

Fibonacci phyllotaxis: An appraisal

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Abstract

Phyllotaxis is the regular geometric patterning of organ primordia at shoot apices and consequentially their corresponding fully developed structures such as leaves, flowers, fruits and seeds on plant shoots. Phyllotaxy has enthused scientists and mathematicians alike and has been their favourite subject of study for nearly a century. However, even after intensive research, practical explanations still remain elusive. Among the different types of phyllotaxy, Fibonacci spiral phyllotaxy is most prevalent in nature and is the most studied. Recent investigations on the flower heads of Asteraceae incorporating mathematical and computational modelling along with biochemical and molecular methods have provided certain enlightening observations and interpretations. The studies could provide clues for the occurrence of this phenomena across different evolutionary lineages. It is assumed that further studies would identify the interlinking principles that facilitate the wide-spread occurrence of spiral phyllotaxy in plants.

Keywords: Phyllotaxis, Fibonacci sequence, Parastichies, Asteraceae, Flower heads

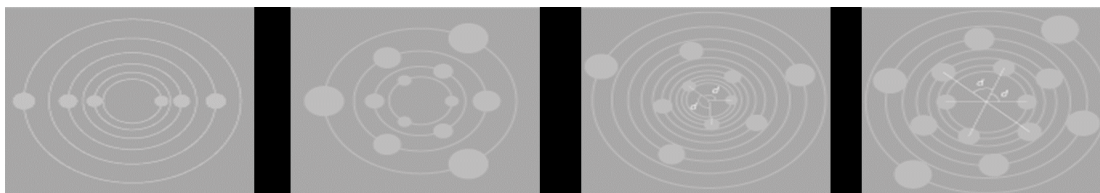
Introduction

Phyllotaxis is the mode of arrangement of developing leaves or floral bracts on the stems of plants (Rutishauser, 1998; Smith *et al.*, 2006; Rutishauser and Peisl, 2001). This regular patterning of leaves and floral bracts occurs due to the origin of organ initials or primordia in pre-determined patterns on the summit of the plant shoot during development (Newell and Shipman, 2005, Okabe *et al.*, 2019). When forming a pattern, the organ initials maintain a specific distance from one another as they develop and follow an angular placement. The angle between any two such consecutive primordia is called the divergence angle ' d ' and is characteristic for a particular pattern (Okabe, *et al.*, 2019).

Research has shown that patterning is omnipresent in the plant kingdom and is a rule rather than an exception. Scientists have identified basically four different types of phyllotactic patterns - Distichous, whorled, spiral and multijugal (Rutishauser, 1998; Roger and Denis, 1998). In distichous phyllotaxy, the initials are placed one at a time on concentric whorls, the second initial being farthest from the first ($d = 180^\circ$), and this pattern continues through the whorls. In whorled phyllotaxis, two or more

initials grow simultaneously on one whorl but at maximum possible distances (equidistant) from one another and in the subsequent whorl, each initial is placed midway between any two in the previous whorl. Here, the divergence angle is constant. In spiral phyllotaxis, the initials grow

one by one on concentric whorls, each at a constant divergence angle ($d = 137.5^\circ$) from the previous one. In multijugate phyllotaxis, two or more initials grow in one whorl and this constancy is maintained through the whorls and also in their corresponding divergence angles (Figs.1a-d).



Figs. 1a-d. Schematic representations of different types of Phyllotaxy **a.** Distichous **b.** Whorled **c.** Spiral **d.** Multijugate Courtesy: <https://www.science.smith.edu/phylo/Assets/Images/About/>

Okabe *et al.* (2019) considers only two types of phyllotaxy – spiral and non-spiral. Accordingly, in the spiral arrangement, the divergence angle of nascent leaves at the shoot apex is fixed at the divergence (golden) angle 137.58° . However, distichy, decussate and whorled phyllotaxis are grouped together as non-spiral phyllotaxy. Herein the divergence angle between successive initials is a simple fraction of 360° .

Phyllotaxis and Parastichies

Among the different phyllotactic patterns, spiral phyllotaxis is the most common in plants (Hotton *et al.*, 2006). All basic phyllotactic patterns can be described by connecting neighbouring primordia with either straight lines (orthostichies) or curved lines (parastichies). The orthostichies and parastichies may vary from one to many in either clockwise or anticlockwise directions or even both may occur together. The spiral phyllotaxis can be described in terms of their 'parastichies' which in turn refers to 'the count of the number of visible curved spirals that join each initial/primordia to its nearest neighbor(s)'. Here, the spirals normally come in pairs (winding in clockwise and anticlockwise directions) (Rutishauser and Peisl, 2001).

