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Phyllotaxis: Theories and Evaluation

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ABSTRACT

The lively topic of phyllotaxis is based on ever improving descriptions of two important parameters, the divergent angle and parastichy patterns, along with several minor aspects, including the roles of stem size and leaf primordium diameter. Most theories to explain these features are quite old yet continue to hold botanists' attention. The major theories are Hofmeister's available space theory, Schwenderen's packing theory, Schüepp's biophysical theory, Schoute's field theory including Reinhard's auxin efflux theory, and Larson's vascular theory. Each theory explains some feature but falls short on explaining others: the available space theory is not a mechanistic explanation and so it describes only what is observed; the packing theory cannot explain fern apices having well spaced primordia; the biophysical model has not yet generated the precision of leaf siting; the field theory cannot explain the false whorled pattern of phyllotaxy; the auxin efflux theory does not distinguish auxin's role in leaf siting from that of leaf development; and the vascular theory predicts nothing as it is a correlation phenomenon. It is recommended that two new features be considered in explaining leaf arrangement as a complex biological process, the precision of leaf siting and the occurrence of node and internodes. Some workers prefer the surface theories (available space, field, contact pressure), others the internal (vascular) theory and progressively more see it as a combination of the two.

Keywords: Fibonacci angle, field theory, mechanical theory, parastichies, phyllotaxis, orthostichies, PIN1, stem apex, vascular theory
Abbreviations: NPA, N-1-naphthylphthalamic acid; **TIBA**, triidobenzoic acid

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INTRODUCTION

Among all patterns in plants and animals that of phyllotaxis, or leaf arrangement, has attracted the interest of botanists, mathematicians and mystics alike. Actually, it is not so much for leaves but the more amplified patterns of ovuliferous scales in pine cones, seeds in sunflower heads and fruitlets of pineapple that express the beauty of iteration. In 1861 the botanist Hugh Falconer sent Charles Darwin a letter suggesting that phyllotaxis was a deeper phenomenon than Natural Selection and he should look into it. Darwin did so, getting help from his mathematician son George and botanists Aza Gray and Joseph Hooker. He became frustrated with it claiming that it was "enough to drive the quietest man mad." He eventually responded to Falconer two years later that "those angles are a most wonderful problem and I wish I could see someone give a rational explanation of them" (Darwin 1861). How lateral organs such as leaves and flowers are arranged remains a serious challenge.

Part of the difficulty in understanding phyllotactic patterns is the seamless way different developmental pathways integrate into shoot ontogeny. Each leaf is associated with the stem by way of one or more vascular bundles that collectively form a similar pattern to that of leaf arrangement. Also, leaves develop a peculiar shape leading to efficient packing and are later separated by internodes. How phyllotaxis, vascular growth and branching as well as early leaf ontogeny and internodes are related as to cause-and-effect is a question that makes what seems at first to be a simple problem is actually a compound expression of complexity.

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Invited Review

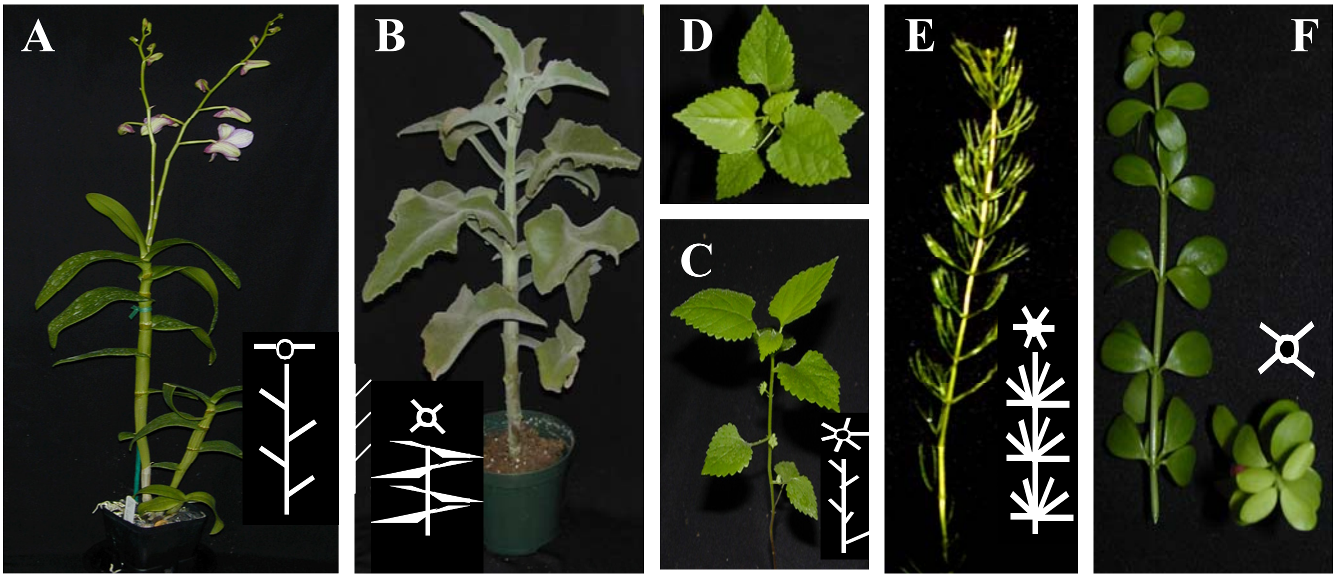

Fig. 1 Types of phyllotactic patterns with stick models from side and top views. (**A**) Alternate, *Dendrobium* or Deb Hiong Beauty orchid. (**B**) Decussate, *Kalenchoe* sp. (**C, D**) Spiral, three-seeded mercury. (**E**) Whorled, *Ceratophyllum*, hornwort. (**F**) False tetramerous whorled, *Peperomia clusiifolia* (when one leaf is missing the others are still 90° apart).

Recent reviews have covered this subject from different points of view including history (Adler *et al*. 1996), a general treatment with good coverage of phyllotactic types (Rutishauser and Peisi 2001), mostly mutant genes (Fleming 2005) and the molecular approach (Kuhlemeier 2007).[1] This review will have an emphasis on evaluating various theories of phyllotaxis including the “old idea” (Kuhlemeier 2007) of the vascular hypothesis.

DESCRIPTION OF PHYLLOTAXIS

Two views are needed to describe phyllotaxis geometrically, centric and cylindrical. First, the centric, or planar, view is from the top of the structure such as when looking at a sunflower head and the bottom of a conifer cone. Second, the cylindrical aspect is viewing a shoot from the side as in vegetative leaves along a stem, the typical view of a pineapple or the lateral view of a conifer cone. Consecutive units generate a genetic spiral up the stem. The standard approach to inspecting phyllotactic patterning is by inspecting plants from the side or the cylindrical view. Five types of patterns are easily discernable.

1. One is the alternate or distichous view where consecutive leaves of the genetic spiral are 180° apart as in pea, grasses and some orchids (**Fig. 1A**). Observed from the top, or planar view, the alternate arrangement has two files or orthostichies (**Fig. 1A**, white sticks).
2. The decussate pattern has pairs of opposite leaves with pairs 90° to each other (**Fig. 1B**). Coleus, snapdragon and some kalanchoes have this pattern. Viewed from the top it has four files or is 4-ranked.
3. The most common type of pattern, found in about 80% of higher plants, is the spiral arrangement as in red mulberry (**Figs. 1C, 1D**), *Arabidopsis* and tomato. Theoretically there are an infinite number of files (**Fig. 1C**, white sticks).
4. The whorled pattern is where more than one leaf is sited at the same level followed by another set of leaves at an adjacent node as in *Hippuris*, *Myriophyllum*, *Fuchia* and *Ceratophyllum demersum* (**Fig. 1F**). Here there are an indefinite number of files of leaves as seen from top view. When the whorl is composed of only two leaves at each node and the pair are 90° to each other it is called decussate.
5. The false whorled leaf arrangement has leaves with a stable number of files as in *Peperomia clusiifolia* (**Fig. 1F**; Malygin 2006, Fig. 10) and most stem segments of *Cephalanthus occidentalis* (Bailey 1949). This is a rare pattern but will be discussed later as important in evaluating various theories of phyllotaxis.

Of critical concern in describing phyllotaxis is the Fibonacci angle, d (Jean 1984). The summation series

1, 1, 2, 3, 5, 8, 13, 21, 34, 55, 89, 144, 233. . . (a)

is formed by adding the two previous numbers, $f_n = f_{n-1} + f_{n-2}$, where n is the position in the sequence of numbers with magnitude f. The Fibonacci fraction is f_n / f_{n-2}, or

1/2, 1/3, 2/5, 3/8, 5/13, 8/21 . . . ≈0.381.

