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students in their areas of strength. This is as it should be. Somehow, too, we must devise a federal support system to retain our best young people in a university or industrial research environment. If the marketplace phenomenon of few job opportunities for scientists and engineers is allowed to reign unchecked (that is, appreciably reduce the input of graduate students), the nation will lose that enormous research effort now contributed by graduate and postdoctoral students. One solution to this problem, as I mentioned earlier, would be an increase in federal formula grants, from which we could support these young people.

A direct effect of the lead institution concept that may cause consternation in research universities is that departments would feel pressure to bend their efforts toward interdisciplinary research, perhaps at the expense of "small science," the kind of basic unarticulated research

that has been the lifeblood of research universities. While I clearly do not advocate diminishing such research, the pressure, on balance, may be a healthy one. With some very notable exceptions, the traditional departmental structures of universities often remain as barriers to interdisciplinary research. To help us overcome these barriers—and still preserve the departments as basic academic and administrative units—we need to rethink ways of subsidizing our research efforts in the interdisciplinary, problem-focused mode. If the research universities do not adjust to society's needs, society's dollars for high-priority research may simply go elsewhere.

Ideally, the university should be the focus for both basic and interdisciplinary research on long-range issues. Federal laboratories, corporations, and special university institutes and centers would be responsible for the shorter-term

approaches closer to practical application.

It will not speak well of the scientific community if we must be dragged into the global age kicking and screaming, with a debilitating case of future shock. If we can protect and strengthen basic research—and you will recall I made particular note of the health of our universities and the support of young investigators—if we can encourage more problem-oriented research and better articulation between research sectors, then, I believe, we can do better than muddle through my so-called global age. In my optimism I think we are bending in this direction now, but my great hope is that these tendencies will accelerate—for our sake and for the sake of future generations.

References

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Phyllotaxis and the Fibonacci Series

An explanation is offered for the characteristic spiral leaf arrangement found in many plants.

G. J. Mitchison

The spiral patterns of leaves, bracts, or florets of plants are a familiar mathematical curiosity of nature. Anyone who has counted the spirals which catch the eye on the head of a sunflower, or on a pine cone, will have discovered that their number is generally a term of the series 1, 1, 2, 3, 5, 8, 13, 21. . . . This is the famous Fibonacci series, each of whose terms is the sum of the preceding two. Although the study of phyllotaxis (leaf arrangement) goes back to classical antiquity, the attempt to find a plausible mechanism or a mathematical explanation for this Fibonacci phyllotaxis began more recently. It is perhaps to Richards that we owe the most lucid treatment of the subject. In particular, his paper on the "Geometry of phyllotaxis" (1) seems to offer a key to the problem. However, it falls short of an

explanation: a suggestive diagram and several pregnant sentences culminate in the assertion that Fibonacci phyllotaxis must inevitably occur, given certain plausible assumptions. It is clear that even Richards' authority has not convinced later investigators, for the problem has continued to be regarded as unsolved. In response to this, Adler (2) recently proposed a somewhat elaborate mathematical theory. I show here that such complexities are unnecessary, and that a simple geometric argument, in the spirit of Richards' paper, suffices to explain the phenomenon.

A proviso is necessary, however, since this argument only applies when the mechanism which positions new leaves meets a certain condition: loosely speaking, the influence of existing leaves in determining the position of a new leaf must be short-range. Experimental evidence suggests that this is so (in some plants at

least), but it is clearly important to know what happens otherwise. Here, simple geometrical reasoning does not suffice, and I have resorted to a computer model. I find that Fibonacci phyllotaxis persists under a wide range of conditions; an observation of some mathematical interest, whatever its botanical pertinence.

The Phenomena

Two types of phyllotaxis predominate in the plant world. One is the decussate pattern, where a pair of leaves springs from opposite sides of the stem at each level, and successive pairs are at right angles. The other, which is my concern here, is the spiral pattern, where there is a single leaf at each level of the stem, and successive leaves make a roughly constant angle, viewed along the plant axis. This spiral, which follows the leaves in the sequence in which they are created by the growing apex, is called the genetic spiral. Near to the apex, or in a bud, the leaves are often closely packed together, and the genetic spiral may be discerned as the shallowest descending spiral. In this situation, each leaf will generally be pressed against two leaves further down the stem, these being called its contacts. In looking at the arrangement of leaves, the eye will tend to follow the sequence of contacts from leaf to leaf, and so to trace out a spiral, of a steeper pitch than the genetic spiral, called a parastichy (Fig. 1). There are two contacts to each leaf, and therefore two sets of parastichies, wind-

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ing in opposite senses. If one counts the number of distinct parastichies in each set, it is generally the case that these numbers form two consecutive terms in the Fibonacci series (3). Thus, in a pine cone, one might find five parastichies in one direction and eight in the other; in sunflower heads the numbers may be far higher, for example, 89 and 144.