Rutishauser (1998) classified the more frequent phyllotactic patterns in plants based on the quantitative parameters such as parastichy numbers, divergence angle, and the range of plastochrone ratios. For better comprehension, the parastichy numbers are usually represented by the alphabets 'm' and 'n'. If 'k' is the greatest common divisor of m and n, then $m=ki$, $n=kj$. Based on this, the notation $k(i, j)$ may be used to describe the particular phyllotaxy. The parastichy numbers may or may not have a common divisor

other than 'one'. Biologically, the alphabet 'k'- can be inferred as the number of initials per whorl.

All types of phyllotaxy can be notated based on the above information. In spiral phyllotaxis, the parastichy numbers have only 'one' as the common divisor ie $k = 1$. For eg. If parastichy numbers $m=2$, $n=3$ indicate the spiral pattern and the common divisor $k=1$, then it can be notated as $1(2,3)$.

Distichous phyllotaxy is usually said to have parastichy numbers (1,1).

If the parastichy numbers have a common divisor k , then they can be either whorled or multijugate. In whorled, when $k>1$ and $i=j$, it is said as k -merous [with parastichy numbers (k, k)]. For whorled parastichies numbers, $m=2$, $n=2$, the highest common divisors $k=2$ ($k>1$), $i=1$, $j=1$ ($i=j$), then the notation would be $2(1, 1)$. In multijugate, when $k>1$, and i, j are distinct ($i \neq j$), for the parastichies $m=2$, $n=4$ and $k=2$ ($k>1$), $i = 1$, $j = 2$, the notation would be $2(1,2)$.

More about Spiral phyllotaxy

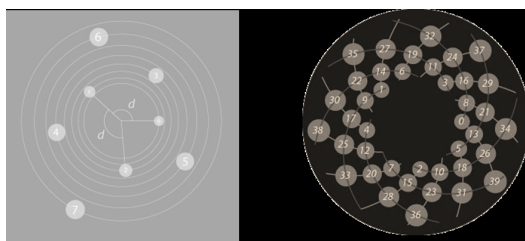
Spiral phyllotaxis can be regarded as similar to the spiral lattices. Mathematically, spiral lattices are visualized as points placed on concentric circles. The divergence angle between any two points on successive circles is constant and the radius of the concentric circles increases from the center by a constant factor represented by G (expansion parameter). The spiral parastichy numbers occur in concentric whorls and have a constant divergence angle ($d = 137.5^\circ$). This divergence angle is usually referred as the 'Golden angle' (Hotton *et al.*, 2006).

When the spiral parastichies ($m =$ Number of clockwise and $n =$ anticlockwise spirals) are consecutive numbers in the Fibonacci sequence, it is referred to as 'Fibonacci phyllotaxy'.

Fibonacci phyllotaxy

As is known, the Fibonacci sequence is a sequence of numbers such that a number at a particular position in the sequence is the sum of the preceding two numbers. The Fibonacci sequence is 1,1,2,3,5,8,13,21,34,55,89,144.....*etc.* The next number in the sequence is derived by adding the two previous consecutive numbers. For eg. $0+1=1$, $1+1=2$, $1+2=3$, $2+3=5$, $3+5=8$, and so on. Thus, the fibonacci spiral phyllotaxy is a naturally occurring design that makes use of the fibonacci sequence and the golden angle.

In order to better understand the Fibonacci spiral phyllotaxis, let us present one situation with the parastichy numbers, $m=8$, $n=13$ (two consecutive numbers of the Fibonacci sequence). Here, the highest common divisor ' k ' =1 and may be represented by the notation 1(8,13) (Figs.2a,b).



Figs 2 a-b. The origin of initials in concentric circles ($d = 137.5^\circ$) **a.** numbered circles (1-7) are initials in their order of origin **b.** the initials depicted with parastichies, $m=13$, $n=8$ (Courtesy: <https://www.science.smith.edu/phyllotaxy/Assets/Images/About/>)

In the figure (Fig.2a,b) numbered circles increasing in size correspond to the sequence in which the initials originate (Fig. 2b, indicated by serial numbers from 0-38). Here, there are 13 clockwise (m) and 8 anticlockwise spirals. Two curved spirals (clockwise and anticlockwise) can be identified, starting from point '0'. It can be noted that '0' is closest to points '13' and '8'. One of the clockwise spiral (m) passes through the points labeled 0, 13, 26, 39...*etc* and the anticlockwise spiral (n) passes through 0, 8, 16, 24, 32,...*etc.*

