Chapter 12

MODELING MERISTIC CHARACTERS OF ASTERACEAN FLOWERHEADS

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1. Introduction

1.1. Symmetry and Organ Numbers in Plants

According to Weyl (1952), the word symmetry commonly has two different meanings. In one sense, symmetry is defined as a group of transformations that map an object onto itself. This usage is reflected in expressions such as bilateral or rotational symmetry. In a broader sense, “symmetric means something like well-proportioned, well-balanced, and symmetry denotes that sort of concordance of several parts by which they integrate into a whole. Beauty is bound with symmetry” (Weyl, 1952). We will use the word symmetry in this broader sense.

A conspicuous aspect of symmetry in plants is the number of organs of a particular type (meristic character) in flowerheads and flowers. The preference for a certain number is called numerical canalization (Huether, 1968; Bachmann, 1983; Vic et al., 1992) and is often closely related to the phyllotaxis of flowers and flowerheads. For example, flowers of the Brassicaceae have whorls of two or four organs, and the numbers of organs of different types are usually multiples of two (Huether, 1992). Similarly, flowerheads from the Asteracean genus Mikania have four florets per flowerhead inserted in two decussate pairs (King and Robinson, 1987). In contrast, the numbers of different floral organs in flowers of the
Ranunculaceae frequently vary among Fibonacci numbers (Endress, 1987). The preference for Fibonacci numbers occurs together with a Fibonacci-type spiral phyllotaxis of the flower (Meinshaeumer, 1979). An equally tight relationship between spiral phyllotaxis and organ numbers exists in flowerheads of the Asteraceae (Hirmer, 1987; Church, 1992; Battjes, 1991; Battjes et al., 1993). A distribution curve of the number of ray florets or phyllaries (involute bracts) in a sample of heads from the same Asteracean species often has one or more peaks at Fibonacci numbers, and lower frequencies between these peaks (Ludwig 1887; later Blanken summarized in Battjes and Bachmann, in press). Only organs that are inserted in a single row at the rim of flowerheads show these remarkable non-random distributions (Battjes and Bachmann, in press). The preferred numbers of organs in predictable positions are thought to give Asteracean flowerheads their symmetrical appearance (Hirmer, 1981; Dormer, 1972; Leppik, 1977).

A developmental explanation for numerical canalization is that the mechanism responsible for the formation of phyllotactic patterns in flowers or flowerheads is capable of dampening the effect of genetic and environmental variation on organ numbers. An indication of the validity of this hypothesis is the fact that whole flowers exhibit less variation in numbers among and within species than flowers with spiral phyllotaxis (Endress, 1990). This suggests that different phyllotactic patterns may have different capacities for keeping organ numbers constant. The aim of this chapter is to clarify the relationships between the phyllotaxis of flowers and flowerheads, the preferred number of organs, and the degree of numeric variation. We focus on flowerheads of the Asteracean genus Microseris because their phyllotactic patterns are relatively easy to analyze, and their morphological variation has been extensively documented.

1.2. Previous Work on the Relationship between Spiral Phyllotaxis and Numerical Canalization

1.2.1. Hirmer's Work and the Collision Model

In many whorled flowers and in decussate flowerheads there is an obvious relationship between patterns of organ insertion and organ numbers, since each organ has a clearly defined position and associated identity. On the other hand, in flowerheads with spiral phyllotaxis it is more difficult to see why the numbers of organs at the periphery are canalized towards Fibonacci numbers, and when deviations from these numbers occur. Although several authors discussed the relationship between Fibonacci numbers of organs and spiral phyllotaxis in flowerheads (reviewed in Battjes and Bachmann, in press), Hirmer (1931) was the first to propose a convincing explanation. Selected ideas of Hirmer were captured and formalized in the collision model of phyllotaxis (Fowler et al., 1992; Battjes, 1994), which is summarized below:

- Consecutive primordia are placed on the receptacle with a constant divergence angle of 137.5° with respect to each other, as seen from the receptacle's center. This value is assumed a priori in the model.
- Radially primordia are placed on the circular rim at the circumference of the receptacle. This process takes place as long as there is enough space, that is, the distance between a new primordium and its closest previously placed neighbor exceeds a predefined threshold.
- A primordium that does not fit on the rim is translated radially towards the center or the apex of the receptacle, so that the distance between the new primordium and its closest neighbor is equal to the threshold value. This process continues until there is no space available on the receptacle.
- The developmental fate of primordia is determined by their position on the receptacle. Ray florets or inner phyllaries develop from primordia positioned on the rim of the receptacle.

Hirmer also observed that the distance between neighboring primordia can become smaller than a critical threshold only after a Fibonacci number of primordia have been placed on the rim. This observation holds for any value of the radius and threshold distance (see Appendix A for an elementary proof). Consequently, the collision model implies that the number of organs resulting from primordia placed on the rim will always be a Fibonacci number.

1.2.2. Confirmation of the Collision Model

It is not immediately obvious that the collision model is sufficient to explain the arrangement of primordia into smooth opposite parastichies. Nevertheless, computer simulations demonstrate the emergence of spiral patterns on receptacles of various shapes for a wide range of primordia sizes (Fowler et al., 1992).

One implication of the collision model is that primordia are placed in circular rings, starting at the rim of the receptacle. In contrast, most other models of spiral phyllotaxis assume a continuously decreasing distance between consecutive primordia and the midpoint of the receptacle (e.g. Vogel, 1979; Erickson 1983; Jean, 1994). Observations confirm that Asteracean flowerheads exhibit some of the ring-like properties postulated by the collision model. Three-dimensional measurements of organ positions in Microseris pygmaea have shown that there are sudden decreases in distance to the midpoint between primordia 13 and 14 and between primordia 20 and 21, numbered from the rim inwards. These decreases are significantly larger than the decrease between subsequent primordia within the outermost rings of 13 (Battjes et al., 1993).

