BIOLOGY SERIES

Phyllotaxis and Symmetry in Angiosperms

Jean-Paul Walch
Solange Blaise

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First published 2024 in Great Britain and the United States by ISTE Ltd and John Wiley & Sons, Inc.

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ISTE Ltd
27-37 St George's Road
London SW19 4EU
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www.iste.co.uk

John Wiley & Sons, Inc.
111 River Street
Hoboken, NJ 07030
USA

www.wiley.com

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Library of Congress Control Number: 2024935368

British Library Cataloguing-in-Publication Data
A CIP record for this book is available from the British Library
ISBN 978-1-78630-989-1

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Foreword

The understanding of phyllotaxis in plants has been of major interest to botanists for a very long time and remains a hot and still unresolved topic of discussion. Additionally, phyllotaxis and symmetry are intrinsically linked, as transitions between spirals and whorls are essentially responsible for the floral diversification among angiosperms. Symmetry in flowers, especially the causes of shifts between different types of symmetry, follows specific patterns that are ruled by developmental and genetic factors.

Solange Blaise and Jean-Paul Walch have recently arrived at the forefront of botanical research, but their contributions have already delivered great impact. A comprehensive book on phyllotaxis models was published in 2023 and has sown the seeds for this new book on symmetry in flowers and its links with phyllotaxis.

The authors' approach goes beyond that of traditional botany, adding their expertise in mathematics and physics to deal with fundamental questions on floral morphology. The book clearly demonstrates the intimate relationship between phyllotaxis and symmetry in flowers. The authors explore this connection from different angles, including experimental models, genetics and physics. They also discuss different types of symmetry and how these relate to major groups of plants. The law of symmetry is represented by continuous growth processes, demonstrating the intricate relationships between organs in time and space, leading to a wonderful pattern in the sequential differentiation of inflorescences and flowers.

The authors explore patterns of symmetry in major groups of angiosperms, citing several studies of specific species related to the causes of changes in symmetry patterns. The book is well illustrated with clear examples of symmetry and their causes taken from other works and is beautifully redrawn. The book emphasizes the fundamental link between growth and form, highlighting the importance of undertaking developmental studies. As such, they revisit the contributions of the

great floral morphologists of the 20th and early 21th century but with a novel, contemporary approach. Most of the observations and conclusions are based on published studies of the early development of flowers, as young stages provide a much better picture of the processes affecting symmetry. Understanding the kind of symmetry necessitates a combination of different approaches, including evidence of spatial constraints and genetic shifts. Through a series of clear examples, the authors provide a detailed overview of the difference between early ("constitutional") and the late ("positional") zygomorphy. They clearly demonstrate the intricate relationship of genetic stimuli and spatial constraints in shaping the floral structure and demonstrate how important it is to approach flowers from different angles.

This book will contribute to our understanding of the intricate mechanisms shaping flowers and should find a space on the bookshelf or computer of anyone interested in the structure of flowers and their evolution.

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Preface

> There cannot possibly be a physical or dynamical, though there may well be a mathematical Law of Growth, which is common to, and which defines, the spiral form in the Nautilus, in the Globigerina, in the ram's horn, and in the disc of the sunflower.
>
> The essential facts of [Phyllotaxis] are not difficult to understand, but the theories built upon them are so varied, so conflicting and sometimes so obscure, that we must not attempt to submit them to detailed analysis and criticism.
>
> In the morphology of living things, the use of mathematical methods and symbols has made slow progress, and there are various reasons for this failure to employ a method whose advantages are so obvious in the investigation of other physical forms.
>
> "On Growth and Form", D'Arcy Thompson (1917)

D'Arcy Thomson suggested that there could be a mathematical law common to the spirals of plants and animals. We have discovered this law: it is a law of symmetry, in the same way that radial and bilateral symmetry are. This law allows us to bridge phyllotaxis and floral symmetry, and explains why purely physical phenomena, in particular magnetic, also generate spirals.

Furthermore, it was necessary to identify the physical and biochemical process which ensure the implementation of this law in plants. Using a unified system of equations, we have modeled the molecular mechanisms and pressure forces that act on inflorescence and floral meristems. Thus, mathematical methods allow us to gain insight into what gives flowers their shapes: our model is an instrument for

evaluating the forces on meristem from their effect on the geometry of this meristem. With this powerful tool, we have revisited many important notions of plant biology.