This value of 0.381 is one of the Golden Mean values, the other is phi, φ, or 1.618 such as where the height and width of Greek Temples are 1.0:1.628, or 0.381:0.618. The value of 1.618 can be calculated as

$$\varphi = \frac{(1+\sqrt{5})}{2}$$

It can also be calculated by the continued fraction approach where φ is converted into a whole numbers fraction. The whole fraction is

$\varphi = 1/(1+a)$

where

$a = 1/(1+a)$

so

$\varphi = 1+1/(1+1/(1+1/(. . .)$

$= 1+1/1=1+1 \rightarrow 2$

$= 1+ 1/(1+1) = 1+1/2 = 2/2+1/2 \rightarrow 3/2$

$= 1+ 1/(1+1/(1+1) = 1+ 1/(1+1/(2)) = 1+1/(2/2+1/2) = 1+1/(3/2) = 1+2/3 = 3/3+2/3 = 5/3 \approx 1.66$

giving a series of Fibonacci fractions that converges to 1.618.

Hence the Golden Mean number of φ is the ultimate irrational number as its continued fraction never ends. The Fibonacci angles are fractions of a circle, or 360° x f_n / f_{n-2}, to give the sequence

180°, 120°, 144°, 135°. . . 137.507°

the nearly mystical value in phyllotaxis.

Another summation series is

2, 1, 3, 4, 7, 11, 18, 29, 47, 76, 123, 199. . . (b)

When used as dominators and the numbers in the Fibonacci series as the numerators

1/2, 1/3, 2/7, 3/11, 5/18, 8/29 . . . . 0.2726

so the angles are

180°, 120°, 102.8°, 98.1°, 100°, 99.3° . . . 99.503° . . .

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[1] It is interesting that two of these four reviews use the term phyllotaxis (Adler *et al*. 1997 and Kuhlemeier 2007) and the other two use the variant phyllotaxy term (Rutishauser and Peisis 2001 and Fleming 2005).

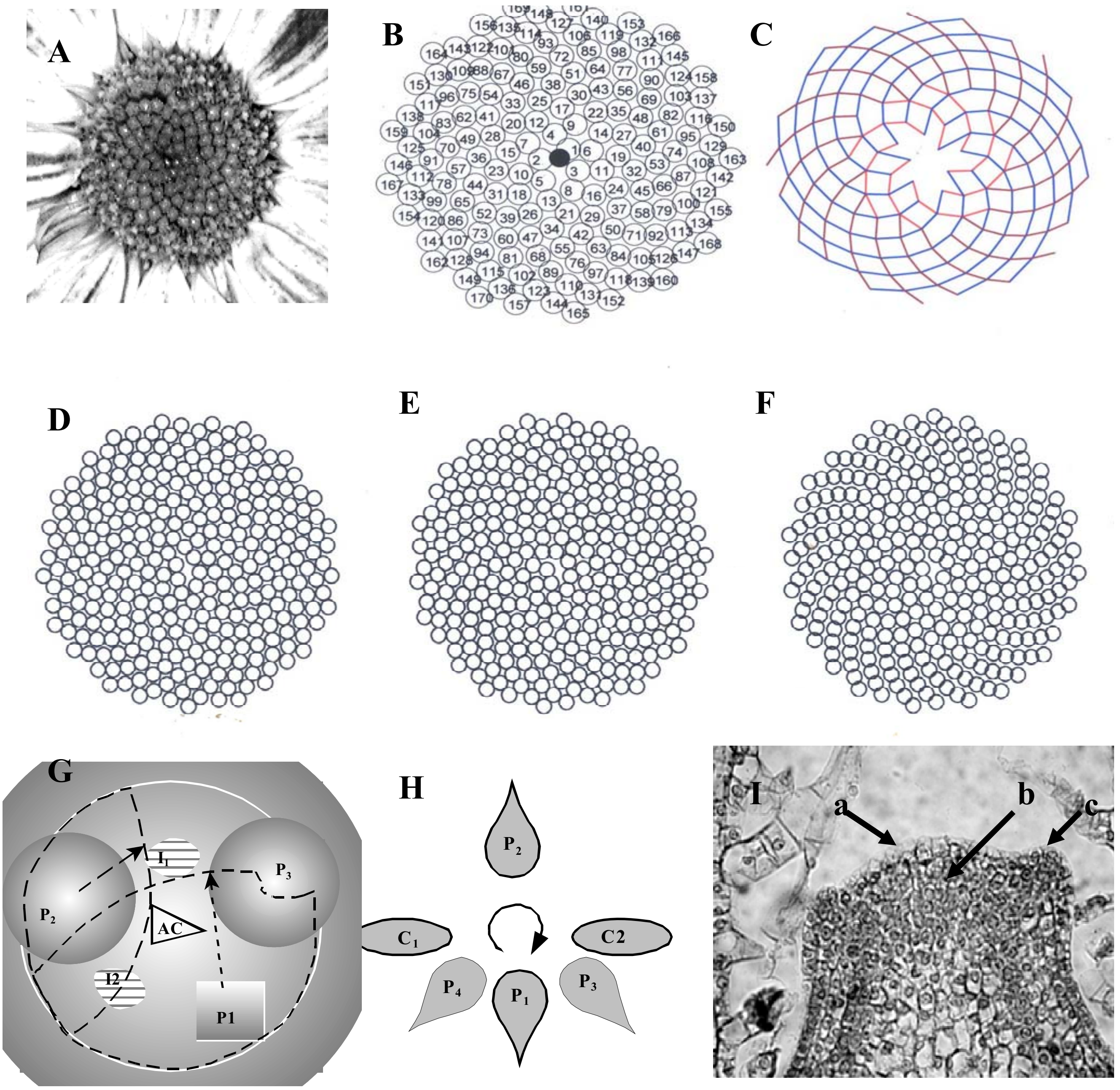

Fig. 2 Centric or top view of phyllotaxis. (**A**) Daisy. (**B**) Computer model with sequence of elements included. (**C**) Computer model giving parastichies. (**D**) Computer model with 137.5° divergent angles. (**E**) Computer model with Lucas 99.5° angles. (**F**) Third type of pattern with 150.1° angles. (**G**) Diagram of apex with locations of P_1, P_2 and P_3 leaves and I_1 and I_2 future primordial along with a triangular apical cell, AC. Dashed arrows and dashed arcs represent inhibitor origin and areas, respectively (after Wardlaw 1949). **(H)** Apex of *Arabidopsis* with cotyledons C_1 and C_2 being opposite, leaves C_1, C_2, P_1 and P_2 being decussate and P_2, P_3 and P_4 being spiral phyllotaxis (after Woodrick *et al*. 2000). (I). Side view of minimal stage of SAM of coleus with tunica (a), corpus (b) and leaf primordium (c).

and are known as the Lucas angles, named after a nineteenth century French mathematician who also coined the term ‘Fibonacci series’. Interestingly, the Lucas series is a compound Fibonacci series

3 (1 + 2), 4 (1 + 3), 7 (2 + 5), 11 (3 + 8), 18 (5+ 13), 29 (8+21) . . .

And hence it is a modified Fibonacci series. The Lucas series is rare, found in about 1% of most plants, all plants in some *Sedum* cultivars and about 15% of sunflower heads. Another series, unnamed, is the series

1, 2, 5, 7, 12, 19, 31, 50, 81, 131, 212. . . (c)

to give a divergent angle of 150.1° and is found in even fewer plants.

A classification system has been developed for all types of phyllotactic patterns. k is the number of elements at each node and the numbers of parastichies are m and n. The notation k(i, j) gives the phyllotactic pattern as i and j are the number of parastichies for m and n, respectively. When k is greater than one and i = j the pattern is whorled, k-merous, and when k is more than one and m is not n then it is k-jugate. The decussate system is 2(1+1), found in about 20% of plants, as in coleus, is dimerous, and the bijugate pattern is found in about 2.5% of plants as in the cutleaf teasel, *Dipsacus laciniatus*, where a double Fibonacci set occurs, 2(m + n).

The centric view

By far the most cited example of phyllotaxis is the sunflower as seen head-on, that is, in the centric or planar view, with about 600 seeds creating a complex swirling pattern. The most visible patterns are spirals, or parastichies running clockwise and counterclockwise (**Fig. 2A, 2B** and **2C**). Those spirals of contiguous seeds are contact parastiches although another less obvious spiral can be often identified. The number of spirals running in the same direction is a family of parastichies, and the numbers of parastichies in the clockwise and counterclockwise families follow consecutive Fibonacci numbers. As examples, the sunflower head usually has 34 and 55 parastichies while most pine cones have 5 and 8 parastichies, or daisies with 8 + 13 parastichies. The number of contact parastichies, m + n, changes as the pattern is followed from apex center to the margin. In this rising phyllotaxis series of the sunflower head m + n may first be 8 + 13 then shifts to 13 + 21, then 21 + 34 and finally 34 + 55. This visible sequence is the result of slight shifting of units during apical growth to realign contacts. Intersection of lines drawn connecting consecutive seeds in a parastichies are at right angles (**Fig. 2C**), a feature that only further highlights these spirals.