This observation may be expressed in another way. If we number the leaves in their genetic sequence, beginning at the apex (with the most recently formed leaf), then the contacts of a given leaf will be m and n further on in the sequence, m and n being the same Fibonacci terms we encounter in counting parastichies. The reason for this is that a parastichy passing through a given leaf is, by definition, the same as that through the appropriate contact. So, if we follow leaves in the genetic spiral counting parastichies, we return to the same parastichy after n leaves (or m , in the other set).

Not all plants have contacts, in the sense of closely adpressed leaves. In ferns, for example, leaf primordia near the apex are small regions widely separated from each other. Even here, though, we find something analogous to Fibonacci contacts; if we look at the nearest leaves, measuring between leaf-base centers, then these are m and n away in the genetic sequence, m and n being a Fibonacci pair. For example, in *Dryopteris dilatata* m and n are commonly 5 and 8, respectively. The analogy between nearest neighbors and contacts may be questioned. In plants with contacts, the leaves may be seen in cross section as rhomboid or crescent-shaped regions, often extending much further circumferentially than radially (Fig. 1). A contact therefore need not be a nearest neighbor in this section. Yet, if we trace each leaf back to its base—that is, its origin in the stem—we often find (4) that the bases form regions which more nearly approximate a circle (or a rhomboid, since the interface between leaves is flattened). Thus, contacts may be nearest neighbors on the stem surface, although a horizontal plane of section distorts this relationship.

Closely related to Fibonacci parastichies and contacts is the observation that the angle between successive leaves in the genetic spiral, the divergence angle, approximates closely to the so-called golden angle, defined by dividing the circumference of a circle in golden section (the ratio of the larger to the smaller sector equals the ratio of the whole perimeter to the larger sector), and having a value of about 137.5° . It is not

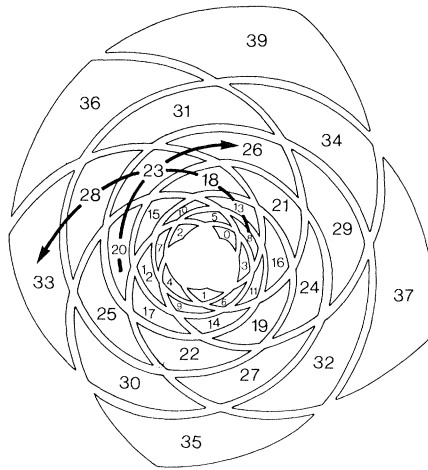


Fig. 1. An idealized plant apex, sectioned in a plane at right angles to the axis. Leaves are numbered from the center outward, following the genetic spiral. The two contacts of a leaf are recognized by their flattened interface. The eye follows parastichies such as the two marked with heavy arrows. There are three right-handed and five left-handed parastichies, so this is 3,5 phyllotaxis.

difficult to show that, if a plant has contacts m and n , then the divergence angle must lie between certain bounds, containing the golden angle, and that these bounds become rapidly narrower as the numbers m and n increase (5). For example, in a plant with contacts 5 and 8 the divergence lies in the range $136.8^\circ \pm 1.8^\circ$. This fact follows from the properties of a regular lattice.

The Changing Apex

The central question is, why do plants show these Fibonacci arrangements of leaves? It is not, as D'Arcy Thompson (6) believed, an inevitable property of a regular leaf arrangement, for it is perfectly possible to construct a lattice with any chosen contact numbers m and n , or any chosen divergence angle from 0° to 180° . The answer is to be found in the way a plant grows. The first true foliage leaves of a plant, after its seed leaves, often initiate a 180° opposite (distichous) or a decussate pattern (7), which eventually gives way to a spiral. This spiral goes through a sequence of increasing Fibonacci contacts; at the same time its divergence converges in an oscillating fashion toward the golden angle. To understand why these changes occur we must look to the plant apex. New leaves are added in succession in a region close to the apical tip; the "anneau initiale" of Buvat (8). It is here that the future patterns are established; a new leaf primordium appears between its contacts, positioned by a mechanism that is little under-

stood. During the growth of a plant from embryo to maturity its apical diameter increases (9). As a result, the pitch of the genetic spiral must decrease, and a new leaf come into contact with leaves further down the genetic spiral. This loose description can be made precise by means of a formal representation.

