

A Collision-based Model of Spiral Phyllotaxis

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ABSTRACT

Plant organs are often arranged in spiral patterns. This effect is termed spiral phyllotaxis. Well known examples include the layout of seeds in a sunflower head and the arrangement of scales on a pineapple. This paper presents a method for modeling spiral phyllotaxis based on detecting and eliminating collisions between the organs while optimizing their packing. In contrast to geometric models previously used for computer graphics purposes, the new method arranges organs of varying sizes on arbitrary surfaces of revolution. Consequently, it can be applied to synthesize a wide range of natural plant structures.

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1 INTRODUCTION

Phyllotaxis, or a regular arrangement of organs such as leaves, flowers, or scales, can be observed in many plants. The pattern of seeds in a sunflower head and the arrangement of scales on a pineapple are good examples of this phenomenon. It is characterized by conspicuous spirals,

or *parastichies*, formed by sequences of adjacent organs composing the structure. The numbers of parastichies running in opposite directions usually are two consecutive Fibonacci numbers. The *divergence angle* between consecutively formed organs (measured from the center of the structure) is close to the Fibonacci angle of $360^\circ \tau^{-2} \approx 137.5^\circ$, where $\tau = (1 + \sqrt{5})/2$ [3]. Computer simulation has shown that the quality of the pattern depends in a crucial way on this angle value [10, Chapter 4]. The intriguing mathematical properties have led to many models of phyllotaxis, which can be broadly categorized as *descriptive* and *explanatory* [9].

Descriptive models attempt to capture the geometry of phyllotactic patterns. Two models in this group, proposed by Vogel [12] and van Iterson [5, 8], characterize spiral arrangements of equally-sized organs on the surface of a disk or a cylinder, and have been applied to synthesize images of plant structures with predominantly flat or elongated geometry [7, 10]. Unfortunately, the assumptions that simplified the mathematical analysis of these models limited the range of their applications. In nature, the individual organs often vary in size, and the surfaces on which they are placed diverge significantly from ideal disks and cylinders. Spherically shaped cactus bodies provide a striking example, but even elongated structures, such as spruce cones, are not adequately described by the cylindrical model, which fails to characterize pattern changes observed near the base and the top of a cone.

A larger variety of organ sizes and surface shapes can be accommodated using explanatory models, which focus on the dynamic processes controlling the formation of phyllotactic patterns in nature. It is usually postulated that the spirals result from local interactions between developing organs, mechanically pushing each other or communicating through the exchange of chemical substances. Unfortunately, no universally accepted explanatory model has yet emerged from the large number of competing theories [9].

In this paper we propose a *collision-based* model of phyllotaxis, combining descriptive and explanatory components.

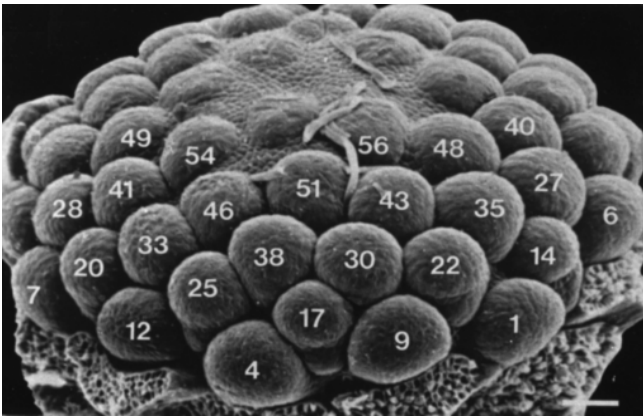


Figure 1: Microphotograph of a developing capitulum of *Microseris pygmaea*. Numbers indicate the order in which the primordia are formed. The scale bar represents $50\mu m$.

Section 2 presents the principle of this model and places it in the context of biological observations. Section 3 applies it to realistic image synthesis, using compound inflorescences (clusters of flowers) and cacti as examples. Section 4 concludes the paper with an analysis of the results and a list of open problems.