Sunflower seeds and pine cone ovuliferous scales do not form simultaneously but in sequence and the angle between consecutive units using the center of the head or cone as the vertex approximates the Fibonacci angle of 137.5°. Davis (1939) measured 685 angles in the stem apex of *Ailanthus* and found an average of 137.4° ± 8.58°. The sequence of units generates an logarithmic spiral which Allard (1946) found from 33,897 tobacco plants there were 16,931 clockwise and 16,966 counter-clockwise shoots, essential equal in numbers. The two seed leaves of a dicot shoot are opposite and the first two true leaves are in an opposite pattern, so where the fifth leaf forms is partly accidental and determines the direction of the genetic spiral (**Fig. 2H**).

An important question is how the divergent angle and the pair of contact parastichies are related since both have Fibonacci values. It seems that parastichies are derived from the divergent angle according to the following argument. Suppose the divergent angle is 90° (6.26318/4 radians) then four leaves form before the next, fifth, overlies the first and, continuing on, leaves will form four rows, or orthostichies. The angle is 1/4 of a circumference or four leaves will form over one revolution. If the angle is 91° then 91/360 is close to 1/4 and four orthostichies form but slightly curved as four parastichies running clockwise, and if the angle is 89° the four parastichies run counterclockwise.

What if the divergent angle is 60°? The fraction is 1/6 of a turn or revolution and six orthostichies form. An angle of 216° is 216°/360° or 0.6 of a turn and can be converted into an exact fraction of 3/5. This 3/5 fraction means that there are five leaves for every three revolutions. But a problem arises when the divergent angle of 137.5° is considered. First, it can be converted into the Fibonacci value of 0.3819… but how is this irrational number converted into an exact fraction?

The solution is found in using continued fractions whereby a decimal is converted into an exact fraction. Here a short cut gives approximations

137.5°/360° = 0.3819/1 = 1/1/0.3818 = 1/2.618 – 10/26 = 5/13

so there are 13 parastichies. The value of 2.618 is φ^2, that is $1.6218^2 = 2.6180$ and for multiplying any Fibonacci number by φ^2 moves it up in the sequence by two positions. Multiplying both the numerator and denominator by ever increasing Fibonacci numbers brings the denominator closer and closer to another Fibonacci number. Hence the sequence 1/2.618, (½), 2/5.2 (2/5), 3/7.8 (3/8), 34/89.01 (34/89), with the approximations in parentheses. When the genetic spiral is counter clockwise odd-numbered positions in the sequence give the number of counter clockwise parastichies and even numbered position give the number of parastichies running clockwise. It is reversed when the genetic spiral runs counterclockwise. Why there are two families of contact parastichies, clockwise and counterclockwise, is because the pattern is always changing as units are added, equilibrium is never reached. In general, the pattern of parastichies seems to form from the divergent angle. This generalization, if correct, greatly simplifies any mechanistic explanation of phyllotaxy. As will be shown later the divergent angle in some theories is only a secondary feature. Also, the dual families of parastichies seem to pack the apex most economically, so the divergent angle is an indirect expression of Natural Selection.

The various divergent angles do not appear that much different from each other (**Fig. 2D, E** and **F**). F. Bookstein claimed he could tell the Lucas sunflower heads from the Fibonacci ones when walking through a field of sunflowers (Ralph Erickson, pers. comm.). Curiously each of these three summation series, the Fibonacci series with a divergent angle of 137.5°, the Lucas series with an angle of 99.5° and a third series with an angle of 150.1° all approach the Fibonacci value of φ, i.e., 233/144 = 1.618, 199/123= 1.617 and 212/131 = 1.618. Here the numbers are from the last two in aforementioned series (a), (b) and (c)).

The cylindrical view

Inspecting a shoot from the side leads to two different types of analysis, depending upon whether units are well spaced and non-contiguous or are packed and contiguous to express contact parasticies. Well-spaced leaves along a stem were originally packed together in the apex and telescoped out as internodes elongated. The only noticeable sequence is the genetic spiral with divergent angles of 180° (alternate and opposite), 137.5° (spiral) or variable (whorled). As stated above, the fraction x/y describes phyllotaxy in which the denominator is the number of leaves before a leaf overlaps the initial leaf in the sequence and the numerator is the number of revolutions from the first leaf to the one before the overlapping leaf. Characteristically elm, linden and grasses are 1/2, beech and hazel are 1/3, apple, holly and plum are 2/5, popular, rose and pear are 3/8 whereas almond, cranberry and pussy willow are 5/13. Overlapping leaves implies orthostichies, namely straight lines, an alignment of leaves not found in apices. It is thought that as leaf sites are teloscoped out nearly straight parastichies are viewed and are taken as vertical alignments. In many higher plants with spiral phyllotaxy buds are formed in the angles between leaf and stem, hence branches coming from lateral buds can also express a phyllotactic pattern.

Packed units include the cylindrical pineapple where fruits are arranged along a vertical fleshy shaft (**Fig. 3A**). Here the packed units in the apex with their parastichies do not teleoscope out by internode elongation but remain contiguous and the pattern of units entering the shoot remains unchanged to give a uniform arrangement along the shoot, unlike the parastichy pattern in the apex which changes as more units are added and the older ones continuously spread out.

The pattern of units on a cylinder can be inspected more carefully if the cylinder is unrolled into a lattice (**Fig. 3B**). The two families of parastichies can be easily recognized and like those in apices, one is clockwise and the other is counterclockwise with both expressing Fibonacci numbers of spirals. The overall pattern can be described by five parameters.

1. The divergent angle between consecutive units, d.
2. The vertical distance between consecutive units, h.
3. The radius of the cylinder, r.
4. The number of units, n, on the cylinder.
5. The size and shape of the unit at the cylinder's surface, D.

As asked previously, how much of the phyllotactic pattern can be explained by the divergent angle alone? The divergent angle, d, determines the positions of units around the vertical axis and the increment of growth, h, places the unit vertically. To pack the units as tight as possible the size of the unit, or diameter if circular, D, must coordinate with d and h. Again if units are circular they pack so there are six touching each unit and there are three families of parastichies, m + n + (m + n) (**Fig. 3C**, lines blue, red and black, respectively), but if units are arranged so there are only four contiguous neighbors there are two parastichy families having two consecutive Fibonacci numbers (m + n).

The geometric features of planar and cylindrical parasti-

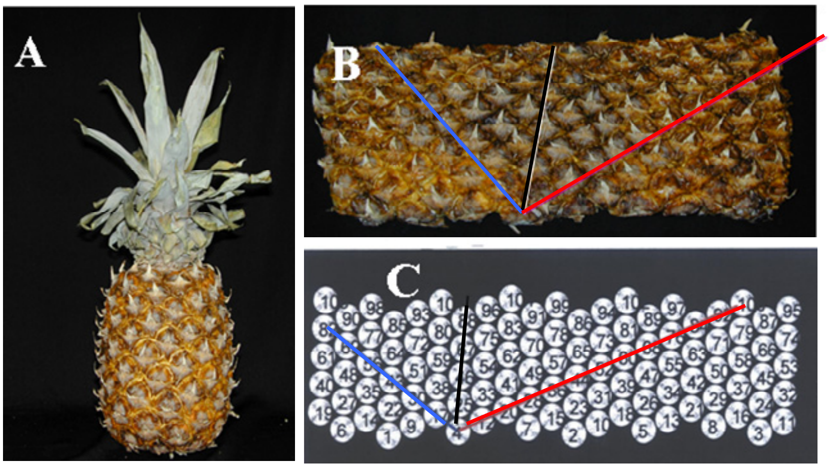

Fig. 3 Cylindrical or side view of phyllotaxis. (**A**) Pineapple with 8 + 13 parastichy pattern. (**B**) Same pineapple unrolled showing parastchies all at once. (**C**) Model of pineapple with 8 (red) + 13 (blue) +21 (black) parastichy families.

chies should be those that have primary developmental importance. What seems critical as primary features are the divergent angle, number of units, displacement rate and possibly unit size. Secondary geometric features are number and size of parastichies as they can be explained by the divergent angle. However, the divergent angle is a human device that is probably the expression of a more fundamental relationship.

Shoot apical meristem

Leaves originate from the shoot apical meristem (SAM) after a plastochron and in predictable locations. The SAM is usually hemispheric as in *Arabidopsis* but can be either flat or concave as in *Helianthus* without altering the phyllotactic pattern. In many plants an apex begins a plastochron as a small dome (**Fig. 2I**), the minimal size, and enlarges to a hemispheric shape of maximal size (**Figs. 4A** and **4B**) at which time one or more new leaf primordia appear. In dicots the surface is usually a single layer tunica covering the corpus within. These layers pass into a leaf to become the epidermis and mesophyll, respectively. Those cells of SAM that become a new leaf primordium are called founder cells and as the leaf develops fewer and fewer of these cells become progressively greater parts of the new leaf.