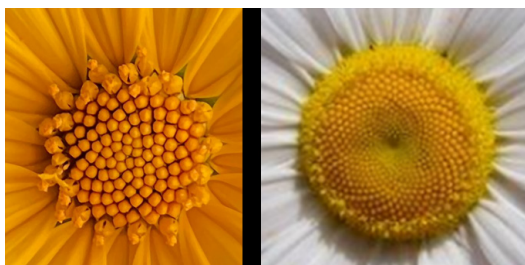
In the Fibonacci sequence, the ratio between any two Fibonacci numbers is referred to as 'Phi'. The ratio between all of these numbers comes closer and closer to 1.618 as we proceed through the sequence (Phi for $3/2=1.5$; $5/3=1.66$; $8/5=1.6$; $13/8=1.625$). This ratio ($\phi = 1.618$) was considered by the Greeks and Romans to be a "Golden Section" or "divine proportion" and could be correlated with the 'divergence angle' in spiral phyllotaxy (Hotton *et al.*, 2006).

As the illustration (Fig 2b) depicts, the arrangement of the spiral parastichies in the golden angle allows for the most compact containment of the petals in a flower and is probably responsible for their aesthetic beauty. The Golden Spiral is not only beautiful, it is functional. It is thought that the golden spiral attracts pollinators through their beauty and may also promote the natural selection in flowering plants. (Gardiner, 2012).

Fibonacci sequence is of rampant occurrence in the floral geometry of aesthetically beautiful flowers of many higher plants for eg. Lillies have 3 petals. Buttercups and wild roses have 5. Delphiniums have 8, and Cinerarias have 13. Most asters have 21 petals, while ordinary field daisies have 34 petals, 55 or 89 petals. It is presumed that it is just nature's way of getting maximum resources made available to it, and taking the easiest path to these goals (Minarova, 2014). To date, the most extensive studies have been carried out on the model plants *Arabidopsis* and tomato (Prusinkiewicz *et al.*, 2022). Although there has been extensive research on this topic, scientists are still unsure about the repeated origin of this sequence during the course of evolution.

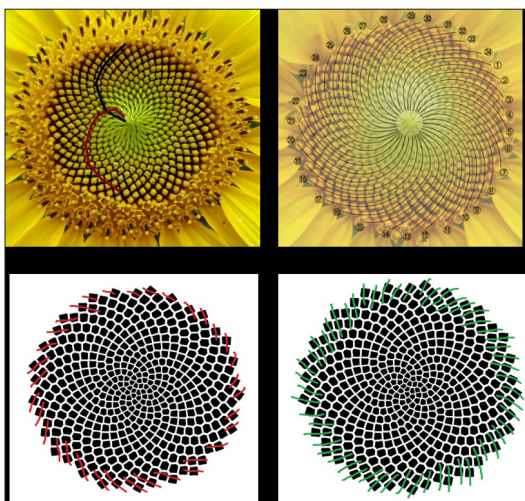
Flower heads of Asteraceae

One of the largest plant families that has been studied as the best examples for Fibonacci phyllotaxy is the Asteraceae. This phenomenon is very evident in almost all members of the Asteraceae. The head inflorescence (capitulum) of Asteraceae resembles a solitary flower but is in fact a cluster of florets (assemblage of hundreds of individual flowers) and is therefore considered a pseudoinflorescence/pseudanthia. Among the florets there are two distinct types – (i) ray florets present in 1-2 layers in the outermost whorls and (ii) disc florets packed in many concentric whorls, towards the head center. The showy ray flowers resemble the petals in solitary flowers, and the hermaphrodite disc flowers resemble the reproductive organs (carpels/stamens) giving the impression of single flowers. The difference in the size, shape, and colour of the ray and disc florets in the different genera of Asteraceae, different species of a particular genus, cultivars of a species or flowers on different plants offer unlimited floral diversity (Figs.3a-b).