2 THE COLLISION-BASED MODEL

2.1 Morphology of a Developing Bud

Although phyllotactic patterns can be observed with the naked eye in many mature plant structures, they are initiated at an early stage of bud development. Consequently, microscopic observations are needed to analyze the process of pattern formation.

Figure 1 depicts a developing bud of *Microseris pygmaea*, a wild plant similar to the dandelion. The numbered protrusions, called *primordia*, are undeveloped organs that will transform into small flowers or *florets* as the plant grows. The primordia are embedded in the top portion of the stalk, called the *receptacle*, which determines the overall shape of the flower head (*capitulum*). The numbers in Figure 1 indicate the order in which the primordia are formed. The oldest primordium differentiates at the base of the receptacle, then the differentiation progresses gradually up towards the center, until the entire receptacle is filled. The divergence angle between position vectors of consecutive primordia approximates 137.5° .

2.2 Biological Origin of the Model

The collision-based model originates from a study of *numerical canalization* [13]. This term describes the phenomenon that in capitula of many plants, organs such as petals or bracts are more likely to occur in certain quantities than in

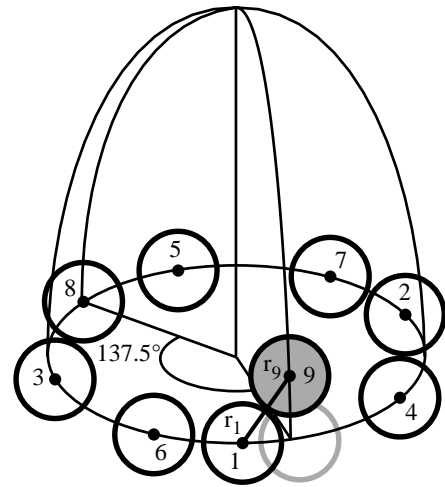


Figure 2: The collision-based model of phyllotaxis. Primordia are distributed on the receptacle using a fixed divergence angle of 137.5° and are displaced along the generating curves to become tangent to their closest neighbors. In the case shown, primordium 9 collided with primordium 1.

others. Fibonacci numbers of organs, relating canalization to phyllotaxis, are found with a particularly high frequency. We developed the computer model to simulate the effect of canalization in *Microseris* [2], and observed that it provides a flexible model of phyllotaxis, free of restrictions present in the previous geometric models. Specifically, it operates on receptacles of arbitrary shapes, and accommodates organs of varying sizes. In this paper, we extrapolate this collision-based model beyond its strict observational basis, to visualize phyllotactic patterns in a variety of plants.

2.3 The Proposed Model

The purpose of the model is to distribute primordia on the surface of the receptacle. The principle of its operation is shown in Figure 2. The receptacle is viewed as a surface of revolution, generated by a curve rotated around a vertical axis. Primordia are represented by spheres, with the centers constrained to the receptacle, and are added to the structure sequentially, using the divergence angle of 137.5° . The first group of primordia forms a horizontal ring at the base of the receptacle. The addition of primordia to this ring stops when a newly added primordium collides with an existing one. The colliding primordium is then moved along the generating curve towards the tip of the receptacle, so that it becomes tangent to its closest neighbor. The subsequent primordia are placed in a similar way — they lie on generating curves determined by the divergence angle, and are tangent to their closest neighbors. The placement of primordia terminates when there is no room to add another primordium near the tip of the receptacle.