At the maximal size the number of cells, ACN or apparent cell number, of SAM ranges enormously. In *Arabidopsis* Smith *et al.* (2006) noted the circumference at the

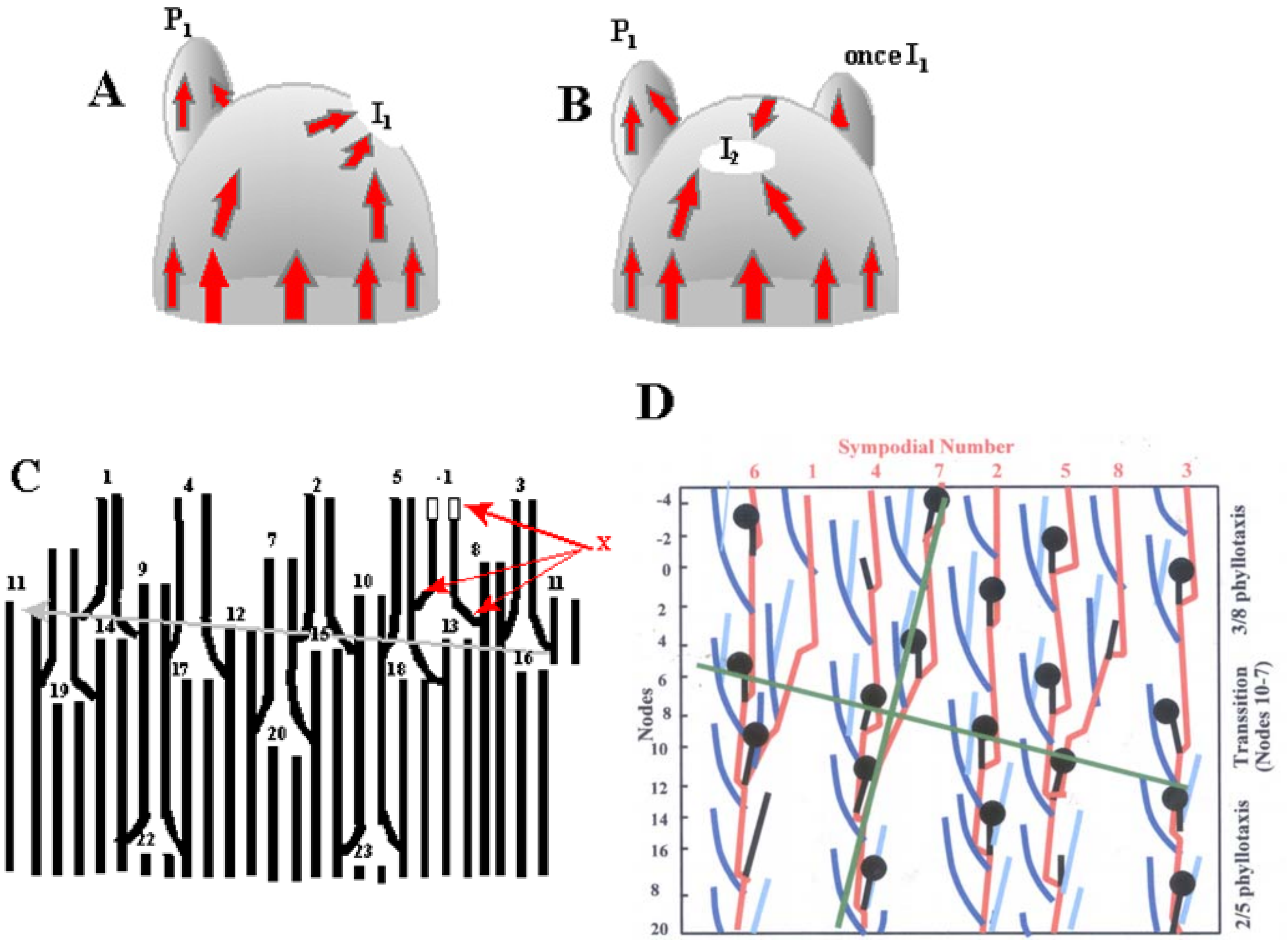

Fig. 4 (**A, B**) The auxin (arrows) carrier model into old and then new primordia (after Ruhemeier 2007). (**C**) Sympodia of *Ginkgo* with dark lines of existing veins and open rectangular of future veins (x). Arrows indicate period of time (five plastochrons) during which veins exist before primordium arises (after Gunckel and Wetmore 1946). (**D**) Cottonwood sympodia (red) with central leaf trace in black, left trace in dark blue and right leaf trace in light blue. Genetic spiral in green (after Larson 1975).

base of the hemisphereic SAM is about 24 cells, thus making the ACN of Sam composed of about 115 cells, close to 110 calculated by Irish and Sussex (1992) by mutant sector size, with a tunica of 90 and a corpus of 25 cells. For coleus at the maximal phase ACN is about 2800 cells and for some very large cactus apices the ACN is more than five million cells (Mauseth 2004). Irish and Sussex (1992) suggest there are about 25 leaf founder cells in SAM.

How many cells of SAM are induced to start a new leaf is unclear? Is it like ferns where one apical cell is induced to begin a leaf and it induces adjacent stem cells to become the founder group? Is this initial cell in the tunica or corpus? Or are a group of cells induced by the phyllotactic mechanism all tunica or all corpus or a mixture of both types of cells? In models of Veen and Lindenmayer (1977) and Smith et al (2006) a single cell starts a new leaf, a reasonable assumption as an initial group of cells requires complex interactions to become coordinated as a single unit.

THEORIES OF PHYLLOTAXIS

Thirty-two theories of phyllotaxis have found their way into the literature (Schwabe 1984), and the past twenty years have witnessed at least two more. They can be separated into two categories, (a) models that are basically chemical, physical or histological and (b) models that are essentially geometric. While the former are preferable as explaining how leaves are sited they can be cloaked in pre-Darwinian teleology while the latter seem too abstract to be of any use botanically yet in some cases they can provide new insights to the problem.

Available space theory

Hofmeister (1868) was the first to propose a theory of how leaves are sited yet by today's standards it is little more than a simplistic description. He proposed that a new leaf forms in the largest available space and this space is usually located somewhat opposite the last one or two that formed (**Fig. 2G**). He viewed the apical meristem as a bald spot residing at the summit and small bumps appear along it's flanks, the smaller ones at the upper flank regions and larger ones below which he interpreted correctly that as a leaf primordium is sited near the apex it both grows in size and recedes basipetally by apical growth. In viewing a mature shoot where leaves are separated by distinct internodes he assumed that in the apex one primordium appears at a time to form the sequence of leaves seen in the mature stem. The three rules of Hofmeister are:

1. A new leaf forms periodically in the place around the central disk where it is the least crowded by other leaves.
2. Once they form, leaves move radially away from the center.
3. As time increases, the rate at which new leaves move away decreases.

Later the Snows (1931) elaborated up the available space theory based on their studies in *Lupinus*. They added the rules that all primordia are of the same size. Also, more than one can be added at a time which then explains whorled patterns. Finally, as more leaves are added the pattern stabiles into a particular phyllotactic arrangement.

The available space theory states where a new primordium will arise and it's only a small step to see how this latest primordium geometrically fits into the overall scheme. Schewendener (1878) proposed an idea of how leaves are packed. He saw young small primordia as spheres nicely arranged in hexagonal order and as they and the apex grows with fluctuations in location, minor shifts of primordia bring out noticeably new parastichies. His mechanical explanation and his reputation as a botanist influenced workers to drop the idealistic, teleological view of pre-Darwinian morphology (i.e., points, *givens*, etc.) and to take up a more developmental cause-effect interpretation of form and pattern (i.e., chemicals, cells).

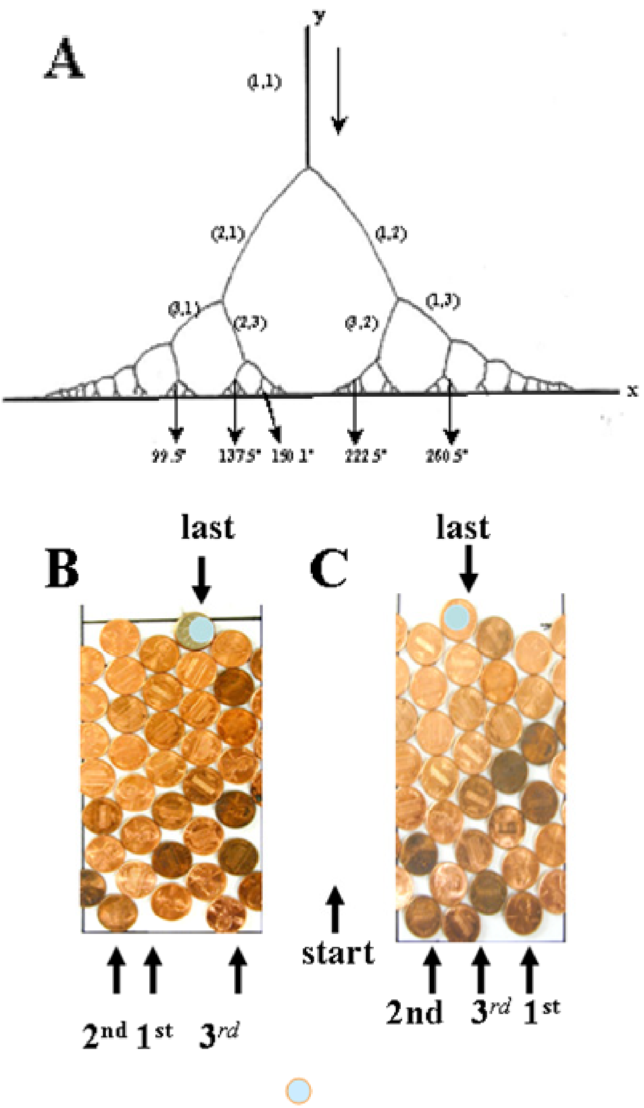

Fig. 5 Origin of various parastichy patterns. (**A**) Redrawn from van Iterson (1907). (**B**) The penny model of Atela and Gole (Atela *et al*. 2002). Somewhat random array of coins at the start gradually become organized into a 3 + 5 parastichy pair of families. (**C**) A different origin results in a Lucas (3 + 4) pattern.