The Lattice of Leaves

Let us represent the leaf-bearing region of a plant as a cylinder with the leaves forming a lattice on its surface (Fig. 2). If this cylinder is cut along an axial generator we have a plane figure, a strip. The leaves are depicted as touching circles. The numbering I use is from the apex downward; L_0 being the most recently formed leaf primordium (leaf for short). Note that the numbering is changed every time a leaf is formed. I use L_0 as the origin for coordinates x, y . The distance along the x -axis measures the angular separation of leaves. Thus, if C is the width of the strip and x is the distance between two consecutive leaves, the divergence is $(x/C)360^\circ$. The y -axis corresponds to distance along the plant axis; in most plants the axial separation of leaves is not constant, but increases approximately exponentially down the stem. But, by a suitable transformation (for example, logarithmic) we can make the vertical distance between successive leaves a constant in the diagram. If the successive divergences are also constant, this means that the leaves form a regular lattice (the vector between L_n and L_{n+1} is parallel and of equal magnitude for all n).

This diagram is the most convenient traditional way of representing the leaf pattern (4). I shall use the terminology of contacts, these being represented by the two circles (leaves) that touch a given circle. In a plant without contacts these must be interpreted as nearest neighbors. I assume that leaf diameters remain constant, so that there is a fixed *contact circle* measuring the center-to-center distance of a leaf from its contacts as shown in Fig. 3a. I also assume that the lattice remains approximately regular. This will hold true if changes in the stem circumference occur slowly. More precisely, the lattice can be treated as regular over small distances. This suffices, since the ensuing argument only concerns leaves that lie close together in the genetic sequence.

Now consider the early growth of a seedling. Suppose the first foliage leaves form a distichous pattern. This means that each leaf lies on the opposite side of the stem from the preceding leaf, touch-

ing it at two points on either side of the vertical axis through its center. As the diameter of the apex increases the two sides of the preceding leaf L_1 will draw apart,

and eventually allow the new leaf L_0 to touch L_2 (Fig. 3c). When this first occurs L_0 can occupy one of two positions, on either side of the summit of L_2 , and will

then initiate a spiral. There is a breaking of symmetry here: the spiral may be left- or right-handed, a choice which appears to be random in plants. When L_0 touches L_1 and L_2 the first stage of Fibonacci phyllotaxis has been reached, since 1,2 is the first distinct pair of the series.

I next make the inductive hypothesis that we have consecutive Fibonacci contacts m and n , with $n > m$ and L_m and L_n on opposite sides of the y -axis (as are L_1 and L_2 in the initial spiral). As C increases, the pitch of the spiral must decrease. This may either be taken as obvious, or be deduced directly from the formula (5)

$$C = m|x_n| + n|x_m| \quad (1)$$

which shows that x_m and x_n must increase with C , hence y_m and y_n decrease.

Which is the next leaf to become a contact of L_0 ? By regularity of the lattice we can draw contact circles around L_m and L_n which no lattice point can enter (shaded region in Fig. 3a). The intersection of these circles is L_{m+n} , and it follows from this that the next lattice point to meet the contact circle of L_0 can only be L_{m+n} . Moreover x_{m+n} is opposite in sign to x_n , since $x_{m+n} = x_m + x_n$ and $|x_n| < |x_m|$; so L_{m+n} lies on the opposite side of the y -axis from L_n . The next contact pair is therefore $n, n+m$, and since $m+n$ is the next Fibonacci term, the inductive hypothesis is established. This proves the following.

Suppose that the leaves of a plant can be represented by a lattice of touching circles. Then Fibonacci phyllotaxis will be generated from the appropriate initial conditions given a gradually increasing circumference of the anneau initiale (or, more generally, an increasing ratio of circumference to leaf diameter). I shall refer to this as the contact circle argument. A specific example may help to illustrate the geometry (Fig. 3c).