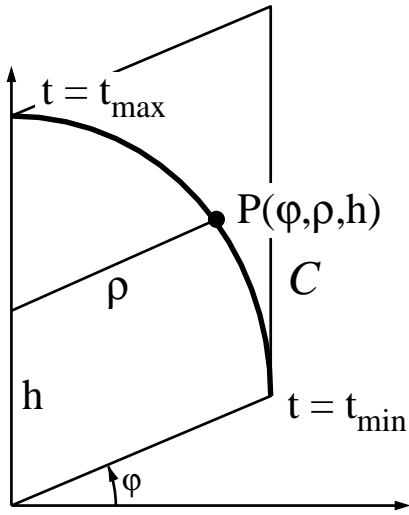


Figure 3: Variables used in the description of the collision-based model

2.4 Formalization

In order to calculate positions of consecutive primordia, we assume that the model is placed in a cylindrical coordinate system φ, ρ, h (Figure 3). The receptacle is described by the parametric equation $\rho = \rho(t)$, $h = h(t)$, and can be conceptualized as the result of the rotation of a generating curve $\mathcal{C}(\varphi = 0, \rho(t), h(t))$ around the axis h . In our implementation, \mathcal{C} is specified as one or more Bézier curves [6]. Parameter t changes from t_{min} , corresponding to the base of the receptacle, to t_{max} , corresponding to the tip. Thus, a point P on the receptacle can be represented by a pair of numbers: $\varphi \in [0, 360)$ and $t \in [t_{min}, t_{max}]$. Assuming that the radii of consecutive primordia form a given sequence $\{r_0, r_1, r_2, \dots\}$, the pattern generated by the collision-based model satisfies the following recursive formulae:

$$\begin{cases} \varphi_0 = 0, \\ t_0 = t_{min}, \end{cases}$$

$$\begin{cases} \varphi_{n+1} = \varphi_n + 137.5^\circ = (n+1) \cdot 137.5^\circ, \\ t_{n+1} = \min\{t \in [t_{min}, t_{max}] : (\forall i = 0, 1, \dots, n) \\ \quad \|P(\varphi_i, t_i) - P(\varphi_{n+1}, t)\| \geq r_i + r_{n+1}\}. \end{cases}$$

The expression $\|P(\varphi_i, t_i) - P(\varphi_{n+1}, t)\|$ denotes the Euclidean distance between the points $(\varphi_i, \rho(t_i), h(t_i))$ and $(\varphi_{n+1}, \rho(t), h(t))$. The formula for t_{n+1} has a simple interpretation — it specifies t_{n+1} as the smallest value of parameter t , for which the center of the newly added primordium $P(\varphi_{n+1}, t)$ will be separated by at least $r_i + r_{n+1}$ from the center of any previously placed primordium $P(\varphi_i, t_i)$. The angle φ_{n+1} at which the new primordium will be placed is fixed at $(n+1) \cdot 137.5^\circ$.

In practice, the value t_{n+1} is computed using a binary search

of the interval $[t_{min}, t_{max}]$. The recursion ends when no value $t \in [t_{min}, t_{max}]$ satisfies the inequality:

$$(\forall i = 0, 1, \dots, n) \|P(\varphi_i, t_i) - P(\varphi_{n+1}, t)\| \geq r_i + r_{n+1}.$$

A modification of the formula for t_{n+1} is useful when consecutive primordia decrease in size ($r_0 > r_1 > r_2 \dots$). In this case, small primordia that should be positioned near the top of the receptacle may accidentally fit in a gap between much larger primordia near the base. This undesirable effect, distorting the phyllotactic pattern, can be avoided by limiting the maximum decrease of parameter t between consecutive primordia to a heuristically selected value δ . The change in the formula for t_{n+1} consists of replacing the constant value t_{min} by $t'_{min} = \max\{t_{min}, t_n - \delta\}$. We have found δ corresponding to the radius of the new primordium satisfactory in most cases.

2.5 Model Validation

The collision-based model describes the formation of a capitulum in a simplified way. The crudest assumption is that primordia emerge on an already developed receptacle, while in nature the differentiation is concurrent with the receptacle's growth. Despite this simplifying assumption, the placement of primordia resulting from the collision-based model corresponds closely to the microscopic observations.