van Iterson (1907) was inspired to study the packing problem from a physical model Airy carried out, the description of which will be discussed later. van Iterson used only one variable, *b*, the ratio of the diameter of a circular leaf to the perimeter of the cylindrical stem. As *b* varies so does the divergent angle and parastichy pair, m + n, beginning with a 1 + 1 to 1 + 2 then bifurcates repeatedly into a large number of pairs, only a few of which are Fibonacci values (**Fig. 5A**). Clearly, as the apex grows in size parastichy pairs bifurcate into higher parastichies. Two useful terms are the plastochron which is the time between the initiation of two consecutive leaves and Richard's (1948) plastochron ratio (PR) which is the ratio of the distances of two consecutive leaves from the apical center (d_{n+1}/d_n).

Ridley (1982) envisioned leaf arrangement as coming from two separate events, first, the siting of a primordium and, second, an adjustment of this site due to contact pressures between adjacent sites that together give the observable rising parastichies. A primordium is seen as an elastic group of cells that responds to pressures created between contiguous primordia and this response occurs over a period of time as more primordia are laid down and old ones recede from the stem apex. His computer simulation produces various parastichies and divergent angles including the Fibonacci and Lucas patterns.

Recently, Atela *et al*. (2002) advanced the Hofmeister-

Snows theory of available space, by viewing a cylindrical arrangement not only by a regular lattice of circles but of rhombic (diamond-shaped or equal-sided quadrilateral) tiling. This allows for observed irregularities of zig-zaging parastichies often encountered in cones and fruits. The available space for siting circular units must be of required size and any new unit must touch at least two older units. As the system enlarges parastichies with m and n values of the Fibonacci series arise. While the Fibonacci angle varies enormously in their model the average of many angles is close to 137.5°. They devised a coin game as a simple demonstration of this idea. Given the width of the rolled out cylinder and common radius of all units added, a new coin is placed in a space of sufficient size and where it touches two older coins (**Figs. 5B** and **5C**).

The packing sub-theory of the available space theory does not use the divergent angle because pattern is considered to emerge by self-organizing processes as seen in **Figs. 5B** and **5C**.

Field theory

Schoute (1913) proposed a field theory whereby each new primordium produces an inhibitor that diffuses out in circular fashion preventing any new primordium from arising within the field (**Fig. 2G**). With growth along the flanks of the apex some tissues are removed from the inhibitory field and produce new primordia. He neither developed a mathematical demonstration of this theory nor found any evidence for such a chemical.

A computer-mathematical approach to the inhibitor-field theory was devised by Veen and Lindenmayer (1977). Using permissible diffusion and decay rates for an inhibitor on a field of an hexagonal array of dots representing cells they found new dots appeared in a variety of patterns. Depending upon the diameter of the inhibitory field different values of m and n rose along with the Fibonacci angle. The patterns were similar to those of van Iterson's packing theory making the results from this model equivocal in supporting a number of theories.

An interesting chemical study was carried out by Schwabe (1971) where he treated *Chrysanthemum* with TIBA, an auxin transport inhibitor. The geometry of the apex and the position of primordia shifted vertically. The phyllotactic pattern changed from decussate to a stable spiral. He explained these results by the field theory where the latest two primordia (P_1 and P_2) inhibit the next primordium, I_1, from forming in proximity. Later Meicenheimer (1979) exposed apices of *Epilobium* (Great Willowherb) with N–1 naphthylphthalamic acid, another auxin transport inhibitor, and α-4-chlorophenoxyisobutyric acid, an auxin antagonist, and both led to similar angular shifts in new primordia causing the decussate pattern to become spiral. Different from Schwabe's findings, the change in phylotaxy was not due to a change in vertical shift of primordia placement but an immediate one in divergent angle.

An interesting mutation in *Arabidopsis* is *pin1* (*pin form1*) where no flowers are present on a naked stem. This feature is similar to tomato apices cultured in a medium with auxin transport inhibitors (Okada *et al.* 1991) and it was found these inhibitors affected a protein that is a putative auxin efflux carrier (Gütweiler *et al.* 1998). Reinhardt *et al.* (2003) proposed a model of phyllotaxy based on auxin efflux carrier results in tomato. Essentially, auxin moves up the stem towards the apex and as it passes through primordia they act as sinks and absorb the auxin. Hence there is much auxin in the apex at P_1, P_2, and the available space and much less between these three sites. A high level of auxin then induces leaf primordium at position I_1 (**Figs. 4A** and **4B**). They explain the distichous pattern when only P_1 is a sink and progressively higher phyllotactic patterns arise as more primordia become sinks.

Biophysical theories

In 1873 Charles Darwin communicated a letter to the Royal Society of London from his acquaintance Hubert Airy about some experiments on leaf arrangement. He glued small spheres (oak-galls) on a stretched out India-rubber band with the spheres running alternately on opposite sides of the rubber band. Upon relaxation, the rubber band twisted into a spiral with the balls following certain phyllotaxis patterns. First there was the 1/3 pattern, when balls were displaced slightly farther from the axis the patterns were next 2/5 and then 3/8. He was convinced that leaf arrangement was for the most economical use of space.

A mechanical theory not of packing but of siting of leaves has been developed by Schüepp (1917). He assumed that the tunica (protoderm) grows faster than the corpus (ground tissue) which creates tangential (vertical) compression. This force results in a buckling, a localized bulge, which becomes a primordium. The location of the bulge on the apex is determined by the geometry of the apex. Appearance of several bulges simultaneously would explain the whorl arrangement, especially of flower parts.

A more recent biophysical theory of phyllotaxis has been proposed by Green (1999). Here the tunica grows slower than the corpus leading to compression in the latter and tangential tension in the former. The tunica yields to form a bulge as a leaf primordium and its specific location is determined by the geometry of the apex and local variation in cell wall extensibility and microfibril orientation. Kirchoff (2003) finds Green's explanation suitable for the arrangement of inflorescences and flowers in *Phenakospermun* and *Heliconia* following the available space theory.

Vascular theory

Morphologists have long noticed the close relationship between leaf positions and the vasculature of the stem as first emphasized by Hanstein (1858). Each leaf extends one or more vascular bundles from the midrib into a complex set of vascular bundles, sympodia, of the stem (**Fig. 4C** and **4D**). Bolle (1939) noticed this relationship in the work of Szabo and put a theoretical spin on it. He proposed there are two induction lines (*Antriebe*) originating in the cotyledons of dicots, one extends upwards and undergoes progressive bifurcation to form all the leaves and the other also passes acropetally without dividing. Bifurcated daughter lines have different lengths and angles leading to the collection of leaves generating divergent angles and parastichies, respectively. A slightly different vascular theory, as proposed by Plantefol (1948), has two foliar helices neither of which is the genetic spiral. They are two of the members of a parastichy family which produce two sets of leaves in a subapical generative center as dictated by an "organizer" at lower levels of the foliar helices. Both Bolle and Plantefol have mixed observable anatomy with abstract givens (*Antreibe*, "organizer") and hence their ideas are not mechanistic explanations of phyllotaxis.

