

DOI: 10.5586/asbp.3535

**Publication history**

Received: 2016-12-30

Accepted: 2016-12-31

Published: 2016-12-31

**Handling editors**

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**Authors' contributions**

Both authors equally contributed to writing the text.

**Funding**

This work did not involve any financial support.

**Competing interests**

Beata Zagórska-Marek holds the position of the editor-in-chief of ASBP. We declare no other competing interests.

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**Citation**

Zagórska-Marek B, Prusinkiewicz P. Phyllotaxis and related topics. *Acta Soc Bot Pol.* 2016;85(4):3535. <https://doi.org/10.5586/asbp.3535>

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## EDITORIAL

# Phyllotaxis and related topics

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Phyllotaxis, a keystone problem in structural plant biology, has attracted the interdisciplinary interest of biologists, mathematicians, physicists, crystallographers and, more recently, computer scientists for almost two centuries. The continuing interest in phyllotaxis has led to this special issue, bringing together nine papers from authors who responded to our invitation or call for papers from early 2016. We thank the authors for their contributions, which we have the pleasure of presenting here.

The papers focus on two aspects of phyllotactic patterning: its universality across a very broad spectrum of plants, and the interplay between the regularity and irregularity of the patterns. Addressing the first aspect, Gola and Banasiak [1] present a systematic survey of phyllotactic patterns in land plants and show that the same pattern types can be found in analogous (not homologous) axial organs present in different plant groups, from bryophytes to angiosperms. The question of what mechanisms, undoubtedly different in their physiological nature, guarantee this convergence, is still open. Gola and Banasiak also discuss individual features of specific plant groups: for example, the presence of true main Fibonacci pattern in gametophytic shoots of Bryophytes is questionable, and in sporophytic shoots of Lycophytes it is rare.

The universality of phyllotaxis is further illustrated by the observation of Fibonacci phyllotaxis in brown algae, a lineage of phototrophic eukaryotes phylogenetically very distant from land plants. In the study of the architecture of the highly organized thallus of the invasive brown alga *Sargassum muticum*, Peaucelle and Couder [2] emphasize the generic character of self-organizing processes leading to Fibonacci-related spirals, but also point out that, although auxin presence in lower phototrophic eukaryotes has been confirmed, the physiological mechanisms of phyllotaxis in these phototrophs are still unknown.

For a long time, the regularity of (real or idealized) phyllotactic patterns, and their relation to the golden section and Fibonacci numbers, have been at the center of studies of phyllotaxis. In this context, Okabe [3] gives a historical account of ideas emphasizing the importance of a constant divergence angle – especially, the golden angle – to the geometry of phyllotactic arrangements. In particular, he brings to light the largely forgotten German-language contributions from the first decades of the twentieth century by Hirmer. More recently, however, it is the irregularity observed in real phyllotactic patterns that has gained increasing attention. Combining the interest in both regular and irregular patterns, Golé, Dumais, and Douady [4] raise two fundamental questions: (i) what is the developmental origin of Fibonacci patterns, and (ii) what are the origins and manifestations of departures from this idealized pattern. Extending a line of geometric models going back to van Iterson [5] and Mitchison [6], and building upon the analogy between the dislocations in crystals and the “imperfections” of phyllotactic patterns introduced by Zagórska-Marek [7], Golé et al. present a model focused on the front of an emerging pattern, where new primordia are being added. This focus emphasizes local configurations and interactions between primordia, while deemphasizing other notions traditionally used in the description of phyllotactic patterns, in particular that of the divergence angle (as Okabe [3] points out, the progress in phyllotactic research does not follow a straight line). Using a series of

in silico experiments in which primordia are represented as disks sequentially stacked on the surface of a cylinder, and novel quantitative characterizations of phyllotactic patterns, the authors show that the emergent parastichy numbers follow the Fibonacci recursion if the size of consecutively placed primordia changes slowly as a function of their position. For moderately faster rates, the Fibonacci recursion is maintained even though individual primordia may emerge out of the order implied in idealized models, resulting in large fluctuations of the divergence angle. This result is remarkably consistent with experimental data, e.g., [8,9]. At even faster rates a qualitative change takes place and “quasi-symmetric” patterns emerge, characterized by approximately equal numbers of parastichies running in opposite directions. Two examples of such patterns are given by Douady and Golé in Part II of their study [10], which illustrates various classes of the patterns simulated in Part I with case studies of phyllotaxis in nature.

The paper by Zagórska-Marek and Szpak [11] provides further examples of departures from idealized patterns using a combination of simulations and experimental data. The authors use the terms  $\gamma$ - and  $\lambda$ -dislocations rather than the triangle and pentagon transitions proposed by Golé et al. [4] and Douady and Golé [10], but the key message is similar: rapid changes in the size of primordia and noise (represented as random changes in the radius of primordia or their out-of-the order placement) modify phyllotactic patterns by splitting or merging the parastichies.

It is intuitive that drastic changes in parameters will likely lead to the development of strongly irregular phyllotactic patterns. Rutishauser [12] provides scanning electron microscopy images illustrating such patterns as produced by the vegetative shoot apical meristems of acacias and the floral meristems of the cananga tree. The chaotic phyllotaxis within the domain of stamens in the flowers of cananga tree is certainly caused by a drastic change in organ identity and size (from large tepals to small stamens). Entirely different is the chaos observed in acacias, which results from the insertion of additional meristematic structures among primordia already set in a regular phyllotactic pattern. The phenomenon of additive plant organs is analyzed by Kitazawa and Fujimoto [13]. They show how meristic variation in the perianth of the Japanese species of *Anemone* leads to the formation of different floral phenotypes, a species-specific trait. An interesting aspect of this case study is that it involves a change not only in the number of flower parts, but also in the way they are distributed.

This special issue concludes with a paper by Beyer and Richter-Gebert [14]. Inspired by the biological reality of phyllotactic patterns, the authors ask the mathematically intriguing question of how phyllotactic patterns would look in higher dimensions. Instead of new primordia being created within a one-dimensional ring on the growing two-dimensional surface of the meristem, the “primordia” are created on the expanding surface of a sphere. Simulations reveal a richness of emerging patterns, with the appropriately generalized divergence angle converging to a constant value, oscillating periodically, or changing in a chaotic manner.

The diverse perspectives, results and open problems highlighted in the papers presented in this special issue demonstrate that the study of phyllotaxis is still far from complete, and will remain an important and enjoyable research area for many years to come.

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