3 APPLICATION TO COMPUTER GRAPHICS

3.1 Principles

Once the phyllotactic pattern has been formed in the early stages of bud development, the bud grows and develops into a mature flower head. The actual organs — florets or seeds — may have totally different shapes from the primordia, yet the original spiral arrangement will be retained.

The collision-based model is applied to image synthesis following a similar scheme: first the phyllotactic pattern is generated by placing spheres on a receptacle, then the spheres are replaced by realistic models of specific organs. In our implementation, the organs are constructed from Bézier surfaces.

For placement purposes, each organ is represented by a contact point and a pair of orthogonal vectors \vec{v} and \vec{w} . The organ is translated to make its contact point match the center of the sphere that it will replace, then rotated to align the vectors \vec{v} and \vec{w} with the normal vector to the receptacle and the vector tangent to the generating curve. The radius of the sphere representing the primordium may be used to determine the final size of the mature organ.



Figure 4: Green coneflower

3.2 Results

The first example, a model of green coneflower (*Rudbeckia laciniata*), is shown in Figure 4. The receptacle is approximately conical. The flower head includes three different types of organs: ray florets (with petals), and open and closed disk florets. The size of disk florets decreases linearly towards the tip of the cone.

Almost flat receptacles have been used to synthesize the composite flower heads shown in Figure 5, yielding similar results to the geometric models based on Vogel's formula [7, 10, 12].

The operation of the collision-based model on a spherical receptacle is illustrated in Figure 6, where individual berries of the multi-berry fruits are represented as intersecting spheres. A change of organs and proportions yields the flowers of buttonbush (*Cephalanthus occidentalis*), shown in Figure 7. In this case, the spherical receptacle is confined to the center of the inflorescence. The individual flowers, at the ends of long pedicels, form a ball with a much larger radius.