A far more meaningful approach is to determine the timing of leaf formation and that for the appearance of corresponding leaf traces. Gunckel and Wetmore (1946) found a strong parallel between sympodial and phyllotactic patterns in *Gingko* (**Fig. 4C**). The vasculature sends two traces into each new leaf and these traces can be identified five plastochrons before their corresponding leaf primordia appear. These traces form and elongate during a time when the apex is undergoing reorganization so the apex at the time of trace entry is not the same as when the trace was first formed. Also, the two traces originate at different times, the earlier one is anodic (runs upwards in the direction of the genetic spiral) and the later one is kathodic (away from the upward direction of the genetic spiral), and arise from different symposia. Here is a complex but highly regulated pattern. Sterling (1947) found procambial strands arise seven to eight plastochrons before their corresponding primordia appear, a difference of almost three complete turns,

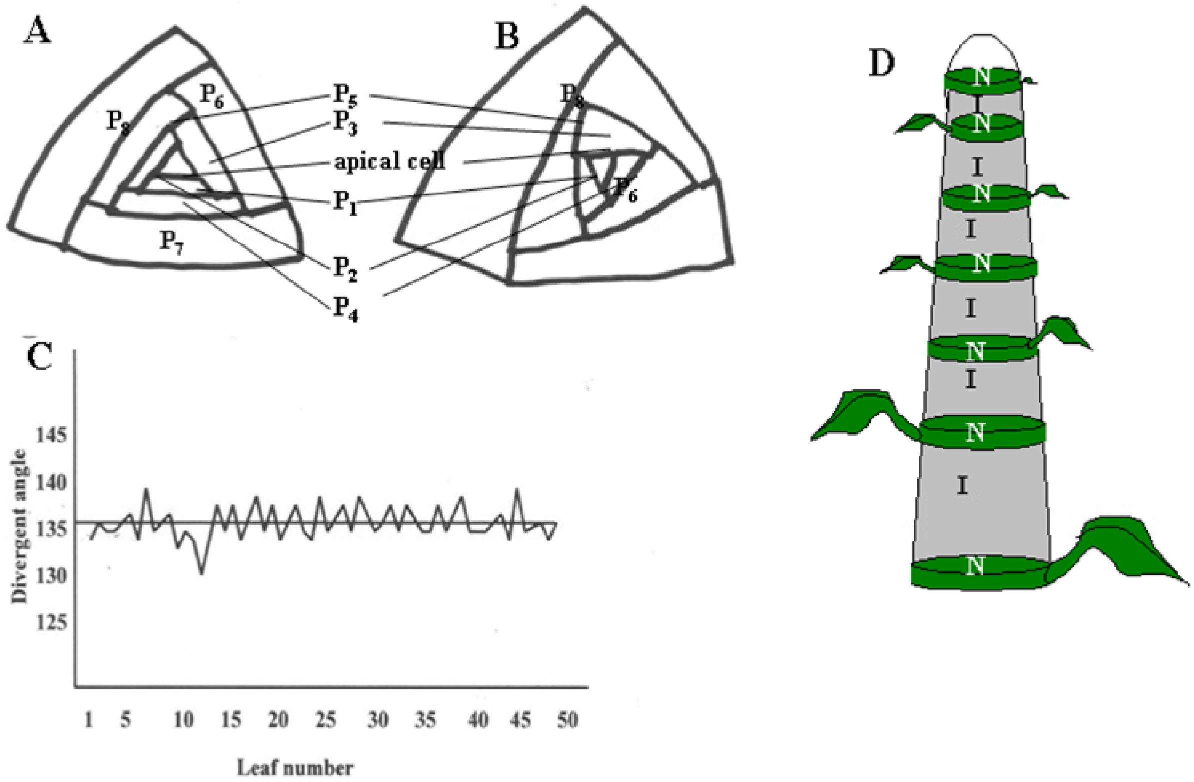

Fig. 6 Moss 'shoot' apical cell division. (**A**) Cell division pattern that generates 120° divergent angles. (**B**) Cell division pattern that generates 137.5° divergent angles (after Westermaier 1896). (**C**) Consecutive divergent angles in sunflower head with cycles of two plastochrons. (**D**) Diagram of node (N)-internode (I) sequence (after Zobel 1989).

3 ≈ (137.5° × 7)/360°.

In cottonwood, *Populus deltoides*, Larson (1975 found the procambial strands could be seen six plastochrons ahead of their leaf primordia (**Fig. 4D**). These early leaf traces also were positioned to lead to new a new pair of parastichies long before they were expected in leaves. While cottonwood has a leaf 3/8 pattern and a divergence angle of about 137.5° Larson felt there are neither orthostichies nor divergent angles, they are simply convenient measures but with respect to the vasculature they do have a structural reality. As with others before him he felt the leaf traces induce leaf primordia, the influence for leaf initiation comes from below the apex.

EVIDENCES FOR AND AGAINST VARIOUS THEORIES

Once all theories of phyllotaxis have been put on the table they can be comparatively evaluated according to the evidence available. Mathematical theories are not included but results from models help in judging how a theory behaves under various conditions. For example the divergent angle cannot be a primary feature of any theory as apices cannot measure angles but a theory should be able to generate the various divergent angles found in different plants. Also, the divergent angle varies and only averages 137.5°, so any theory has to generate this variation. A necessary assumption is that the phyllotactic mechanism(s) are the same in all plants for the sake of simplicity (Kelly and Cooke 2003). An obvious exception of the phyllotactic mechanism is found in mosses (**Figs. 6A** and **6B**). Some mosses have "leaf" arrangement along a stem as a 120° spiral and others have a 137.5° spiral. The basis for these two patterns is the cell division geometry of the terminal apical cell (Leitgeb 1874). How the apical cell measures itself to form an unequal cell division is unclear but at least the morphological location of the phyllotactic mechanism is known. That this is not the way higher plants site leaves has been noted by Bierhorst (1977) for ferns and by Ball (1960) for angiosperms.

Surgical experiments

Mary and Robert Snow (1931) performed a series of surgical cuts to the apex of *Lupinus alba* which has an average 137.5° divergent angle and a 2 + 3 pair of parastichies families (**Figs. 7A-D**). Primordia are numbered from the latest, P_1, to the next older, P_2, and to the oldest, P_n. Likewise then next primordium to form is I_1, then after that one comes I_2 and so forth. First, they cut a vertical slit with a scalpel separating P_1 from the rest of the apex (**Figs. 7A** and **7B**). The apex continued growth with the addition of more primordia. I_1 primordium developed in a normal position, about 137° from P_1 but I_2 was atypically close to the slit, or P_1, and about 165° from I_1. Since *Lupinus* has a 2 + 3 phyllotaxy, primordium I_2 is in contact with P_1 and P_2 while I_1 is in contact with P_2 and P_3. Perhaps P_1 has an influence on contiguous primordia, one of which is I_2 or perhaps I_1 was already determined but not expressed. To test these interpretations they made another series of trials by making a vertical cut to separate I_1 from the rest of the apex (**Figs. 7C** and **7D**). This time I_2 was in its normal position but now I_3 was moved by an angle of about 200° from I_2 and atypically close to the cut. Based on these experimental results the Snows preferred to conclude that the altered sites were closer to where available space was the largest. But these most interesting experimental results are equivocal as they also support Schoute's theory of inhibitory fields as the altered sites were the farthest from recent primordia where the inhibitor would be the least. The results can also be explained by the vascular theory as incisions force recruitment of procambial strands to be diverted sideways.

Of considerable interest but played down by other authors is that often when the divergent angle is more than 180° the direction of the genetic spiral is reversed, indicating the siting mechanism has been damaged.

Wardlaw (1949) carried out a series of somewhat similar surgical experiments on the fern *Dryopteris dilatata*. Instead of separating a primordium by a slit, he damaged the leaf site with an incision. Destroying site I_1 led to normal siting of I_2 and I_3 but I_4 was closer to I_1 cut. This result is

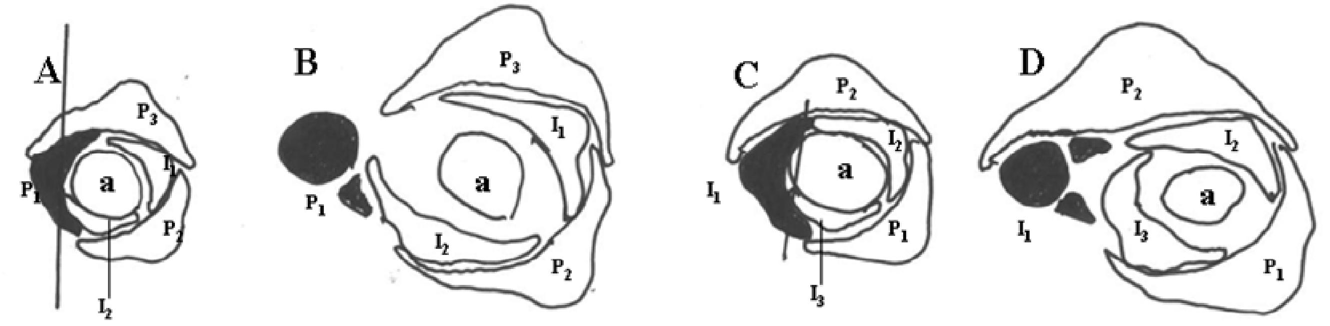

Fig. 7 The Snows‘ experiment on *Lupinus* apices. (**A**) Incision (straight line) so P_1 (shaded) is separated from rest of apex. (**B**) Results of P_1 (shaded) isolation with I_2 moved closer to P_1. (**C**) Apex with incision (straight line) to separate I_1 (shaded) from rest of apex. (**D**) Results of separating I_1 (shaded) with I_3 moved closer to I_1.

similar to those from *Lupinus* in that the fern has a 3 + 5 parastichy pattern and I_4 is normally closest to P_2 and I_1. Again the altered leaf is the one closest to the injury. Despite the similar findings and their equivocal interpretations Wardlaw took just the opposite view of the Snows by supporting the inhibiting field theory.