Spiral phyllotaxis optimizes the packing of primordia (e.g. sepals and petals on the floral meristem), but there is no clear boundary between organ types: thus, organ number is labile, as seen in early-diverging angiosperms. Packing is less optimal in whorled phyllotaxis; however, organs within a whorl have the same identity and therefore each species has a well-defined number of organs of each type. Magnoliales and Laurales use a "strategy" to align organ identity with spiral phyllotaxis based on "pseudo-whorls", that is, sets of organs of the same type that look like whorls but are less regular because they are derived from Fibonacci spiral initiation (with divergence angles between successive primordia equal to the golden angle (137°), e.g. quincuncial aestivation) as opposed to rational angles dividing the circle into equal parts (e.g. 72° = 360°/5 in a pentamerous flower). Each pseudo-whorl corresponds to the periphery of the apex of the meristem where Fibonacci spirals are initiated, which explains why the number of organs in a pseudo-whorl is a term of the Fibonacci sequence (3, 5, 8, 13, etc.). This is why monocots are trimerous and dicots are often pentamerous.

Inflorescences themselves display obvious symmetrical patterns (e.g. distichous, opposite-decussate or spiral). These patterns are transmitted to the perianth via the bracteoles in cymose inflorescences and a few racemose inflorescences, or by contact pressure in the absence of these transitional organs. In a flash of genius, Eichler (1875, 1878), in his monumental work on floral diagrams, identified the rules of the influence of bracteoles on the arrangement of the calyx, but despite his efforts, he was unable to give these rules a "mathematical" explanation. This is what our modeling has been able to do.

We show that although tetramerous perianths can be radially symmetrical from initiation, in general, pentamerous perianths are initiated as irregular pentagons. The transition to regular pentagons (radial symmetry: for example, valvate aestivation) requires an equalization of the pentagon angles before anthesis.

If spirals have remained the preserve of phyllotaxis, the study of the genetic causes of floral symmetry has taken off since the characterization of floral symmetry genes in *Antirrhinum majus* (Luo et al. 1996). More than 100 studies using molecular methods (RT-PCR and RNA in situ hybridization) have shown that closely related members of the *TCP* gene family play a crucial role in the control of floral symmetry in diverse angiosperm lineages.

By transposing the conclusion of Curie's (1894) thesis on electromagnetic phenomena, stating that "when certain causes produce certain effects, the elements of symmetry of the causes must be found in the effects produced", to the symmetry of flowers, we were able to state a general principle whereby the symmetry of the perianth (the effect) is derived from the symmetry of certain *TCP* gene expression (the cause).

The model developed in our previous book, *Phyllotaxis Models*, by Jean-Paul Walch and Solange Blaise made it possible to identify the general mechanisms responsible for the location of organ primordia within the floral meristem. In this book, we highlight the interplay between the symmetry of the expression of certain *TCP* genes and previously described phyllotactic mechanisms, be they of molecular inhibition or mechanical (contact pressure) origin.

Endress (1999) defined two categories of zygomorphy, constitutional (apparent as early as the initiation of perianth primordia) and positional (appearing late in floral development), and asked: what is the genetic difference between these two categories? We show that these two categories of zygomorphy correspond to two different temporalities of floral asymmetrical *CYC*-like gene expression: early or late. Late zygomorphy is caused in particular by the development of a spur (e.g. *Delphinium* (Ranunculaceae)) or by elongation of the flower (ligules of Asteraceae).

May 2024

Acknowledgments

We would like to thank Florian Jabbour, Associate Professor at the Muséum National d'Histoire Naturelle, Paris, for his encouragement, Hélène Citerne for her review of the manuscript, and Line and Michèle Walch for their superb drawings.

Introduction

In our previous book, *Phyllotaxis Models*, by Jean-Paul Walch and Solange Blaise, we developed a mathematical model of phyllotaxis that made it possible to reproduce in silico the arrangement of the floral organs in dozens of species; these patterns matched the SEMs (scanning electron micrographs) of developing flowers, as well as the floral diagrams of Eichler (1875, 1878). In this book, we studied a number of species from angiosperm orders with mainly bilaterally symmetrical flowers from a phyllotactic and genetic point of view.