The most delicate point of the argument is the transition from one pair of contacts to the next. Here the leaves L_0, L_m, L_n , and L_{m+n} will form the vertices of a 120° parallelogram (Fig. 3b). It is a property of the Fibonacci series that the ratios $m/n, n/(m+n)$ of consecutive terms tend to a limit, g , the golden ratio (5). From this it follows that the parallelogram is approximately repeated at every transition. This was remarked by Richards (1), who concluded that no greater accuracy of leaf positioning was required from one pair of contacts to the next, even though the divergence angle converges to the golden angle (10).

The stem diameter increases from one transition to the next by a factor of about 1.6 (11). Thus a fourfold increase in apical

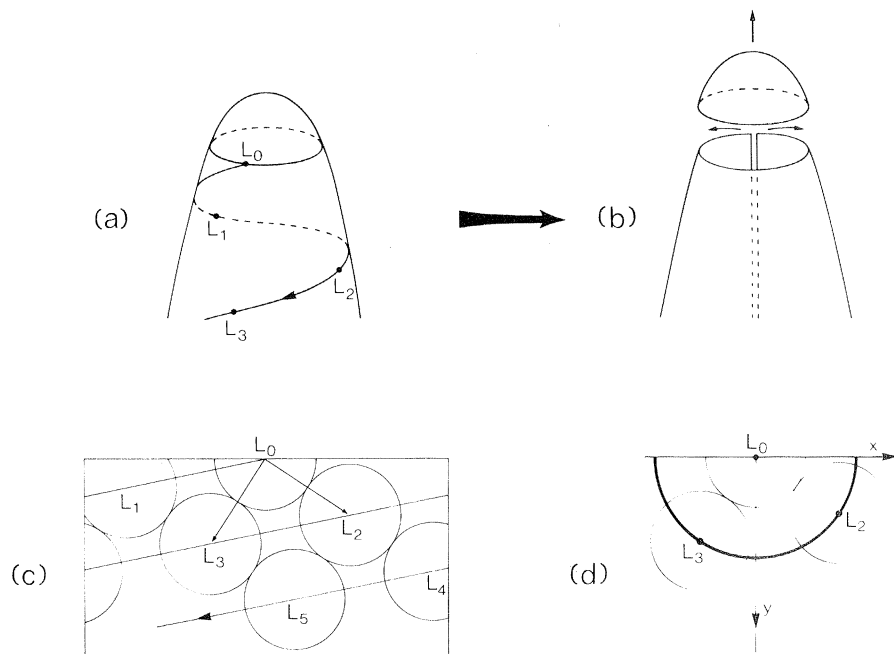


Fig. 2. An apex (a) is decapitated (b) at the anneau initiale, and opened up and laid out in a plane (c); a strip of constant width is made by a suitable transformation. The leaves are depicted as circles, although they would usually be flattened along common boundaries. The contact circle [heavy circle in (d)] is the locus of possible positions for the center of a contact.