The collision model also postulates that the position of primordia with respect to the rim of the receptacle, rather than the ontogenetic order of initiation, determines the developmental fate during their differentiation. Again there are indications that this assumption is realistic. For flowers it is known that genes determining the developmental fate of floral organs (sepals, petals, stamens, carpels) are expressed in rings. These expression patterns are thought to be independent of floral phyllotaxis, and thus of the ontogenetic order of primordia, because the identity of the organs...
may change as a consequence of mutations, while the arrangement and number of organs remains constant (Coen and Carpenter, 1993). For flowerheads, Rinser (1931) and Backmann and Chambers (1990) postulated that the differential development of peripheral versus central primordia is determined by a concentration gradient that indicates the distance of a primordium from the rim. No gene expression patterns confirming this hypothesis have yet been found, but the existence of a gradient that provides positional information is likely. For example, during the early development of M. pygmaea flowerheads, primordia on the rim subdivide into an inner phyllary and a floret. This subdivision appears to be controlled by the distance from the rim rather than the strict ontogenetic order of the primordia (Battjes et al., 1992).

1.2.3. Discrepancies between Flowerhead Development and the Model

Although the assumptions of the collision model discussed above are realistic, the model does not accurately capture several aspects of flowerhead phyllotaxis and meristic variation.

The divergence angle in the model is assumed to be constant, but observed angles vary considerably. For instance, Microseris exhibits divergence angles much less than 137.5° at transitions between rings of 13 primordia. This phenomenon can be explained by assuming that a new primordium attempts to minimize the distance to both of its closest neighbors (Battjes et al., 1993), rather than simply preserving a threshold distance to its nearest neighbor. Similar deviations from the average divergence angle after Fibonacci or Lucas numbers of florets were observed in Helianthus heads (Ryan et al., 1991), although in that study numerical calculation was not considered. In vegetative shoots, regular deviations from the average divergence angle have been found as well, for example in subdecussate shoots (Dome, 1972).

Another unrealistic assumption of the collision model is the absence of growth on the surface on which the phyllotactic pattern is generated. Flowerheads usually grow considerably in size during the initiation of involucral bracts and florets (Pupin and Chan, 1932; Rauh and Resnik, 1953; Horridge and Cockshull, 1977; Palmer and Steer 1985; Sharmann and Sedgley, 1988; Brown and Menary, 1994). For example, in a variety of sunflowers the capitulum radius increased fivefold during the initiation of about 1500 bracts and florets (Palmer and Steer, 1985). In the much smaller flowerheads of Microseris douglasii with only 80 florets, the increase in circumference during floret initiation alone is almost twofold (Battjes and Backmann, 1994). The diameter of the individual primordia also increases over time, although the measured growth rates are lower than those of the receptacle (Battjes et al., 1994).

Finally, the collision model yields a strict preference for Fibonacci numbers of inner phyllaries, whereas observed numbers are canalized less rigidly. Copi numbers are more variable than numbers of parastichies (Battjes and Backmann in press), which in Asteraceae flowerheads are almost always Fibonacci numbers.

(Ryan et al., 1991; Battjes et al., 1993; Szymanowska-Pulka, 1994). Consequently, non-Fibonacci numbers of ray florets or inner phyllaries may occur in flowerheads with Fibonacci numbers of parastichies (Weisse, 1887). This aspect of flowerhead phyllotaxis is not captured by the collision model, although it is essential for an understanding of meristic variation in flowerheads.

1.3. Objectives of the Current Work

In the present paper we analyze in detail the relationship between spiral phyllotaxis and the number of organs in flowerheads. The central questions are:

- how can a non-Fibonacci number of inner phyllaries arise in a Microseris flowerhead with a Fibonacci number of parastichies, and
- what is the relationship between the ontogenetic order of primordia and their chance of developing into inner phyllaries.

We hypothesize that the answers to these questions can be found by introducing two modifications into the collision model, inspired by observations listed in Sec. 1.2.3.

The first modification is the incorporation of receptacle growth during floret initiation. The second is the adjustment of divergence angles that maximizes local density of primordia packing on the surface of the receptacle. The model predicts that:

- receptacles with higher growth rates have more variable numbers of organs, and
- when the number of inner phyllaries is not a Fibonacci number, some primordia are likely to develop into inner phyllaries out of the ontogenetic order.

Two modes of receptacle growth were simulated and analyzed: uniform and non-uniform; the latter is characterized by a slower growth rate at the periphery of the head. To test the validity of the model, we compared floret and inner phyllary positions measured in M. pygmaea with the results of simulations. In both cases, the model is in agreement with observations of the positions of inner phyllaries in the flowerheads of M. pygmaea. The non-uniform growth model leads, however, to a more realistic distribution of organs on the receptacle.

2. The Modified Collision Model

2.1. Placement of Primordia with Adjustments in the Divergence Angle

In this paper, we consider two-dimensional, circular receptacles. We also conceive the primordia as being circular, with a constant radius r. The position of primordium i at time t is specified by the radius \( r_{i,t} \) (distance between the center of the primordium and the center of the receptacle) and azimuth \( \psi_{i,t} \) (angle between
The problem of the collision of two primordia is to be solved. The solution is based on the assumption that the primordia are spherical and that the collision is head-on. The distance between the centers of the primordia is given by the formula:

$$d = r_1 + r_2$$

where $r_1$ and $r_2$ are the radii of the primordia.

The time of collision is given by the formula:

$$t = \frac{d}{v}$$

where $v$ is the velocity of approach.

The problem is solved by considering the collision as a series of collisions of smaller primordia. The process continues until all primordia have collided.

The final result is that the primordia fuse to form a single, larger primordium.

This process is known as the growth of the receptacle.
Figs. 2–7. Pattern formation on a static (non-growing) receptacle according to the modelled collision model. (2) Like all primordia on the rim of the receptacle, the first primordium is divided into an inner phyllary (p) and a floret (f). (3) Initially, the divergence angle between adjacent primordia is equal to $137.5^\circ$. (4) After eight primordia have been placed on the rim, there is space for the next primordium (*). (5) Primordium 9 is placed in a more inward position. (6) The position of primordium 9 is adjusted so that it rests on its two closest neighbors. As a result, the divergence angle deviates from $137.5^\circ$. (7) Receptacle filled with primordia.

We also consider non-uniform growth, assuming that the relative element growth is slower in the outer zone of the receptacle, where primordia have already been formed, than in the remaining inner part. In the extreme case of no growth in the zone with primordia, the distance between any point in this zone and the disk border is constant in absolute terms:

$$R_{t+1} - \rho_{t,t+1} = R_t - \rho_{t,t}.$$  

(3)

The growth of the inner part of the receptacle is described as in the uniform case (Eq. 2). The above equations describe the growth of any point on the receptacle.
and thus apply, in particular, to the points that represent the centers of primordia, which are of focal interest in this paper.