The second finding of the Snows was repeated by Cris Kuhlemaier’s and Didler Reinhardt’s group (Reinhardt *et al.* 2003) using tomato instead of white lupine and cultured apices instead of whole plants. They also observed apices repeatedly from immediately after surgery up to several weeks later instead of only once weeks after cutting as carried out by the Snows. I_1 did not appear as it was destroyed, I_2 arose in the normal position but I_3 was displaced away from I_2 more than normal and closer to the expected I_1 location, exactly what the Snows found. At first the center of the apex shifted away from the incision, most likely due to damage but the apex realigned itself correctly. The question then is how much damage is done to the apex by surgery?

They also used laser ablation on the meristem as it causes less damage than does surgery. I_1 was isolated from the rest of the apex by killing cells at that position. In 50% (n =26) of the apices I_1 still formed but to either side of the ablated region giving either a larger or smaller than average angle with P_1 with subsequent primordia appearing in the correct locations. In 12% of the cases I_1 formed between I_2 and where I_1 usually formed with a reversal of the genetic spiral. In the remaining 38% of apices I_2 appeared below the lesion with no alteration of divergent angles or direction of spiraling. The results from laser ablation indicate that, first, incisions cause general damage to the apex and, second, I_1 and therefore all presumptive sites have a flexibility, a feature not detected by incision. They also concluded that nearest neighbors to I_1, both P_1 and P_2, are important in determining its position.

These most informative results have been interpreted by the authors as supporting the field theory but again are equivocal in that they can also support the first available space as well as the vascular theory. Ablation and cell death can lead to a new available space or by the vascular theory the shift of I_1 could be interpreted as procambial initials recruit cells in a new location beneath nearby living tunica cells.

Chemical experiments

The model for phyllotaxis in tomato was based, in great part, on the findings of Okada *et al.* (1991) of the *pin1* mutant in *Arabidopsis* where during the floral stage only a finger-like stem was formed with no flowers and on the results of Galweiler *et al.* (1998) that PIN1 is a protein that is an auxin efflux carrier. Further experiments by Reinhardt *et al.* (2000) were most instructive. NPA (an inhibitor of auxin transport) resulted in a leafless stem, namely an NPA pin. When a small amount of auxin was added to the flank of an NPA pin, primordia appeared but only at the site of auxin application. When NPA was added at the summit of the apex, primordia appeared on the flanks in no particular pattern. When a small amount of NPA was added to an untreated apex at the expected site of I_1 no primordium appeared but later one arose at the I_2 site. More primordia arose but in a reversed spiral, reminiscent of the ablation experiment of the I_1 region described above.

Later Reinhardt *et al.* (2003) studied the *pid* mutant in *Arabidopsis*, that appears like *pin1* in forming a finger-like stem void of flowers. When auxin was added to a *pin1* apex a single donut-shaped primordium formed around the apex and when auxin was applied to the tip of a *pid* apex a whorl of separate organs appeared, sometimes even a second whorl formed. The question arose whether auxin distribution induces new primordia or simply allows a preestablished pattern of primordia to be expressed. They added 2,4-D, a synthetic auxin analogue that is not carried by the efflux carrier, and the donut-shape bulge appeared, similar to the auxin treated *pin1* apex. That the whorl of organs did not form because PIN1 protein could not move 2,4-D indicates it is PIN1 that generates pattern. The path of auxin is upwards in the epidermis/tunica into the apical dome where it moves to the latest formed primordia that behave as sinks and then downwards in the primordium where it activates xylem development. The *Arabidopsis* group at Cal Tech (Heisler *et al.* 2005) monitored the distribution of the PIN1 protein by green fluorescent protein dye distribution of pPIN1::PIN1-GPP and found it is uneven with the highest

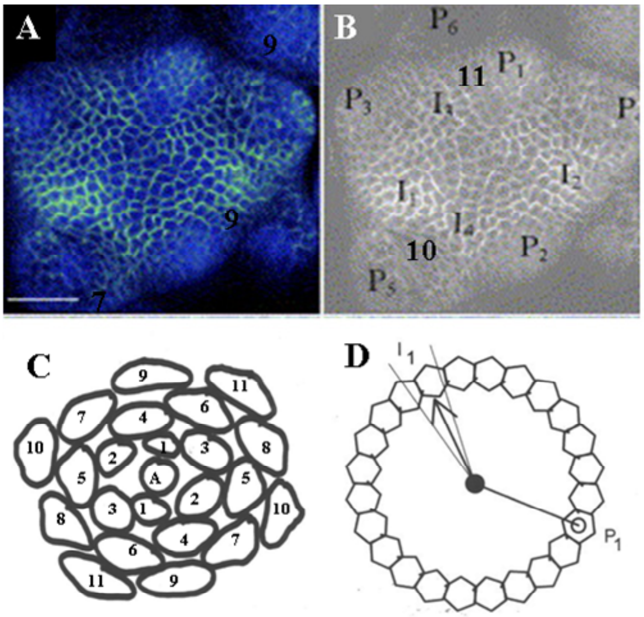

Fig. 8 (**A**) Results of experiment by Heister *et al.* (2003) on *Arabidopsis* stem apex with PIN1 protein by green fluorescent dye distribution (**B**) Locations of primordia and presumptive primordia**.** (**C**) The bijugate Fibonacci pattern. (after Reinhardt 2005). (D) Diagram of *Arabidopsis* apex from top view with bottom ring of cells and divergent angle (P_1 – arrow – I_1) to show precision of one cell in placement of a new primordium.

concentration in L_1 primordium and the tags are mostly on the side of cells facing away from the I_1 site (**Figs. 8A** and **8B**). With each new primordium formed the distribution of PIN1 shifts both on the apex and place in cells.

As Hudson (2007) points out, all this fascinating data are equivocal as they also support the idea that auxin simply stimulates growth at preordained sites (he calls it a permissive role) as well as the theory that auxin leads to patternation *novo* at the apex (an instructive role).

Morphological

Phyllotaxis includes three distinctly different morphological (geometry of form) phenomena, the siting of leaves, the determination of leaves and the development of leaves. They also can be seen as anatomical (internal structure) features defined by cellular behavior. The leaf siting process can be distinguished from the determination of a leaf in *Zeylanidium subulattim* as shown by Imaichi *et al.* (2005) in that leaf determination occurs in the absence of a shoot apical meristem. A new leaf is connected to an older leaf which may, in part, have the initial tissue from which a new leaf arises. Also, apogamous leaves in ferns come from gametophytic tissue where no SAM is present (Korn 2008a).

Perhaps of greater interest is the fact that primordia in ferns are well separated, not even close to forming contact with each other (**Fig. 2G**). This general finding puts a damper on van Iterson's (1907) contact packing theory as well as the ideas of Ridley (1982) and Hellwig *et al.* (2006) of a series of minor adjustments. Also, the coin packing model of Atela, Gole and Hotton (2002) does not work for ferns, and this model also produces divergent angles with enormous variation, much more than measured by Davies (1939).

The distichous phyllotaxy pattern (**Fig. 1A**) can be explained by an inhibitor or efflux carrier as extending over only part of the meristem but the false whorled pattern (**Fig. 1F**) cannot be explained by a field interpretation. Hudson (2007) noted the two-rank pattern in opposite phyllotaxis suggests more than surface fields are involved in leaf siting. All theories except the vascular theory cannot explain the false whorled and opposite phyllotaxies, a situation where the importance of this single pattern is out of proportion to its frequency of occurrence. A detailed morphological examination of false whorled and opposite phyllotaxies is called for in order to make sure it actually is regular and not some variation of other patterns. The bijugate Fibonacci phyllotaxctic pattern, in the cactus *Gymnocalycuen* (**Fig. 8C**) and during the rosette stage of *Dipsacus*, consecutive leaves are only about 68° apart, a feature that is difficult to explain by the field theory (Snow 1951).

An intriguing artificial study was carried by Douady and Couder (1992). They allowed drops of a ferrofluid (having magnetic properties) fall on a film of oil. The magnetic field polarized the drops that became dipoles and so repelled each other. As each drop falls it experiences a repulsion from previous formed drops floating on the surface of the film while the magnetic field pushes it away from the center of the film. Adding drops slowly produces two ranks of drops 180° apart, similar to the distichous pattern. Adding drops faster yields more complex arrangements that eventually settle down to one with 137.5° angles between consecutive drops. Multjugate patterns occur when several drops are added simultaneously. It is difficult to see how primordia equate to fallen drops. A primordium does not first appear at the center of the apex but well down and along its flank; preestablished primordia do not push new primordia away from themselves to form the divergent angle; and the movement of old primordia away from the center is not the same as growth. It certainly does not mimic fern apices where primordia are well spaced (**Fig. 2G**).