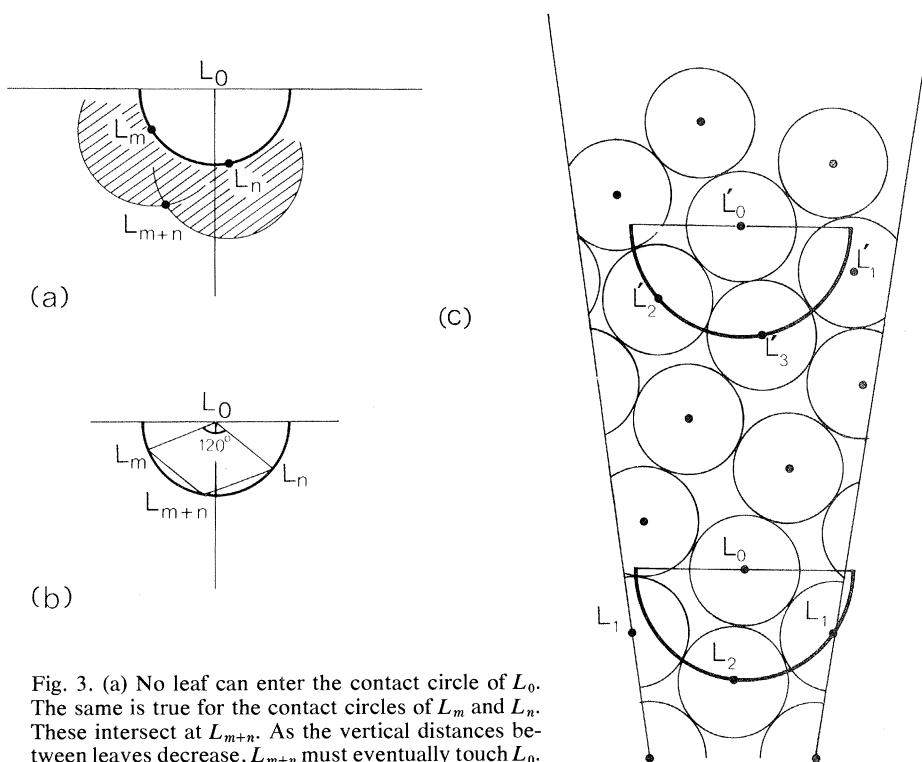


Fig. 3. (a) No leaf can enter the contact circle of L_0 . The same is true for the contact circles of L_m and L_n . These intersect at L_{m+n} . As the vertical distances between leaves decrease, L_{m+n} must eventually touch L_0 . (b) The geometry at the transition. When m and n are large, $m/n \cong g$, the golden ratio (5). The coordinates of L_m, L_n , and L_{m+n} are accordingly $(x_m, y_m), (x_n, y_n/g)$, and $(x_m + x_n, y_m/g^2)$, respectively. If the contact circle has a radius $R, x_m = -0.962R, y_m = 0.332R$, and $x_n = 0.791R$. (c) An expanding apex is represented as a strip of increasing width. Two transitions occur: distichy to 1,2, and 1,2 to 2,3 contacts (primed). Contact circles have been drawn at two leaves close to these transitions. Note that the lattice has small irregularities; a more rapid widening of the apex would increase these, eventually disrupting the pattern.

diameter would suffice for a transition from the initial 1,2 spiral to a 5,8 spiral. In cases where still higher numbers are found, like a sunflower head, the apex is well known to undergo dramatic size increases. A sunflower with contacts 89,144 would require a total 30-fold increase in apical diameter from embryo to capitulum.

So far I have assumed that the foliar spiral is regular, locally at least. Now, the Snows (12) showed that a fault in a lattice of touching circles is endlessly propagated. It might be argued, therefore, that an accumulation of inaccuracies, together with effects due to the expanding apex, would eventually disrupt the pattern. There are two reasons why this need not happen.

First, a smooth and slow increase of stem diameter does not of itself accumulate irregularities. It is the rate of expansion rather than the overall increase in apical diameter that matters (13). Thus Fig. 3c shows a correct sequence of transitions from distichy (180°) to 2,3 phyllotaxis in a succession of ten leaves; doubling the rate of increase of diameter will dislocate the pattern.

Second, there appear to be mechanisms that correct irregularities, as was shown by the Snows' experiments (12). They removed primordia in *Lupinus albus* and found that the ensuing disturbance in the leaf arrangement was rapidly dampened. This was brought about by a change in the size of a leafbase, which increased or decreased with the distance apart of its contacts. The pattern regulates because a larger than average divergence is "filled in" by a larger leaf base.

Of course, not all phyllotactic patterns achieve ideal regularity, and in some plants disruption of the pattern appears to be common (14). This may be due to an early rapid increase of the ratio of stem to leaf diameter.

It should also be mentioned that an "anomalous" spiral phyllotaxis is sometimes found. Here the contacts follow a series such as 1, 3, 4, 7, 11, 18, . . . , analogous to the Fibonacci series but with a different initial pair of terms. In such a case there will be a different limiting divergence; for example, 99.5° with the above series. Such anomalous phyllotaxis can be traced back to the initial leaf pattern. The transition from distichy to 1,2 phyllotaxis that I have previously described is perhaps the most common, but is certainly not the only possible sequence of events. Variants, such as decussate breaking into a spiral, easily account for the anomalous patterns.

The Positioning of Leaves

So far I have taken the touching-circle model of the leaves of a plant as a fait accompli. To see how far this representation is justified, we must consider how leaves are positioned at the plant apex.