3. Evaluation of the Modified Collision Model

In order to evaluate the modified collision model, we compared the results of simulations with the observations of Microseris pygmaea heads using three criteria:

- spatial arrangement of florets on the receptacle,
- numbers of inner phyllaries and their canalization, and
- ontogenetic order of inner phyllary positions.

The methods used for comparisons and the results are presented below.

3.1. Spatial Arrangement of Florets on the Receptacle

3.1.1. Methods for Flowerhead Observations

Immature flowerheads of M. pygmaea strain C96b ranging from 1.5 mm to 6 mm in diameter were collected in the greenhouse of the University of Amsterdam in 1991 and fixed in alcohol (Batjjes et al., 1992). The number of inner phyllaries per flowerhead ranged from 7 to 16, with the Fibonacci numbers 8 and 13 represented most frequently. A non-random sample of 47 heads with the numbers of inner phyllaries distributed as evenly as possible between 8 and 13 were embedded in glycol methacrylate, sectioned and stained using the PAS reaction, according to standard anatomical techniques (Fig. 12). The heads were then projected on glass paper using a camera lucida and drawn by hand. The floret and inner phyllary primordia were numbered in the ontogenetic order, determined by drawing opposite parastichies over primordia positions and counting the numbers of parastichies in each direction. In all heads, except one that was excluded from further analysis, these numbers were consecutive Fibonacci numbers. The ordering numbers were then assigned to primordia using the Bravais-Bravais theorem (Jean, 1994), which states that the ordering numbers of adjacent primordia on an n-parastichy differ by n. Since the Bravais-Bravais theorem characterizes differences between primordia numbers rather than their absolute values, an additional assumption was made: the number 1 would denote the first floret with associated inner phyllary (Fig. 13).

The estimated positions of the centers of all primordia were recorded in Cartesian coordinates. Each inner phyllary was assumed to have the same number in ontogenetic order as the floret in its axil (Batjjes et al., 1992; also see Fig. 13). Positions of outer phyllaries were measured separately, since they do not have florets in their axils. These positions were not included in the further analysis of the spatial arrangement of florets on the receptacle, because the outer phyllaries are located below the rim of the receptacle, whereas our model is limited to the layout of primordia on a planar receptacle.

3.1.2. Methods for Simulations

Simulations were performed on a Silicon Graphics workstation using an in-house software implementation of the modified collision model. Different phyllotactic patterns were created by systematically varying three parameters described in Sec. 2.2: the initial radius of the receptacle $R_1$, the growth constant $c$, and the mode of receptacle growth (uniform or non-uniform). The ranges of the initial radius
yielded flower numbers that correspond to those observed in nature. In one experiment yielding simulated flowerheads with all the numbers of florets from 16 to 60, another experiment, the results of 5000 simulations were used to visually compare the quality of pattern approximation, the number of florets, and the number of the longest inner phyllaries as functions of growth parameters. In all simulations presented in this paper, \( r \) (the primordium radius) was set at 0.25 length units.

### 3.1.3. Methods for Comparing Observed and Modeled Flowerheads

Visual inspection is the most straightforward technique for comparing observed phyllotactic patterns with their models. To make it easier, we superimposed modeled patterns on a measured pattern of primordium distribution, and successively adjusted position, orientation, and scale of the model on the screen of the graphics workstation to achieve as good a fit as possible (Fig. 14). By undoing the adjustments, we abstracted from the position, orientation, and scale of the head, and focused on the relative distances and angles, which are the key attributes of the patterns. Differences in primordium positions which remain after fitting indicate discrepancies between the observations and the model.

![Fig. 14. A simulated head (light) superimposed on a measured head (dark) after the position, orientation, and scale of the model have been adjusted to achieve as good a fit as possible. The symbols are as in Fig. 12.](image)

In order to speed up the process of fitting and to evaluate the results of comparisons more objectively, we introduced the sum of squared distances (SSD) between corresponding primordium positions as a measure of discrepancy. We developed an algorithm that minimizes the SSD automatically by applying optimum transformations without human intervention (Appendix II). This algorithm was used to systematically compare families of simulated patterns with the observed flowerheads. The numbers of florets in the observed flowerheads ranged from 16 to 60 (Sec. 3.1.1), but not all intermediate numbers were present. Consequently, we divided the range of 16 to 60 florets into 14 equal intervals, and selected one interval as the representative for each interval. Thus, the simulated patterns in the 16–60 floret range were compared to heads that had at most two florets more or two fewer than the simulated pattern. The representative heads were characterized by the number of the SSD with respect to most other heads of a similar size, and, in cases of ties, by the number of florets in the simulated or observed pattern (see Appendix II).

![Fig. 15. Deviation (SSD) between an observed flowerhead with 47 primordia and simulated flowerhead with 47 primordia. Light circles represent values obtained for uniformly growing receptors, dark circles represent values obtained for non-uniformly growing receptors.](image)
higher growth rates, as indicated in Fig. 15. A possible explanation of this effect is suggested by Figs. 16–18. In the case of uniform growth (Fig. 17), packing of primordia is much less dense at the periphery than in the center of the head. In contrast, the simulated pattern obtained using the non-uniform growth model (Fig. 18) exhibits a more even distribution of florets and in this respect resembles the observed pattern (Fig. 16) more closely.

![Fig. 16-18. Comparison of floret distribution in heads with equal numbers of florets. (16) Measured Microseris head. (17) Simulated head obtained using the uniform growth model (initial radius: 0.91 length units, growth constant: 0.036 length units per plastochron). (18) Simulated head obtained using the non-uniform growth model (initial radius: 1.03 length units, growth constant: 0.036 length units per plastochron).]

Figure 19 collects the results of comparisons limited to the outermost 13 primordia for all size classes. These primordia play the dominant role in determining the inner phyllary numbers. The large peaks on the right side of Fig. 19 indicate that combinations of small initial radii with large growth constants lead to unrealistic patterns. Primordia distributions generated using larger initial sizes of the spectacle approximate the observed heads more closely, although there still is much variation in the value of the SSD. Inspection of observed and modeled patterns superimposed on each other gives an insight into some of the reasons for this variation (Figs. 20, 21). Figure 20 presents a good fit between the observed head and the model. In this case, both patterns have 8 inner phyllaries. Further analysis demonstrates that the SSD is also low when both patterns have 13 inner phyllaries.