Figure 5: Daisies and chrysanthemums

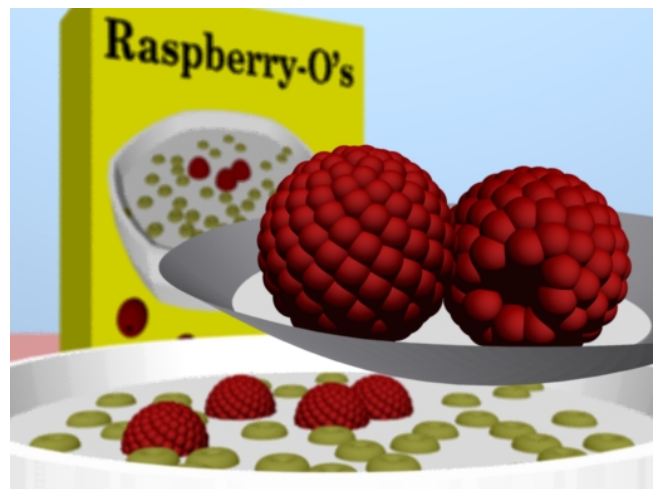


Figure 6: Raspberry-os

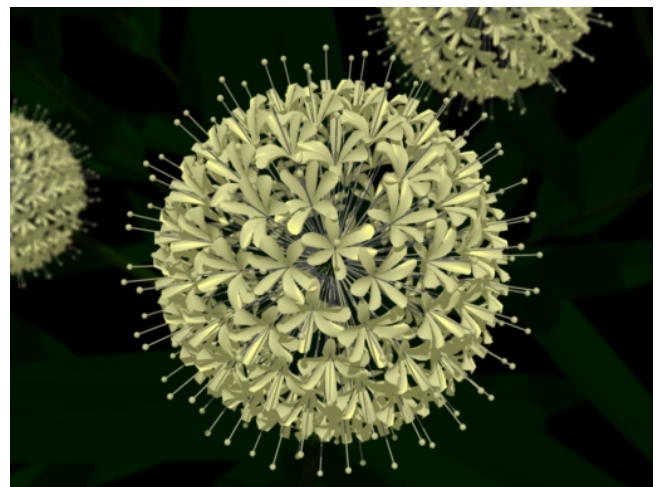


Figure 7: Flowers of buttonbush



Figure 8: Seed head of goatsbeard

In goatsbeard (*Tragopogon dubius*), presented in Figure 8, the collision-based phyllotaxis model is used in a compound way, to capture the distribution of the seeds (*achenes*) on the receptacle, and to construct their parachute-like attachments. The same technique has been applied to model cactus *Mammillaria geminispina*, with a spiral arrangement of spine clusters on the cactus stem (Figure 9). The compound application of the phyllotaxis model has been exploited even further in the models of cauliflowers and broccoli (Figure 10). In this case, the receptacle carries clusters of compound flowers, which are themselves clusters of simple flowers approximated by spheres. Thus, the collision-based model has been applied here at two levels of recursion. In Figure 11, the model governs the positions of spine clusters and flowers, as well as the arrangement of spines in each cluster and petals in each flower.

Since the collision-based model provides a mechanism for filling an area with smaller components, it can be applied to other purposes than the simulation of phyllotaxis. For example, in Figure 12 it was used to place many single-stem plants in each pot. The soil surface was considered as a large, almost flat “receptacle”, and the distribution of spherical “primordia” on its surface determined the position of each stem. As a result, the flower heads form dense clusters without colliding with each other.

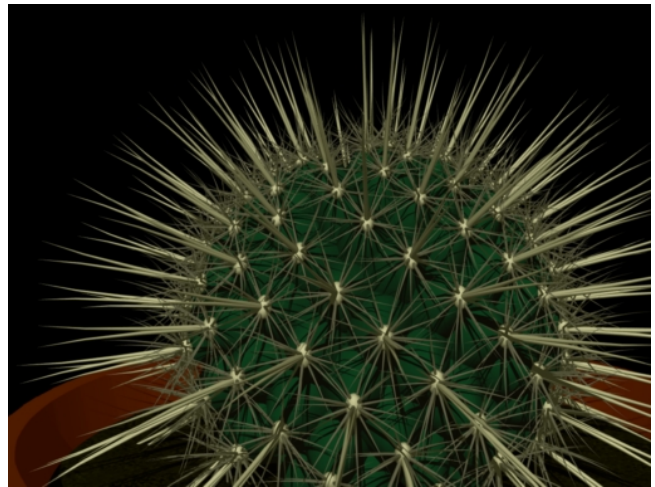


Figure 9: A model of *Mammillaria geminispina*

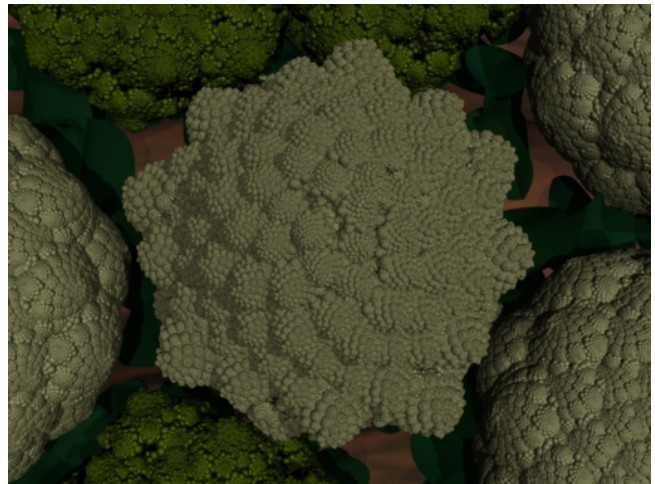


Figure 10: Cauliflowers and broccoli

3.3 Implementation

The modeling environment consists of two programs designed for Silicon Graphics workstations. An interactive editor of Bézier curves and surfaces is used to specify the shape of the receptacle and the organs. A generator of phyllotactic patterns distributes the organs on the receptacle according to the collision-based model.