Figs 3a-b. Disc floret packaging in the heads of two genera of Asteraceae **a.** *Tithonia diversifolia* (Mexican Sunflower) **b.** *Leucanthemum vulgare* (Ox-eye daisy)

Though diverse, almost all members of Asteraceae displayed the unique presence of Fibonacci phyllotaxy. Many studies tried to identify the biological meaning of this patterning. Results of one such experiment on Sunflowers seems the most convincing. The Citizen Science Experiment, conducted on sunflower samples proved that almost 90% of the flowers followed the Fibonacci pattern or nearly similar patterns [The two lesser-known patterns similar to Fibonacci sequence are the double Fibonacci (*i.e.* 2, 4, 6, 10, 16, . . . *etc.*,) or the Lucas sequence (*i.e.*, 1, 3, 4, 7, 11, . . .)]. In both these sequences also, each number at a particular position is the sum of the preceding two numbers]. Only a small percentage (10%) of the flowers tested, exhibited entirely different patterns (Elomaa, 2019; Godin *et al.*, 2019; Swinton *et al.*, 2016).



Figs 4 a-d. Sunflower, head inflorescence and simulated images **a.** Curves tracing clockwise and anticlockwise spirals **b.** Curves tracing 34 clockwise spirals **c.** Simulated representation

of anticlockwise spirals ($n=34$) **d.** Simulated representation of clockwise spirals, ($m=55$) (Adapted from <https://craftofcoding.wordpress.com/2022/05/16/fibonacci-and-sunflowers/>)

Recent investigations (Zhang *et al.*, 2021) on spiral phyllotaxy in Gerbera flower heads showed that the most common parastichy numbers are - $m=34$, $n=21$, and $m=55$, $n=34$ (Figs.4a-d). The patterning is more obvious in flowers with large circumference at the growth ring towards the head centre. The number of florets in the flower head, is related to the expansion growth of the meristem. It should be realized that, the number of florets also have a functional significance as they ultimately enhance seed yield in economically important members of Asteraceae.

Though substantial progress has been made in uncovering the molecular dynamics of phyllotactic pattern development, the specific details underlying the mechanism is yet to be investigated (Okabe *et al.*, 2019). One of the first biological explanations for Fibonacci phyllotaxy was proposed by Hofmeister. According to Hofmeister's rule, regular patterning of disc florets could be explained by the emergence of new primordia only at the time and at a place where there was enough space for them to appear. In other words, new primordia always arise in the largest gap between existing primordia as observable in most phyllotactic patterns (Newell and Shipman, 2005).

A simpler model, based on cellular differentiation, was proposed to explain the *de novo* generation of phyllotaxy (Klar, 2002) wherein the stem-cell proposal predicts that floral meristems growing spirally and divide asymmetrically to produce dexter and sinister arrangements in equal proportions. Three hypotheses were put forward to explain how information is communicated among the cells of the shoot apical meristem (SAM) during patterning. These include the (i) alterations in the active transport of auxin, (ii) mechanical buckling of the plant's tunica and (iii) changes in the material properties of the cell wall (Gardiner, 2012). These hypotheses were actually complementary, as all three assume that new organ sites are established by hypothetical diffusing chemical fields of growth promoters/inhibitors, originating from both the SAM and the youngest primordia (Rutishauser and Peisl, 2021).

The first hypothesis was grounded on the findings of Reinhardt *et al.*, (2000). Accordingly, auxin is required for and is sufficient to induce organogenesis both in the vegetative tomato meristem and in the *Arabidopsis* inflorescence

meristem. Smith *et al.*, (2006) proposed a simulation model which could connect the molecular mechanisms of morphogenesis and the geometry of phyllotaxis. The model further highlights the interaction dynamics between existing and incipient primordia in a growing apex, mediated by actively transported auxin. To be more specific, new primordia emerge in the areas of high auxin concentration and maintain a distance from each other by depleting auxin in their proximity.

Zhang *et al* (2021) could notice certain other interesting facts as they traced the path of origin of primordia in Gerbera heads. For this, they used the microscopic imaging techniques and correlated the information with physiological and molecular changes in the growth zones. They could decipher that there are three phases (Phase I, II, III) during the head growth. Phase I was identified to be the decisive step in the process. The bracts were found to emerge in a specific order (circular pattern with Fibonacci number of primordia) and therefore could guide the placement of the subsequent bracts and florets. There was a simultaneous rise in auxin levels at specific locations on the meristem, which in turn was directly proportional to meristem growth in size. Also, the pattern was such that a new auxin maximum location arose in between two neighbouring auxin maxima locations and was found to move closer to the older of the two neighbours. However, electron microscopic images could not disclose the primordia at this stage. Thus, it is clear that the regular patterning in spirals is due to a local rise in auxin content prior to the initiation of the primordia and the pattern progression could be traced in accordance with the characteristics of the Fibonacci sequence. Earlier a similar patterning was described in the shoot apex. It was suggested that the spiral emergence of leaf primordia follows an approximate golden angle (137.5°), and their positioning in the available space between existing primordia is associated with formation of auxin maxima at incipient primordia and on subsequent depletion of auxin in their vicinity (Elomaa, 2019).