![Fig. 19. Deviations (SSD) between the positions of 13 outermost primordia in measured flower heads and in patterns generated using the modified collision model with non-uniform receptacle growth.]

![Fig. 20 and 21. Comparisons of the distribution of primordia in a measured Microseris head (dark) and in two simulated heads with the same number of primordia. (20) Good fit (SSD = 0.0183) obtained for a simulated head with 8 inner phyllaries (initial radius = 1.0 length units, growth constant = 0.011 length units per plastochron). (21) Poor fit (SSD = 0.0183) obtained for a simulated head with 10 inner phyllaries (initial radius = 0.706 length units, growth constant = 0.0092 length units per plastochron).]

In contrast, Fig. 21 illustrates a case of a larger SSD. The modeled head has 10 inner phyllaries, and primordia 12 and 13 are too close to the rim in comparison to the observed head. The effects of this discrepancy propagate towards the center of the modeled head. In conclusion, the predictions of inner phyllary positions
are most realistic for modeled flowerheads with Fibonacci numbers of inner phyllaries.

3.2. Numbers of Inner Phyllaries and Numerical Canalization

3.2.1. Observations

Eight inbred lines of Microseris pygmaea have been used to study naturally occurring genetic variation in meristic characters of flowerheads (Bachmann et al., 1995; Bachmann, 1991). Each inbred line expressed considerable phenotypic plasticity. The number of inner phyllaries per flowerhead was canalized towards Fibonacci numbers while the number of florets varied in a continuous manner. A similar phenotypic plasticity has been found in other species of Microseris (Bachmann and Battjes, in press).

The developmental causes of the phenotypic plasticity were studied in two of the inbred lines of M. pygmaea by Battjes and Bachmann (1994). In both cases, larger numbers of florets per flowerhead were the result of larger receptacle perimeters at the onset of floral initiation. The size of floret primordia was much less variable. The size of the receptacle increased significantly during phyllary and floret formation.

3.2.2. Simulations

Figure 22 shows the numbers of inner phyllaries generated by the model for different values of the starting size and the growth constant of the receptacle. Predictably, only Fibonacci numbers of inner phyllaries fit on the rim of a non-growing receptacle. Larger receptacles have higher numbers of phyllaries. With increasing growth constants the preference for Fibonacci numbers of inner phyllaries decreases until, at a growth constant of 0.06 length units per plastochron, no preference for Fibonacci numbers remains. The number of florets increases gradually and shows no preference for Fibonacci numbers (Fig. 23).

3.2.3. Comparison Results

The simulation results agree with the records of phenotypic plasticity in Microseris flowerheads in the following points:

- the number of inner phyllaries is canalized to Fibonacci numbers whereas the number of florets shows a continuous variation,
- the same (Fibonacci) number of inner phyllaries can occur in receptacles of different initial sizes,
- a considerable growth rate of the receptacle is associated with a frequent occurrence of non-Fibonacci numbers of inner phyllaries.

The model also predicts that receptacles with lower growth rates have more constant numbers of organs on the rim, but we do not yet have the experimental data to verify this prediction.

3.3. Ontogenetic Order of Inner Phyllary Positions

3.3.1. Observations

Figure 24 shows the ontogenetic order of inner phyllary positions in the same flowerheads of M. pygmaea as described in Sec. 3.3.1. Flowerheads with 8 or 13
inner phyllaries have all first 8 or 13 ontogenetic positions occupied by these phyllaries. An example of a flowerhead with 8 inner phyllaries is shown in Fig. 23 and 13. For numbers of inner phyllaries between 8 and 13, positions 9 and 10 are more often occupied by a phyllary than 11 to 13. Within each of these two groups, however, inner phyllaries at primordium positions higher in ontogenetic order are occupied more frequently. The most frequently observed positions of inner phyllaries are shown in Fig. 25.

3.3.2. Simulations

The ontogenetic order of inner phyllaries simulated with the modified collision model follows a peculiar pattern as well (Fig. 26). Patterns with 8 or 13 inner phyllaries have all of the first 8 or 13 ontogenetic positions occupied by the phyllaries. When the number of inner phyllaries is equal to 9, all first 8 positions and position 13 are occupied. With increasing numbers of inner phyllaries, the intermediate positions from 12 to 9 are occupied by inner phyllaries in descending order. Figures 8-11
4.1.2. Canalization of Inner Phyllary Numbers

The size of the Microseris receptacle may vary while the number of inner phyllaries remains constant. Simulations using the modified collision model agree with this observation. Similarly, variation in growth rate in the model often does not result in a change in the number of organs on the rim. Thus, the modeled algorithm for phylotactic pattern formation is able to buffer meristic characters against considerable variation in developmental parameters of the receptacle.

The modified collision model also predicts that for smaller ratios of the receptacle growth rate to the primordium initiation rate, the numbers of organs on the rim of the receptacle show less variation. At present we only have a circumstantial confirmation of this prediction. In many whorled flowers the petals appear very quickly one after another in the same sequence as is usually found in flowerheads with spiral phylotaxis. The meristem growth rate relative to the petal initiation rate is probably low. These flowers often exhibit Fibonacci number of petals and other floral organs (Endress, 1990). In light of our simulations, we speculate that these two phenomena are connected: the fairly constant number of petals is the consequence of their rapid spiral initiation, combined with slow growth of the meristem. More variable numbers of petals would be a consequence of higher growth rates of the meristem or longer intervals between the initiation of subsequent petals.

4.1.3. Ontogenetic Order of Inner Phyllaries

As described in Sec. 3.1.1, inner phyllaries on the M. pygmaea flowerheads are distributed in a highly predictable manner. Specifically, position 10 is occupied by a phyllary more frequently than 9, and positions 13 to 11 are occupied in a decreasing order of frequency. The modified collision model exhibits a similar preference for positions higher in ontogenetic order, although the sequence of position occupation is not the same. This preference is a result of packing non-growing primordia as a growing receptacle. Thus, the variation in the positions of inner phyllaries can be largely attributed to geometric relationships between primordia on a growing receptacle.