Other data suggests the genetic spiral retains a structural continuity. Skutch (927) found anodic coiling in the banana leaf, anodic axillary buds were described in *Victoria* by Cutter (1959-60) and in *Eucalyptus* by Carr (1998). In *Citrus* Schroeder (1953) reported that thorns were located anodically. I found anodic placement of secondary blades in *Croton variegatus*, anodic location of the larger of two axillary buds in *Acalypha virginica* and anodic bending of the midrib of *Syngonium podophyllum* (Korn 2006). These cases of an anodic behavior indicate some left-right symmetry exists along a structurally continuous genetic spiral which is best interpreted by sympodial organization where leaf traces originate in adjacent sympodia and not temporal, molecular relationships. However, such physical continuity could be established after leaf siting which guides procambial extension. Larson (1975) argues convincingly that it is simpler to have the leaf traces enter a primordium to form a midrib than to have a midrib branch with these branch veins extending downward and linking up with specific sympodia. This idea is supported by Kang *et al.* (2003) who found in *Arabidopsis* procambial strands in SAM extend acropetal instead of basipetal.

EVALUATION

Precision of siting

The most noticeable feature of phyllotaxis is the collection of parastichies and second is the genetic spiral. Although the genetic spiral can run either counterclockwise or clockwise the spiral is reversed in branches (Korn 2006) and after growth spurts in *Citrus* (Schroeder 1953). It can be experimentally altered by incisions placed between primordia (Snow and Snow 1931) such that when the primordium is displaced to generate a divergent angle of about 180° or greater, the genetic spiral is reversed. Reinhardt *et al.* (2005) also found a reversal of spiral direction in some tomato apices when I_1 region cells were ablated. In spite of these exceptions the mechanism that dictates the continuity of the sequence of leaf placements is highly stable.

The variation of the divergent angle is also highly regulated. Of 685 divergent angles measured in *Ailanthus* Davies (1939) found an average of 137.666°, close to the expected mean of 137.5°. The range was from 113° to 165° with standard deviation (SD) of 8.58 for a coefficient of variation (CV) of 100 × 8.58/137.666, or 6.24. Les Bursill's group (Ryan *et al.* 1991) analyzing seeds in the sunflower head found an average divergent angle of 136.8° with a SD of 7.41° which can be calculated here as a CV of 5.4, similar to the *Ailanthus* data. Rutishauser's (1998) data set on *Sagina saginoides* also oscillates on a two-primordia cycle even through it is small, only six angles, with an average and SD of 143.6 and 23.8 to give a CV of 16.2. The minimum and maximum angles were 122° and 152°. These data bring forth two points of interest. First, no reversal of spiraling was encountered and the maximum angles of 165° and 152° are far below that of 180° where reversal is expected to occur. Second, the CV of 6.24 and 5.42 is about the same as that for other well regulated events such as the difference in size of two daughter cells has a CV of 7.2 (Korn 2008b) which is also atypically low compared to the more common value of about 17.0 as was found for number of achenes in *Crepis* capitulum (Lambert 2001). The small SD's reported seem far less that what Green's biophysical and Atela et al. (2002) pennies models can match. The computer model of Smith *et al.* (2006) gives the same divergent angles of the first nine leaves as well as the same standard error as from *Arabidopsis* seedlings.

Smith *et al.* (2006) estimate the peripheral zone in *Arabidopsis* where primordia form is a circle of about 24 cells and so an angle of 137.5° is 24 × 137.5/360, or about nine cells. The ± 8.58 standard deviation of Davies (1939) data is about 24 × 2 × 8.58/360 or 1.1 cells (**Fig. 8D**). Clearly, the mechanism of leaf siting can narrow in with a precision of about one cell. Koch *et al.* (1998) calculated the precision required for seed siting in a sunflower head. The 8 + 13 parastichy pair forms by van Iterson's chart (**Fig. 5A**) a divergent angle between 137.2° and 138.2°, or within only 1°. Assuming the meristematic ring is about 100 cells then each cell is 3.6° and a requirement of 1° is far less than one cell. The observable parastichy pair of 55 + 89 makes the requirement even greater. Their answer to this dilemma is to invoke a second mechanism, that of adjustment forced upon older primordia by younger ones, as previously proposed by adherents to Schwendener (1878) pressure contract theory. Perhaps in relatively simple arrangements as in *Arabidopsis* shoots leaf siting is the only mechanism whereas mature systems with crowding of elements as in composite heads, conifer cones and fruitlet packing a second mechanism is required to achieve the efficient arrangement of these elements.

The sequence of divergent angles is also of considerable interest. Analysis of the data of Bursill (Ryan *et al.* 1991) as reconstructed in **Fig. 6C** gives a coefficient of correlation, *r*, of -0.43 indicating a strong negative correlation between consecutive angles. When one angle is more than average the next is less and visa versa giving a phase duration of about two plastochrons. Fifty consecutive angle measurements from Davies' (1939) data give an *r* value of -0.20. Rutishauser's data give an r value of -0.96. These cases of negative correlation can be explained in either of two ways. First, the summit of the apex is misplaced by the investigator slightly off-center so an angle vertex close to the two youngest primordia gives an angle larger than it actually is and a subsequent angle on the other side of the apex farther from the last two primordia will be smaller, hence the artificial oscillation with a phase of two plastrochrons. The lesson is one of caution in determining the center of the apex as methods now exist for a more objective determination (Hotton 2003). If this interpretation is correct the small SD's of 8.58 and 7.41 include technique errors making the true SD even smaller and the siting mechanism even more precise. The other interpretation is primordia move from contact pressure as this oscillation has been found from computer modeling (Hellwig *et al.* 2006).

Internode formation

By definition leaf primordia are attached to stems at nodal regions and consecutive nodes are separated by internodes. A critical question is how leaves that are well packed into the apex recede from each other by elongating internodes? Where do internodes come from? Zobel (1989) inspected decussate shoots where nodes and internodes are clearly distinct especially in those plants where either nodal or internodal cells store phenolic compounds. Both nodes and internodes are stacked like blue and red poker chips all the way up into the apex where the smallest of each is only two cells in depth (**Fig. 6D**). Her interpretation is that the cells in the layer beneath the protoderm, L_2 under L_1, divide periclinally to form alternately sheets of mother nodal cells and mother internodal cells. It would seem these "differentiating divisions" occur lower in the apex where cells change from dividing in three directions to dividing only longitudinally (Korn 1993) so cell sheets can be more easily established and maintained.

The presence of alternating nodal and internodal sheets in the apex helps explain several anatomical features. First, the monocot leaf has a basal sheath that often surrounds the stem, as a tubular structure as in *Tradescantia zebrna*. Another curious anatomical case to be explained is the whorled arrangement, as in *Ceratophyllum*, where as many as eight leaves originate at the same node. Placing eight leaves at the base of the apex, essentially in individual cells equally spaced apart and yet at the same distance from the apex is close to impossible but if they are placed in the same node the whorled pattern becomes commonplace. Also, the wide but thin scale leaf scars on woody stems are closely packed, yet are still separated into distinctly different nodes.

The presence of nodal and internodal sheets does not help to distinguish between surface field and internal induction theories, they are both forced to initiate leaves in a restricted belt-like region. For the field theory an inhibitor could come down from the summit of the apex and limit how far up the stem the node/internode pattern can ascend. This theory would also work as either an inhibitor or efflux carrier would restrict a new primordium only circumferentially because vertically restriction is established by the nodal sheet of cells. By the vascular induction theory an apical inhibitor from the summit would again be required but the location of leaf siting in the sheet is determined by the placement of upwards advancing sympodia.

CONCLUSIONS

There has been a gradual improvement in collecting information, larger data sets and statistics have given greater validity to description. Approaches of morphology and physiology have been augmented by molecular biology and computer simulation. Also, data is gradually being separated into primary which is useful to understand the mechanism of leaf siting and secondary which can be explained away by primary data.

Alas

The location of the leaf siting mechanism remains problematical as it can be either located at the surface of the apex in the L1 cell layer or within SAM, namely, the procambium. Presently, some workers consider leaf siting a tunica phenomena through inhibitor or efflux carrier gradients (Heisler *et al.* 2007; Hudson 2007), other prefer the procambial interpretation (Larson 1975; Korn 2006) and still others see an interaction between these two types of mechanisms in order to explain the precision of placement (Reichardt *et al.* 2003). The interaction of leaf siting, node-formation, apex stability during growth, tunica-corpus separation and dorsoventrality of leaf primordia become one complex system, as noted by Fleming (2005), only one component of which, the first listed, has been emphasized here. Workers on phyllotaxy should best be aware of this complexity that has evolved in plant evolution, perhaps to resolve a number of problems simultaneously.

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