Angiosperm orders are not presented following the APG IV (2016) phylogenetic system but rather a pedagogical order. However, in each chapter, families within an order follow the APG IV classification system. Species were selected according to the availability of data for phyllotaxis modeling: SEMs, floral diagrams of Eichler and drawings of plant organogenesis (Payer 1857). The expression patterns of floral symmetry genes were compiled from reverse transcriptase polymerase chain reaction (RT-PCR) and RNA in situ hybridization data. Chapters 3–7 are therefore made up of case studies.

In Chapter 1, we give readers the keys to understanding this "new phyllotaxis", which is one of the two pillars of our approach to floral symmetry. The other pillar is the genetics of floral symmetry. In particular, we focus on *CYC*-like genes from the *TCP* family that are implicated in the control of floral symmetry in angiosperms.

Chapter 2 is the only chapter to use mathematical concepts. We show that phyllotactic spirals are a form of symmetry. If Fibonacci spirals are the most common, with the number of spirals corresponding to numbers in the Fibonacci sequence (3, 5, 8, etc.), other configurations show spiral numbers corresponding to the Lucas sequence (3, 4, 7, 11, etc.). We show that the latter are the consequence of dislocations within the lattice of primordia.

In Chapter 3, we model floral organogenesis in Ranunculales (early-diverging eudicots) and analyze the genetics of floral symmetry in species where data are available. The flower of bleeding heart (*Lamprocapnos spectabilis*, Papaveraceae) presents an unusual symmetry (disymmetry), which corresponds to a disymmetric expression of a *CYC*-like gene. The bilateral symmetry of *Capnoides sempervirens* (Papaveraceae) is linked to the growth of a lateral spur (the single axis of symmetry is transverse). Again, the tepal arrangement is consistent with the symmetry of *CYC*-like gene expression. In the actinomorphic corolla of *Aquilegia* (Ranunculaceae), *CYC*-like gene expression is itself radially symmetrical. These genes are not expressed in the actinomorphic corolla of *Nigella* (Ranunculaceae). *Delphinium* is one of the rare genera in Ranunculaceae with zygomorphic flowers (associated with the development of a large spur): its *CYC*-like genes present a late asymmetric expression along the dorsoventral axis. As in many Ranunculaceae, the perianth of *Ranunculus repens* is initiated in a spiral. We show how the arrangement of the perianth shifts toward actinomorphy, due to contact pressure between organs during growth.

Antirrhinum majus, from the order Lamiales, is the model plant for the genetics of floral symmetry. We study the perianth of six Lamiales with either actinomorphic or zygomorphic flowers by simulating their floral phyllotaxis using our model and showing the influence of *CYC*-like gene expression patterns on the phyllotaxic mechanisms (Chapter 4). In accordance with Curie's principle, the symmetry of the expression of these genes determines the symmetry of the perianth.

In Chapter 5, we distinguish constitutional zygomorphy (early zygomorphy, e.g. Lamiales) from positional zygomorphy (late zygomorphy). For example, in *Tropaeolum longifolium* (Brassicales), zygomorphy is not the consequence of the arrangement of floral organs during their initiation, but of their differential growth, in particular, with the formation of a spur. In *Impatiens* (Ericales), the weight of the spur causes the flower to rotate at anthesis (resupination). In Asteraceae, the causes of the actinomorphy of disc florets and the zygomorphy of ray flowers are also consistent with Curie's principle.

Unlike in most core eudicots, the first sepal in Caesalpiniodeae and Faboideae (Fabales) is generally located on the abaxial side of the flower, which requires that the adaxial inhibition source be much stronger than that of the bract, in the vicinity of which this first sepal arises. Modeling a zygomorphic perianth requires that couples of primordia appear simultaneously and symmetrically with respect to the dorsoventral axis ("twinning"), for example, initiation of twin petals forming the two keels or the two wings, as in *Cercis*. In *Mimosa* (Mimosoid clade), the symmetry of the inflorescence (a raceme), as well as the synchronous development of the flowers within it, underlies the radial symmetry of these flowers. In *Pisum*

(Faboideae), with typical papilionoid flowers, the symmetry of *CYC*-like gene expression in the flower is the cause of zygomorphy (Chapter 6).

Most early-diverging monocots are actinomorphic, while more derived monocot families, such as Orchidaceae, Iridaceae, Poaceae, the order Zingiberales and Commelinaceae, are mainly zygomorphic. Curie's principle applies just as well to the perianths of monocots as to those of eudicots. Therefore, in Commelinaceae, *TCP* genes are not expressed in the actinomorphic flowers of *Tradescantia pallida* but are expressed asymmetrically with respect to the transverse axis in the zygomorphic flowers of *Commelina communis*. These two species are a perfect illustration of scorpioid cymes, the former having a bracteole, while the latter does not (Chapter 7).