Although the geometric aspects of incorporating non-growing areas into a growing surface should be further analyzed, there are good reasons for keeping the size of a primordium constant during the simulations. Floret primordia of M. pygmaea measured during several consecutive days of flowerhead development do not show a significant increase in size, although the receptacle expands considerably (Battjes and Bachmann, 1994). This indicates that rates of expansion may be important and different between florets and the receptacle. Furthermore, the developmental mechanism that creates phylotactic patterns on the receptacle may be of a chemical rather than mechanical nature. If this is the case, the primordium size used in the model could be re-interpreted as the radius of an inhibitory field created by the primordium; the size of this field may be independent of the actual primordium size and receptacle growth.

4.2. Suggestions for Future Work

The present study suggests several topics for future research that may contribute to a better understanding of the geometric aspects of meristic variation and spiral phylotaxis.

- The proposed model postulates that the distribution of florets on the receptacle and the canalization of inner phyllaries are influenced by the growth of the receptacle, with differential growth rates leading to a better agreement between the model and the observations of the Microseris flowerheads. A direct confirmation of this relationship by measurements of the relative elementary growth rate in different zones of the receptacle over time would significantly contribute to model validation.

- It is an interesting question, how the developmental fate of primordia can be controlled by apparently very small deviations in their positions. A more detailed analysis of these positions, for example expressed in relation to the closest neighboring primordia rather than in absolute coordinates, may provide a useful insight.

- The modified collision model does not predict the observed difference in chance to become an inner phyllary between primordia 10-9 and 13-12. Also, for a non-Fibonacci number of the inner phyllaries, some inner phyllary primordia in the model are too close to the rim (see Sec. 3.1.4). These shortcomings may require an explanation. For example, our view of collisions between neighboring primordia may be too simplistic, and more complicated interactions involving several neighboring primordia may have to be considered. Such a different approach might lead to other divergence angles and collision patterns, and consequently to other arrangements of the inner phyllaries.

- An important question is the applicability of the results of the present study to a wide range of Asteraceae species. Although there is no indication that the described distribution of inner phyllaries and florets is specific to Microseris, it is important to confirm that other species can be characterized by the same model, possibly with different values of parameters.

- The divergence angle of 137.5° between sequentially placed primordia is assumed both in the original collision model and its modification presented in this paper, although in the latter case the angle is adjusted as a result of interactions between neighboring primordia. Ideally, this value should not be given a priori, but should result from the model. Models in which the divergence angle in an emergent property have been described in literature (Mitchison, 1977; Douady and Couder, 1992; Van der Linden, 1994; Yotsumoto, 1993; Koch and Meinhardt, 1994), but they are in turn limited in their capability of explaining meristic variation. It would be of great importance to develop a model of phylotaxis, in which:
— the sequence of primordia placement and the divergence angle are not assumed, but result from simulations, and
— the power of the modified collision model to explain the meristic variation and the departure from the ontogenetic order in inner phyllary formation is preserved.

4.3. Concluding Remarks

Spiral phyllotactic patterns have often been idealized as extremely regular, with the divergence angle constant or changing gradually, and the distance from the primordia to the center decreasing in a continuous manner (e.g. Erickson, 1983). In the same manner, larger flowerheads have been viewed as differing from smaller ones only by the addition of extra florets at the periphery (Vogel, 1979; Beem and Faz Xudong, 1988; van der Linden, 1990). Although these approximations may be adequate for many purposes, they promote a simplified view of phyllotaxis. Divergence angles in flowerheads are not constant but show regular, non-proportional deviations from the average (Ryan et al., 1991, Batjtes et al., 1993). The distances from primordia to the head center change discontinuously (Batjtes et al., 1993). In the present study we have further shown that primordia on the rim of a Microcassiea head have different chances of developing into an inner phyllary, which are out of step with the ontogenetic order. These deviations from abstract spiral or helical patterns are typical properties of flowerhead phyllotaxis rather than exceptions. We believe that they can be best understood by taking ontogenesis of the phyllotactic pattern into account, integrating postulated developmental mechanisms into a computer model, and carefully comparing the results with observations.

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Appendix A: Proof of Hirmer’s Conjecture

Hirmer (1931) proposed an explanation for the canalization of the numbers of organs n found at the perimeter of flowerheads. His explanation was based on the postulate that n is the maximum number of primordia of a given size that fit on the circular rim of a receptacle without intersecting each other. Hirmer observed that if the divergence angle between consecutively placed primordia is equal to the golden angle $\phi$ (approximately 137.5°), n is a Fibonacci number for any ratio of the pericarpoid radius r to the rim radius R. Although this observation was later supported by calculations of special cases and computer simulations (Batjtes 1994), in our knowledge it has not been formally proved. The purpose of this appendix is to present such a proof.

Let us consider a set $P(n)$ of n distinct points representing the centers of primordia placed on the rim of a receptacle. We will arrange this set into two sequences.

The ontogenetic sequence, denoted $\{P_i\}$ describes the order in which the sequentially generated points $P_1, P_2, \ldots, P_n$ have been placed on the rim. It is assumed that pairs of consecutive points $P_i$ form a constant divergence angle $\psi$ when seen from the rim center $O$.

$$\angle P_i O P_{i+1} = \psi \quad \text{for} \quad i = 1, 2, \ldots, n-1.$$  (4)

The partitioning sequence, denoted $\{P_P\}$, is a permutation of the sequence $\{P_i\}$ such that $P_{P_1} = P_1$ and $P_{P_{n}}, P_{P_{n+1}}, \ldots, P_{P_n}$ are consecutive points encountered while traversing the rim counterclockwise:

$$0 < \angle P_{P_1} O P_{P_2} < \angle P_{P_1} O P_{P_3} < \cdots < \angle P_{P_n} O P_{P_n} < 360^\circ.$$  (5)

We will denote by $\sigma(n)$ : $\{1, 2, \ldots, n\} \rightarrow \{1, 2, \ldots, n\}$ the function that converts the index $P_i$ of a point $P$ in the partitioning sequence $\{P_P\}$ to the index $i$ of the same point in the ontogenetic sequence $\{P_i\}$.