The arrangement and display of primordia on the receptacle takes one to two seconds, making it possible to manipulate parameters interactively. After the desired pattern has been found, the generator outputs a set of transformation matrices that specify the position of each organ. The organs are incorporated into the final image by the renderer (the ray tracer rayshade) as instances of predefined objects. Instantiation makes it possible to visualize complex plant models, consisting of millions of polygons, using relatively small data files.



Figure 11: Table of cacti, including realistic models of the elongated *Mammillaria spinosissima*

From the user's perspective, the reproduction of a specific structure begins with the design of the receptacle. This is followed by the interactive manipulation of the primordia sizes, leading to the correct arrangement of parastichies. The total time needed to develop a complete structure is usually dominated by organ design.

4 CONCLUSIONS

This paper presents a biologically motivated collision-based model of phyllotaxis and applies it to the synthesis of images of different plants. The model employs local interactions between organs to adjust their positions on the underlying surface and can operate without modification on surfaces of diverse shapes. In contrast, purely geometric models of phyllotaxis used previously for computer graphics purposes [7, 10] have been limited to the surface of a disk or a cylinder.

Below we list several open problems, the solution of which could result in more robust and varied models.



Figure 12: Flower shop. The collision-based model controls the arrangement of plants in each pot.

- *Formal characterization of patterns generated by the collision-based model.* While most models of phyllotaxis were constructed to describe or explain the conspicuous spirals, the collision-based model originated from research on canalization. Consequently, it does not provide ready-to-use formulae relating the arrangement of parastichies to the geometry of the receptacle and the sizes of primordia. Such formulae would improve our understanding of the phenomenon of phyllotaxis, and provide additional assistance in building models of specific plants.
- *Analysis of the validity range.* Although the model operates correctly for various combinations of receptacle shapes and primordia sizes occurring in nature, one can easily produce input data for which it does not generate phyllotactic patterns. For example, this may happen if the receptacle has zones with a small radius of curvature, compared to the size of primordia, or if consecutive primordia vary greatly in size. The model could be therefore complemented by a characterization of the range of input data for which it produces nondistorted phyllotactic patterns.



Figure 13: Grape hyacinths

- *Simulation of collisions between mature organs.* This is an important problem in the visualization of structures with densely packed organs, such as the inflorescences shown in Figures 13 and 14. In nature, individual flowers touch each other, which modifies their positions and shapes. This effect is not captured by the present model, since collisions are detected only for primordia. Consequently, the mature organs must be carefully modeled and sized to avoid intersections. This is feasible while modeling still structures, but proper simulation of collisions would become crucial in the realistic animation of plant development.
- *Comparison with related models.* Mechanical interactions between neighboring primordia were also postulated in other models of phyllotaxis. Adler [1] proposed a *contact-pressure* model which, in a sense, is opposite to ours: it uses constant vertical displacement of primordia and allows the divergence angle to vary, while we fix the divergence angle and let collisions control the displacement along the generating curves. Two other models explaining phyllotaxis in terms of mechanical interactions have been proposed recently by Van der Linden [11], and Douady and Couder [4]. A comparison and synthesis of these results is an open problem. Specifically, the incorporation of a mechanism for the adjustment of the divergence angle into the collision-based model may lead to structures better corresponding to reality, and provide a causal explanation for the divergence angle used. The comparison of phyllotactic models can be put in an even wider perspective by considering non-mechanical models, such as those based on reaction-diffusion [9].



Figure 14: Inflorescences of water smartweed



Figure 15: Window sill — various phyllotactic patterns

In spite of its simplicity, the collision-based model captures a wide range of plant structures with phyllotactic patterns (Figure 15). It also illustrates one of the most stimulating aspects of the modeling of natural phenomena — the close coupling of visualization with ongoing research in a fundamental science.

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