Zhang *et al* (2021) with the help of *in silico* modelling detailed the progression of the growth zone. They suggested that after the initiation of primordia in the outermost whorl, there was a gradual transition to zig-zag pattern and the development of the head filling spiral pattern was entirely based on this zig-zag pattern as template. Also, it was opined that the Fibonacci numbers arise due to the intercalary insertion and lateral displacement of incipient primordia.

This phyllotactic patterning depends on the size of the active growth zone of the flower heads and thus could be coordinated with the growth of the head. They suggested that the asymmetry in the origin of primordia which is caused due to the displacement of incipient primordia toward their older neighbors probably causes Fibonacci phyllotaxy. A strict adherence to the Fibonacci sequence occurs only when the incipient primordia partition the space between their neighbors exactly according to the golden ratio.

Elomaa (2019) has documented molecular studies conducted in some members of Asteraceae to comprehend the genic interactions and molecular pathways regulating capitulum architecture and flower type differentiation. Gerbera is quoted to be an excellent model plant for studying the patterning on the head inflorescence of Asteraceae since the genome is sequenced and transgenic plants have been raised to study gene function. Results revealed that the CYCLOIDEA-like TCP domain transcription factors have a major influence in regulating the development of capitulum architecture. The experiments conducted on the flower meristem identity genes in Gerbera [LEAFY (LFY) and UNUSUAL FLORAL ORGANS (UFO)] gave evidence to show that the capitulum resembles a solitary flower at the molecular level also. Evidence for the evolutionary origin of flower types was also gained through gene silencing experiments. Silencing of Gerbera orthologues of LFY converted ray flowers into branched structures resembling those found in Calyceraceae, the phylogenetically closest relatives of Asteraceae (Elomaa, 2019). These genes might serve as candidate genes for further studies.

Subsequent studies could come up with many interesting discoveries (Prusinkiewicz *et al*, 2022). Though Phyllotaxis is commonly found associated with circular template, it was found that it could even be extended to non-circular growth patterns (fasciated). In a study on fasciated heads of Gerbera, additional information could be gathered. However, the study was limited to a small sample due to rarity of occurrence of fasciated heads in nature. Tracing the molecular aspects of origin of primordia during all the three phases of growth it could be noticed that in spite of the non-circular nature of the organ initials, there was a tendency to follow the Fibonacci parastichy numbers wherein the local circularities of the head rim became determining factors. The lateral displacement of primordia towards their older neighbors during Phase I occurs in fasciated heads also. This was also evident at the

end of Phase III during pattern closure towards the head center. In circular heads, it occurs by the irregular placement of primordia at the head center. In fasciated heads, closures are often linear. Therefore, it appears that pattern closure is different in fasciated heads and the divergence angle, and the plastochron ratio (the distances of primordia as measured from the pattern center) cannot be defined in fasciated structures.

To summarize, the disc florets on the head inflorescence of Asteraceae are arranged in a symmetrical fibonacci phyllotaxy. Aside from the aesthetic beauty, fibonacci patterning has an engrained biochemical and molecular bases. The patterning is more evident in larger and more circular heads, with higher parastichies. This property may find application in the breeding and propagation of cultivars with larger heads in the case of ornamental and economically important members of Asteraceae. It appears that just as in Asteraceae members, spacing between primordia, presence of auxin maxima at critical locations on the head meristem and regulation of the floral identity genes manifest the Fibonacci patterns in many other flowering plants. Since the patterning is nearly similar in many plants across evolutionary lineages, the applications may be extended to such situations as well.

Conclusion

Though phyllotaxy is one of the highly researched topics, simple, comprehensive explanations and interpretations are scarce. It would be interesting to decode the biochemical and molecular bases of all kinds of patterning in plants. Since phyllotaxy is the best example for spatial resource utilization in nature, investigating the process further may serve to improve the structure of specific plant parts such as leaves and flowers of horticulturally important ornamentals as well as fruits and seeds of economically important food crops in terms of their qualitative and quantitative attributes such as colour, size, shape and arrangement. Delving deep into the gene regulation of single plants/crops and understanding the different levels of interactions during patterning might shed light on their altered phenetic attributes.

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