The partitioning sequence divides the full angle into $n$ partition angles:

$$\angle P_{P_1} O P_{P_2}, \angle P_{P_2} O P_{P_3}, \ldots, \angle P_{P_{n-1}} O P_{P_n}, \angle P_{P_n} O P_{P_1}.$$  (6)

We will denote the set of (different) values of these angles by $A(n)$. The notions introduced above are illustrated in Fig. 27.

Lemma 1: Let $\mathcal{S}$ be an infinite ontogenetic sequence of points $P_1, P_2, P_3, \ldots$ generated using a divergence angle $\psi$:

$$\angle P_{P_1} O P_{P_{i+1}} = \psi \quad \text{for} \quad i = 1, 2, 3, \ldots.$$  (7)

If $\psi$ is an irrational number, there exists an infinite set of integers $N$ such that for any $n \in N$, the set of points $P(n)$ satisfies the conditions:

1. $P(n)$ consists of n initial elements of the sequence $\mathcal{P}$,
2. the set $A(n)$ of the values of partition angles has two elements,
3. the two partition angles sharing the vertex $P_{P_i} = P_i$ are different: $\angle P_{P_i} O P_{P_i} \neq \angle P_{P_{i+1}} O P_{P_i}$. 

The proof of Lemma 1 follows from the properties of the golden angle and the properties of the Fibonacci sequence.
Fig. 27. The ontogenetic sequence (labeled inside the rim) and the partitioning sequence (labeled outside) of 12 points, generated using the divergence angle $\psi = 137.5^\circ$. The function $\Sigma^{(n)}$ converts the indices of points in the partitioning sequence to the indices of points in the ontogenetic sequence; for example, $\Sigma^{(12)}(1) = 1$, $\Sigma^{(12)}(2) = 9$, $\Sigma^{(12)}(6) = 2$. The set $A^{(12)}$ of partition angle values has three elements $\alpha$, $\beta$, and $\gamma$.

Proof: by induction on $n$.

Initial step. For $n = 2$ the set $P^{(n)}$ consists of two points $P_1$ and $P_2$. There are two partition angles, $\angle P_1OP_2$ and $\angle P_2OP_1$, which have different values (otherwise the divergence angle $\psi$ would have been equal to 180°, which is a rational number) and share point $P_1$.

Inductive step. Assume that the thesis is true for some $n \geq 2$. Let $\angle P_1OP_2 = \alpha$ and $\angle P_2OP_3 = \beta$, with $\alpha > \beta$ (the opposite case can be considered in a similar way). Rotate $P_1, P_2, \ldots, P_n$ with respect to the receptacle center $O$ by angle $\beta$ and label the resulting points $Q_1, Q_2, \ldots, Q_n$, respectively. Denote the set $\{Q_1, Q_2, \ldots, Q_n\}$ by $Q^{(n)}$. Refer to Fig. 28 for an illustration of the proof.

1. Observe that the rotation of point $P_1$ by $\beta$ makes the resulting point $Q_1$ coincide with the point $P_2$. Denote by $k + 1$ ($k \geq 1$) the index of the point $P_{k+1}$ in the ontogenetic sequence:

$$k + 1 = \Sigma^{(n)}(P_k).$$

Fig. 28. Illustration of the proof of Lemma 1. Small circles represent points of the set $P^{(n)}$, generated using the divergence angle of $137.5^\circ$. Data represent points of the set $Q^{(n)}$, obtained by rotating points $P_i \in P^{(n)}$ by angle $\beta$ with respect to the receptacle center $O$, as indicated by the dashed arrows.

Since the divergence angle between consecutive points in the sequences $\{Q_i\}$ is the same as in the sequence $\{P_i\}$, we obtain:

$$Q_1 = P_{k+1}, Q_2 = P_{k+2}, \ldots, Q_{n-k} = P_n, \ldots, Q_n = P_{n+k}. \quad (9)$$

The first $n - k$ points of the sequence $\{Q_i\}$ coincide with the last $n - k$ points of the sequence $\{P_i\}$ included in the set $P^{(n)}$. The remaining $k \geq 1$ points of the sequence $\{Q_i\}$ are equal to the elements $P_{k+1}, P_{k+2}, \ldots, P_{n+k}$ of the sequence $S$ not included in $P^{(n)}$. Consequently, the set $P^{(n)} \cup Q^{(n)} = P^{(n+k)}$ consists of $n + k > n$ initial points of the sequence $S$.

2. Consider the merged sequence

$$P_{P_1}, Q_{P_1}, P_{P_2}, Q_{P_2}, \ldots, P_{P_n}, Q_{P_n}, \quad (10)$$

and assume formally that $P_{P_1} = P_{P_{k+1}}$ and $Q_{P_1} = Q_{P_{k+1}}$. From the construction of points $Q_{P_1}, Q_{P_2}, \ldots, Q_{P_n}$, it follows that $\angle P_{P_1}OQ_{P_1} = \beta$ for any $i = 1, 2, \ldots, n$. On the other hand, from the inductive assumption it follows that $\angle P_{P_i}OP_{P_{i+1}} \in (\alpha, \beta)$ for any $i = 1, 2, \ldots, n$. Two cases may occur:
• if $\angle P_{n}OP_{n+1} = \alpha$ then point $Q_{n}$ lies between points $P_{n}$ and $P_{n+1}$; then the angle $\angle P_{n}OP_{n+1}$ is divided into two smaller angles:

$$\angle P_{n}OQ_{n} = \beta \quad \text{and} \quad \angle Q_{n}OP_{n+1} = \alpha - \beta = \gamma.$$  \hspace{1cm} \textbf{(11)}

• if $\angle P_{n}OP_{n+1} = \beta$ then points $Q_{n}$ and $P_{n+1}$ coincide.

Consequently, the merged sequence (10) consists of points of the set $\mathcal{P}(n+k)$ of $\mathcal{Q}(n)$ listed in the partitioning order, although some points may be listed twice. From the equalities (11) it follows that the set $\mathcal{A}(n+k)$ of partition angles for the set of points $\mathcal{P}(n+k)$ has two elements: $\beta$ and $\gamma$.