The Conclusion presents the most significant outcomes of our theory.

Our model has been published in the *Journal of Theoretical Biology*, its application in basal angiosperms in *Botany Letters* and the demonstration of the influence of bracteoles on sepal arrangement (initially intuited by Eichler in 1875) in *Flora*. The influence of *CYC*-like genes on phyllotaxic mechanisms in Lamiales has been published in *Botany Letters*.

1

Concepts of Phyllotaxis and the Genetics of Floral Symmetry

1.1. Types of floral symmetry

In the generally accepted classification system, four types of floral symmetry are defined (Endress 1999) (Figure 1.1):

– *Actinomorphy* (radial symmetry or polysymmetry): the flower has n axes of symmetry, where n > 2 is the number of organs in each whorl (e.g. six axes of symmetry; Figure 1.1(A)).

– *Disymmetry*: there are two perpendicular axes of symmetry (Figure 1.1(B)).

– *Zygomorphy*: (bilateral symmetry or monosymmetry): the flower is symmetric with respect to the dorsoventral axis and asymmetric with respect to the transverse axis (Figure 1.1(C)).

– *Asymmetry:* flowers have no axis of symmetry (Figure 1.1(D)).

Bilateral floral symmetry is predominant in certain species-rich families such as Lamiaceae and Fabaceae (legumes) in eudicots and Orchidaceae in monocots. Phylogenetic studies have demonstrated that zygomorphy has evolved many times from ancestors with radially symmetrical flowers and that reversals from bilateral to radial symmetry are frequent. A minimum of 130 shifts from radial to bilateral floral

For a color version of all the figures in this chapter, see www.iste.co.uk/walch/phyllotaxis2.zip.

symmetry and 69 reversals to actinomorphy have been inferred within angiosperms. For example, in Lamiales, bilateral symmetry has evolved early in the diversification of the clade and has been followed by at least 10 reversals to radial symmetry (Reyes et al. 2016).

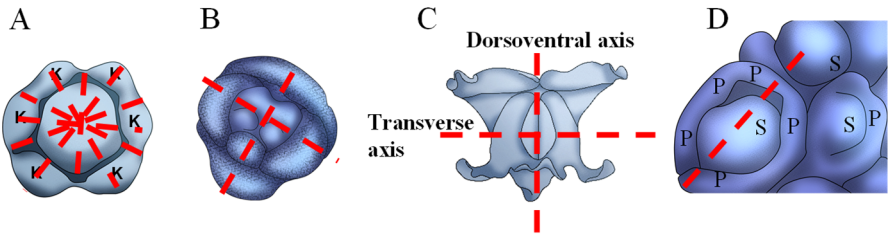

Figure 1.1. *Different types of floral meristem symmetry before anthesis. (A) Actinomorphy: Antirrhinum majus (Plantaginaceae) cyc:dich mutant at an early developmental stage (from Luo et al. 1996) with six axes of symmetry. (B) Disymmetry: Lamprocapnos spectabilis (Papaveraceae) with two perpendicular axes of symmetry (from Damerval et al. 2013). (C) Zygomorphy: wild-type Antirrhinum majus (redrawn from Vincent and Coen 2004). Dashed lines represent the dorsoventral and transverse axes, which intersect at the center of the flower. (D) Flower meristems of Centranthus ruber redrawn from Roels and Smets (1996). The asymmetric flowers have a single stamen that is not on the dorsoventral axis. K = sepals from the German Kelch, not to confuse with S = stamen; P = petal; S = stamen*

In flowers that have spur, the third dimension has to be taken into account, and symmetry is considered with respect to planes instead of axes (Figure 1.2(A)). In the case of *Impatiens* (Balsaminaceae; Figure 1.2(A)), the weight of the spur tilts the flower at 180° at anthesis (resupination).

Jean-Baptiste Payer was appointed professor of geology and mineralogy at the University of Rennes in 1840. In 1844, he obtained the chair of botany at the École Normale Supérieure in Paris. He received a doctorate in medicine from the Paris faculty in 1852 and was appointed that same year as professor of plant organography at the faculty of sciences. He published “On Comparative Plant Organogeny of the Flower” between 1854 and 1859.