \quad (1)$$

where τ is the angle of intersection of any two opposed spirals in the pair (m, n) , the spirals in each family being evenly spaced logarithmic spirals, $R > 1$ is the ratio of the distances to the common pole of the spirals of two consecutively born florets in the capitulum, or primordia in the cross-section, and

$$p(\tau) = \vartheta^3 (5^{1/2} \cot \tau + (5 \cot^2 \tau + 4)^{1/2}) / 2 \cdot 5^{1/2}, \quad (2)$$

where $\vartheta = (5^{1/2} + 1) / 2$. Function $p(\tau)$ decreases monotonically from ∞ to 0 as τ increases from 0 to 180° . By the transformation

$$R = e^{2\pi r} \quad (3)$$

formula (1) becomes

$$r = p(\tau) (m+n)^{-2} \quad (4)$$

where r is the ordinate of primordium 1 in the regular lattice of points expressing for example the arrangement of scales on a cone, or on a pineapple, considered as a cylinder unfolded in the plane. By (3) the spirals in (1) become evenly spaced parallel straight lines in (4). In the former case, we speak about the centric

representation of phyllotaxis, and in the latter case about the cylindrical representation.

Formula (1) has shown recently to be a very accurate tool, much more easy to apply, thus an improvement over earlier methods meant for the practical assessment of phyllotactic patterns. From formula (1) we can deduce formulae involving other phyllotactic parameters (1987), but we will concentrate on the parameters τ , r , $m+n$, and the divergence angle d , on which the symmetry of the systems depend. The model shows an explicit relation between the first three parameters, and an implicit relation between the last two.

4. ANALYTIC, GEOMETRICAL AND ARITHMETICAL SYMMETRIES

Formulae (1) and (4) express the global symmetries of all the systems. Considering (1) for example, if one observes any spiral pattern (m, n) with ratio R , then the point $(\log R, m+n)$ is on the line with slope -2 in the log-log grid. For each given value of τ this remarkable symmetry property is true, whatever be the spiral pattern (m, n) observed. Thus formula (1) is an allometry-type expression of differential growth. Concerning formula (4) the straight line of slope -2 intersects the vertical axis at $(0, \log p(\tau))$, the horizontal axis at $((\log p(\tau))/2, 0)$, and for $\tau \approx 121.43^\circ$ the line goes through the origin of coordinates.

Formulae (2) and (4) involve symmetries expressed by the following relations, for any pair (m, n) and for two symmetrical values of τ around 90° , that is $90 \pm x$, where x is in degrees:

$$p(90-x) p(90+x) = \phi^6/5 = p(90)^2, \quad (5)$$

$$r(90-x) r(90+x) = r(90)^2. \quad (6)$$

They show the importance of the orthogonality of the opposed spirals or straight lines in the respective representations of phyllotactic patterns. In fact, the practical assessment of these patterns is a search for the pair(s) (m, n) for which τ is closest to 90° . The symmetry in formulae (5) and (6) allows one to deduce the value for $90 + x$ from the value for $90 - x$. Also for τ fixed we have

$$J^2 r(Jm, Jn) = r(m, n) \quad (7)$$

where J is a positive integer specifying the number of genetic spirals in the natural system. For each fixed value of r , when τ goes from 0 to 180° , $m+n$ decreases monotonically, and the value of $m+n$ for which τ is closest to 90° gives the conspicuous pair (a, b) of the system such that $a+b = m+n$, and such that $a, b, a+b, 2b+a, 3b+2a, \dots$ is the series corresponding to the observed value of d .

On each straight line of slope -2 in the log-log grid, τ fixed, the distance from the point $(r_1, m+n)$ to the point $(r_2, 2m+n)$, to

the point $(r_3, 3m+2n)$, ... rapidly stabilizes around the value $5^{1/2} \log \phi$. For example, one goes from the orthogonal system $(m, n) = (5, 3)$ to the orthogonal system $(m, m+n) = (5, 8)$, by a jump of $5^{1/2} \log \phi \approx 0.46731$ on the allometric line $r = 1.8944 (m+n)^{-2}$ representing a special case of (4). The number $5^{1/2} \log \phi$ is a condensed expression for the symmetry ratios involved in phyllotaxis.

There are systems for which (m, n) does not change during a period of time while r varies. In that case, the point $(r, \cot \tau)$ moves on an hyperbola given by the relation

$$br \cot \tau = r^2 - a, \quad (8)$$

where $a = \phi^6/5 (m+n)^4$ and $b = (5a)^{1/2}$, with center $(0, 0)$, and asymptotes $b \cot \tau = r$ and $r = 0$. Given that $r > 0$ for the phenomenon concerned, the right-hand side branch of the hyperbola is concerned, underneath the asymptote $b \cot \tau = r$.

Arithmetically, these arrangements (m, n) show symmetries expressed by formulae of the type

$$| m(nd) - n(md) | = 1 \quad (9)$$

where d is the divergence angle (as a fraction of the circle in the centric (spiral symmetry) representation, or as the abscissa of point 1 in the cylindrical (orchard-like symmetry) representation, between two consecutively born primordia, and (xd) is the integer nearest to xd . In fact, (9) is a necessary and sufficient condition for a pair (m, n) to be visible.

5. LITERATURE CITED FROM THE AUTHOR

- 1983 Allometric Relations in Plant Growth, J. Math. Biol., **18**, 189-200.
- 1984 Mathematical Approach to Pattern and Form in Plant Growth, Wiley-Interscience, N.Y., 240 pages.
- 1985 A Geometric Representation of α -Polypeptide Chains Revisited, J. Theor. Biol. **112**, 819-825.
- 1987 A Mathematical Model and a Method for the Practical Assessment of Phyllotactic Patterns, J. Theor. Biol., **129**, 69-90.
- 1988a Model of Pattern on Generation Plants, Based on the Principle of Minimal Entropy Production, in Thermodynamics and Pattern Formation in Biology, I. Lamprecht and A. I. Zotin (eds), W. de Gruyter Pub., West Berlin, pp 249-264.
- 1988b Phyllotactic Pattern Generation: A Conceptual Model, Annals of Botany (London), **61**, 293-303.
- 1988c Number-Theoretic Properties of Two-Dimensional Lattices, J. Number Theory, **29**, #2, 206-223.
- 1989a Phyllotaxis: A Reappraisal, Can. J. Botany, in press.
- 1989b Mathematical Concepts in Shoot Development of Plants, with W.W. Schwabe, to be published by the Consortium for Mathematics and its Applications Project, Lexington, Mass.