3. According to the partitioning sequence (10), the vertex $P_{n}$ is shared by the angles $\angle Q_{n}OP_{n}$ and $\angle P_{n}Q_{n}O$. From the assumptions $\angle P_{n}OP_{n} = \alpha$ and $\angle P_{n}OQ_{n} = \beta$ it follows that

$$\angle Q_{n}OP_{n} = \angle P_{n}OP_{n} - \angle P_{n}Q_{n}O = \alpha - \beta = \gamma.$$  \hspace{1cm} \textbf{(12)}

The angles $\beta$ and $\gamma$ are not equal; otherwise the divergence angle $\psi$ and the full angle $360^\circ$ could be both expressed as integer multiples of $\gamma$ and $\psi$ would be a rational number. Thus, the set $\mathcal{P}(n+k)$ satisfies conditions 1–3 of the thesis for $n + k > n$. □

We will now focus on the special case in which the divergence angle $\psi$ is equal to the golden angle $\varphi = 360^\circ(1 - \tau)$. The golden ratio $\tau$ is defined by the equation

$$\frac{1}{\tau} = 1 - \tau \quad \text{or} \quad \tau^2 = 1 - \tau.$$  \hspace{1cm} \textbf{(13)}

**Lemma 2.** If $\theta_{i} = 360^\circ r$, $\theta_{i+1} = 360^\circ r$, and $\theta_{i+1} = \theta_{i+1} - \theta_{i}$ for $i \geq 1$, then $\theta_{i} = 360^\circ r$ for any $i \geq 1$.

**Proof:** by induction on $i$.

**Initial step.** Obviously, $\theta_{1} = 360^\circ r = 360^\circ(1 - \tau)$, and $\theta_{2} = 360^\circ r = 360^\circ(1 - \tau) = 360^\circ r$.

**Inductive step.** Assume that the thesis is true for some $i \geq 2$. For $i + 1$ we obtain

$$\theta_{i+1} = \theta_{i+1} - \theta_{i} = 360^\circ r + 360^\circ(1 - \tau) = 360^\circ r - 360^\circ r = 360^\circ r = 360^\circ r - (1 - \tau).$$  \hspace{1cm} \textbf{(14)}

**Lemma 3.** If the divergence angle $\psi$ is equal to the golden angle $\varphi$, then:

1. the set $\mathcal{N}$ of integers $n_{1} < n_{2} < n_{3} < \cdots$ satisfying Lemma 1 consists of consecutive elements of the Fibonacci sequence: $f_{1} = f_{2} = 1$, $f_{i} = f_{i+1} + f_{i+2}$, for $i \geq 1$, starting with $n_{1} = f_{3} = 2$;

2. for any $i \geq 1$ the partitioning sequence of points in $\mathcal{P}(n_{i})$ divides the full angle into $f_{i+1}$ angles $\theta_{i} = 360^\circ r$ and $f_{i}$ angles $\theta_{i+1} = 360^\circ r + i$.

3. for any $0 < m < n_{i+1} - n_{i}$, the partitioning sequence of points in $\mathcal{P}(n_{i+1} + m)$ divides the full angle into $f_{i+1} + m$ angles $\theta_{i} = 360^\circ r + i$, $f_{i} + m$ angles $\theta_{i+1} = 360^\circ r + i$, and $m$ angles $\theta_{i+2} = 360^\circ r + i$, with all three angle values occurring at least once.

**Proof:** by induction on $i$.

**Initial step.** By definition, the set $\mathcal{P}(n_{1})$ consists of $f_{2} = 2$ points $P_{1}$ and $P_{2}$ such that:

$$\angle P_{1}OP_{2} = \varphi = \theta_{1} \quad \text{and} \quad \angle P_{2}OP_{1} = 360^\circ - \varphi = \theta_{1}.$$  \hspace{1cm} \textbf{(15)}

Thus there is no integer $m$ satisfying the inequality $0 < m < n_{2} - n_{1} = 3 - 1 = 1$, thus part 3 of the thesis also holds.

**Inductive step.** Assume that the thesis is true for $i \geq 1$. Construct the set $\mathcal{P}(n_{i+1})$ as described in the proof of Lemma 1. From Lemma 2 it follows that $\theta_{i} > \theta_{i+1}$, thus the partitioning sequence of points in $\mathcal{P}(n_{i+1})$ divides the full angle into $f_{i} < f_{i+1} = f_{i+1} + f_{i+2}$ angles $\theta_{i+1} + f_{i+1}$ angles $\theta_{i} - \theta_{i+1} = \theta_{i+2}$. For any $0 < m < f_{i}$, the partitioning sequence of points in $\mathcal{P}(n_{i+1} + m)$ subdivides only $m$ angles $\theta_{i}$, $f_{i}$, then $m$ angles $\theta_{i+1}$, and $m$ angles $\theta_{i+2}$. Consequently, the sequence $\mathcal{N}$ has no elements between $n_{i} = f_{i+2}$ and $n_{i+1} = f_{i+1} + f_{i+2}$.

**Theorem (Hirmer's conjecture).** Let $D$ be a circle with center $O$ and radius $R$. Consider the largest set of circles $\mathcal{C}(n) = C_{1}, C_{2}, \ldots, C_{n}$, with the set of centers $\mathcal{P}(n) = \{P_{1}, P_{2}, \ldots, P_{n}\}$, such that:

1. all points $P_{i} \in \mathcal{P}(n)$ lie on the circumference of the circle $D$;

2. for any $i = 1, 2, \ldots, n - 1$, the divergence angle $\angle P_{i}OP_{i+1}$ is the golden angle $\varphi$;

3. all circles $C_{i} \in \mathcal{C}(n)$ have the same radius $r < R$;

4. no two different circles $C_{i}, C_{j} \in \mathcal{C}(n)$ intersect.

The number $n$ of circles in the set $\mathcal{C}(n)$ is a Fibonacci number.

