



Review

Phyllotaxis: Some progress, but a story far from over

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HIGHLIGHTS

- We review a variety of models for phyllotaxis.
- We derive a model for phyllotaxis using biochemical and biomechanical mechanisms.
- Simulation and analysis of our model reveals novel self-similar behavior.
- Fibonacci progressions are a natural consequence of these mechanisms.
- Common transitions between phyllotactic patterns occur during simulation.

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ABSTRACT

This is a review article with a point of view. We summarize the long history of the subject and recent advances and suggest that almost all features of the architecture of shoot apical meristems can be captured by pattern-forming systems which model the biochemistry and biophysics of those regions on plants.

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1. Introduction

Observe the seeds of sunflowers, bracts on pine cones, spines on cacti, leaves on foliage plants, and analogous structures (leaf homologues) found in pictures throughout this article. In many of these examples, such as on the sunflower head of Fig. 1 and the pine cone and cactus of Figs. 2(a) and (b), the leaf homologues are arranged in spirals. Strikingly, the spiral pattern on the cactus of Fig. 2(b) is almost identical to that on the pine cone of Fig. 2(a). In both cases, the homologues lie at the intersections of two families of spirals, and the numbers of spirals in these families (89 and 55 at the outer edges of the sunflower of Fig. 1, and 13 and 8 on the pine cone and cactus of Figs. 2(a) and (b)) are successive members of the Fibonacci sequence. In contrast, on the cactus of Fig. 2(c), the succulent of Fig. 2(d), and many other plants, the spines or leaf homologues are arranged in opposite pairs that alternate in angle, the so-called decussate or 2-whorl arrangement. Three-whorl patterns, in which triplets of homologues separated by 120° from each other, and for which the following and preceding triplets are rotated by 60° , are also common (see Fig. 10(a)).

The arrangement (*taxis*) of leaves (singular: *phylla*, plural: *phylla*) or their analogs on plants is referred to as *phyllotaxis*. Phyllotaxis has intrigued natural scientists for ages, served as a tool for identifying and classifying plants, motivated questions on optimal packing, and provided challenges and clues to understanding the biochemistry and biomechanics of plant growth. It is surprising that, despite much attention over the years, only recently have quantitative explanations emerged for the wonderful architecture seen near the shoot apical meristems (SAM's) of plants. The goal of this review is to tell the story to date and to provide substantial evidence for the idea that plants and other organisms can pursue optimal strategies by employing naturally occurring patterns driven by instabilities initiated by biochemical and biomechanical processes. Moreover, the length scales associated with the driving mechanisms are not microscopic and connected in any obvious way with genetic instructions but are macroscopic and of the same order as the phenomena observed.

While this article is a review, it adopts, over the telling of a story, a point of view: That all the mysteries and challenges of phyllotaxis will ultimately be explained by the behaviors of instability-generated patterns in auxin and stress fields in the neighborhood of plant SAM's. We provide substantial evidence that points to this conclusion.

To this end, it is good idea to provide the reader with a roadmap spelling out what it is we do in each section and why. The introductory Section 1.1 introduces the reader to some of the landmarks in the history of the subject. A more extensive history of the study of phyllotaxis may be found in [1]. This section also introduces important terminologies used as descriptive tools such as, for example, the notions of parastichies and the fact that the polar coordinates of the phylla lie on cylindrical lattices. These lattices can be characterized by one of two measures. The first arises from an appropriate and 'obvious to the eye' choice of basis vectors for the lattice from which two important further quantities, the rise and divergence angle, can be calculated. Due to plant growth, the rise and divergence angle evolve, the latter often tending to the golden angle in the outer reaches of the meristem. This evolution is captured by a diagram due to Van Iterson which is central to all attempts to



Fig. 1. A seed head of *Helianthus*, the sunflower. Photo courtesy of John Palmer.

explain the observed phyllotactic configurations. But there is also an equally important second set of measures, dual coordinates, associated with the normals to the preferred choice of basis vectors for the lattice. In Section 1.2, we introduce both sets of phyllotactic coordinates and outline why it is that the dual coordinates, which are basically Fourier modes, are more useful in explanations which are based on mechanistic rather than teleological models. In Section 1.3, we discuss the kinematics of phyllotactic pattern formation, namely how the incipient phylla, called primordia, are initiated in a generative annulus in the neighborhood of the shoot apical meristems (SAM's) of plants. Here we learn that the radial position R of the generative annulus changes as the plant grows. In many cases, it increases, but in some cases, such as during the seed formation stage of sunflowers, it decreases. The upshot is that the nature of the pattern, whether it is has a spiral or whorl structure, may change depending on the radius of the generative annulus at which primordia first form. This necessitates a discussion, which we begin in Section 1.4, between spiral patterns with different numbers of spirals in their spiral families or between spiral patterns and whorl patterns. Sometimes the transitions are smooth; sometimes they involve defect formation. The main ideas are discussed in Section 1.4 and we provide conclusions about transitions from our models in Section 3.5.

Section 2 discusses in detail the main two approaches to date which purport to explain phyllotaxis. The first approach is teleological in that it posits rules manifested as cellular automaton algorithms which are based on the plant placing its phylla according to some optimization principle. Some rules have an observational footing. They are based on repeated and careful experiments by the noted botanist Hofmeister, who encoded the outcome of his observations in a set of rules, now named after him, which we list in Section 1.1. Some readers may prefer the use of the word "phenomenological" to the word "teleological" due to the observational motivation of the rules for these discrete models.

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