**Proof:** Circles $C_{i}, C_{j} \in \mathcal{C}(n)$ will not intersect if the distance between their centers satisfies the inequality $|P_{i}P_{j}| > 2r$, or $\angle P_{i}OP_{j} > \pi = 2 \arcsin \frac{r}{R}$ (Fig. 29). Let $\theta_{i}$ be the smallest element of the sequence $\{\theta_{i}\}$ (see Lemma 2), such that $\theta_{i} > \zeta$. According to Lemma 3, a Fibonacci number $n_{i}$ is the largest number of points satisfying assumptions 1 and 2 above, such that the partitioning sequence of points in $\mathcal{P}(n_{i})$ does not include an angle less than or equal to $\zeta$. □
After substituting the right hand sides of Eq. 17 for $x_{li}$ and $y_{li}$ in Eq. 16, the SSD becomes a function of parameters $k$, $l$, $\alpha$, and $s$. Since the purpose of transforming pattern $b$ is to determine the best match possible between $a$ and the resulting pattern $b'$, we seek parameter values for which the SSD reaches minimum. According to elementary calculus, the necessary condition is that the partial derivatives of the SSD with respect to all parameters are equal to zero. To simplify the calculations, we assume that the center of gravity of pattern $a$ lies at the origin of the coordinate system:

$$\sum_{i=1}^{n} x_{ai} = \sum_{i=1}^{n} y_{ai} = 0.$$  

Since it is always possible to position pattern $a$ in such a manner that this assumption is satisfied, no generality is lost.

Considering the translations first, we obtain:

$$\frac{\partial \text{SSD}}{\partial k} = 2s^2 \sum_{i=1}^{n} (x_{ai} + k),$$

and, disregarding the degenerate case $s = 0$,

$$\frac{\partial \text{SSD}}{\partial k} = 0 \quad \text{if} \quad k = \frac{1}{n} \sum_{i=1}^{n} x_{ai}.$$  

Similarly,

$$\frac{\partial \text{SSD}}{\partial l} = 0 \quad \text{if} \quad l = \frac{1}{n} \sum_{i=1}^{n} y_{ai}.$$  

The derivative with respect to the angle $\alpha$ is equal to:

$$\frac{\partial \text{SSD}}{\partial \alpha} = 2s \sin \alpha \sum_{i=1}^{n} (x_{ai} x_{bi} + y_{ai} y_{bi}) - 2s \cos \alpha \sum_{i=1}^{n} (x_{ai} y_{bi} - x_{bi} y_{ai}),$$

then, assuming that $s \neq 0$ and that no division by zero is performed, we obtain:

$$\frac{\partial \text{SSD}}{\partial \alpha} = 0 \quad \text{if} \quad \alpha = \arctan \left( \frac{\sum_{i=1}^{n} (x_{ai} y_{bi} - x_{bi} y_{ai})}{\sum_{i=1}^{n} (x_{ai} x_{bi} + y_{ai} y_{bi})} \right).$$

If the denominator in the above formula is equal to 0, we use the value $\alpha = \pm \frac{\pi}{2}$, determined directly from Eq. 22.

In order to calculate the derivative of Eq. 16 with respect to the scale $s$, we introduce auxiliary variables:

$$\tilde{x}_{ai} = (x_{ai} + k) \cos \alpha - (y_{ai} + l) \sin \alpha,$$

$$\tilde{y}_{ai} = (x_{ai} + k) \sin \alpha + (y_{ai} + l) \cos \alpha.$$
From Eq. 17 it follows that $x_i^{(a)} = x_i^{(b)}$ and $y_i^{(a)} = y_i^{(b)}$. By substituting the right-hand sides of these formulae into Eq. 16, we obtain:

$$\frac{\partial \text{ssd}}{\partial s} = 2a \sum_{i=1}^{n} (x_i^{(a)} - y_i^{(a)}) - 2a \sum_{i=1}^{m} (x_i^{(a)} - y_i^{(a)}) .$$

(25)

As a result,

$$\frac{\partial \text{ssd}}{\partial s} = 0 \text{ if } s = \sum_{i=1}^{n} (x_i^{(a)} - y_i^{(a)}) .$$

(26)

Further inspection reveals that the sss reaches the minimum for the values of parameters $k$, $l$, and $s$ determined by Eqs. 20, 21, and 26 respectively. The value of $a$ obtained using Eq. 23 corresponds to either a minimum or a maximum of the sss. In the case of a maximum, $s$ should be added to $a$ to obtain the minimum.

In the paper, we often refer to a normalized version of the sss, defined by the equation:

$$\text{SSD} = \frac{\text{ssd}}{\text{radius(a) radius(b) n}} .$$

(27)

The purpose of dividing the sss by the radius of patterns $a$ and $b$ and the number $n$ is to make the resulting value more suitable for comparisons involving receptors of different sizes and with different numbers of primordia.

References


Chapter 13

THE SHAPE OF DIRICHLET REGIONS IN A COXETER LATTICE AS A FUNCTION OF DIVERGENCE AND RISE

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1. Introduction

Coxeter (1972) used continued fractions to show that divergence values of the form $\alpha = 1/(t+1/r)$ in cylindrical phyllotaxis have the exceptional geometric property, with plausible botanical utility, of strictly alternating sides in successive nearer approaches to any given ‘leading’ direction by subsequent ‘leading’ directions in the index sequence of ‘leaves’. After Coxeter, we call this ‘Tait’s condition’. Coxeter discussed Tiling’s suggestion to the effect that we imagine a cylindrical phyllotaxis of fixed divergence $\alpha$ undergoing axial compression, so that rise $r$ continuously decreases, causing the changes of conspicuous parastichy pairs. Changing plesocache ratio is a key feature of growth and form in phyllotaxis and through Coxeter’s analysis we see how Tait’s condition becomes a proposition about a changing pattern of nearest neighbours in a cylindrical lattice. What I propose to do in this paper is to take Coxeter’s analysis a stage further, to shift attention from the pattern of directions of successive nearest neighbours in a lattice undergoing compression to the question of space surrounding each lattice point.

I propose to formulate the shape of the Dirichlet region of a phyllotaxis lattice as a fraction of divergence and rise. I will show that among all possible fixed values of $\alpha$ golden mean divergence gives least distortion of shape during continued lattice compression. As Adler points out, to assume a constant $\alpha$ while rise changes contrary to botanical fact, and so the study presented here is not morphogenetic in purpose but mathematical. Adler (1974 & 1977), which is a morphogenetic model, is obtained by setting the equivalent of my Dirichlet shape constant (=1) so as to study changing $\alpha$ with decreasing $r$. Here we shall set $\alpha$ constant so as to study changing shape with decreasing $r$. The result will be a number of mathematical formulations which serve to complement the Adler model.

At any point of compression all the Dirichlet regions of the lattice are identical to each other in shape and size and orientation, but for any fixed $\alpha$ the shape and