There is abundant evidence that the position of a newly forming leaf is determined by the older leaves immediately below it. For example, before a new leaf has appeared, another leaf primordium, which would have become its contact or nearest neighbor, can be isolated by a cut (15, 16). When the new leaf develops it is displaced toward this cut, as though some influence from its contact had been blocked by the cut. This suggests some kind of spacing mechanism, although its nature is unknown.

Perhaps the most attractive proposal, whose consequences I shall explore, is an inhibitor mechanism, as suggested by Schoute (17). This assumes that the leaves and apical tip of a plant produce an inhibitor which prevents new leaves from forming in their proximity. I shall assume that this inhibitor diffuses or is transported away from its sources, and that a new leaf is formed at the first site to appear beneath the growing apex where the inhibitor concentration falls below a fixed threshold.

This has the merit of being the simplest theory which broadly accounts for the experimental observations. The principal rival to inhibition is Schwenender's contact pressure theory (18), recently revived by Adler (2), which assumes that a leaf is positioned by mechanical pressure

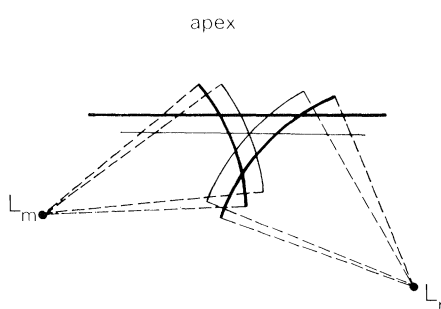


Fig. 4. The threshold is denoted by θ ; heavy lines are θ contours and light lines $\theta/3$ contours. As the apex grows its $\theta/3$ contour must eventually reach the intersection of the two $\theta/3$ contours of the leaves L_m and L_n . When this happens, as shown here, the inhibitor concentration at the triple intersection falls to threshold (assuming additivity). Since the inhibitor concentration is above threshold outside the triangle formed by the θ contours, it follows that the first threshold point must lie somewhere within this triangle. When the distance between θ and $\theta/3$ contours is small (the gradient is steep), this triangle is small and L_0 must therefore lie close to the intersection of the θ contours (or $\theta/3$ contours).

from its contacts. This is in many ways an unhappy hypothesis. It cannot apply to the many plants, including ferns, where the leaves are widely separated. And even in plants where the leaves are in contact, mechanical pressure cannot explain the initial siting of leaves, since a leaf must grow somewhat before it meets its neighbors. The appeal of contact pressure is solely that it leads directly to the geometry of touching circles. However, an inhibitor mechanism can be formally equivalent to contact pressure, as was appreciated by Richards and Schoute.

For suppose that the contours of inhibitor concentration can be represented by circles, and that the concentration gradient is steep near the threshold contour. Then the first subthreshold region to appear during growth will lie close to the intersection of the threshold contours of the two nearest leaves and the apex (Fig. 4). This means that the threshold contour, drawn around L_0 , plays the role of a contact circle. Thus the contact circle argument can be applied, and such an inhibitory mechanism will generate Fibonacci phyllotaxis.

More General Models of Inhibition

There are various ways in which an inhibitory mechanism may depart from the foregoing ideal. An exponential (or non-uniform) growth of the stem may distort the projection onto the cylinder diagram of a contour of inhibitor concentration. Or polar transport [as with indole auxins (19)] may flatten a contour on the stem surface against the direction of flow. There is, however, no difficulty in generalizing the contact circle argument to a large class of contour shapes—in fact, it can be applied whenever the threshold contour is a convex curve (and symmetric about the y-axis through its source). Convexity means that any line segment between two points on the curve lies within the curve, or equivalently, that the tangent to the curve rotates in a fixed sense as we follow the curve (examples are a circle and a parabola). This class of curve is adequately general. Any contour from a point source of inhibitor, with any combination of linear destruction kinetics, diffusion, and polar transport must be convex (20).

The contact circle argument must be modified as follows to deal with the general convex curve. Draw the inverted threshold contour T_0 around L_0 (Fig. 5) and suppose that L_m and L_n lie on T_0 . (This is equivalent to saying that L_0 lies at the intersection of threshold contours of L_m and L_n .) Draw the translated contours

Table 1. Computer simulation of an expanding apex. Here $A = 1.0$, which means that the inhibitor gradient due to a leaf falls sevenfold (to 15 percent of its original value) in the distance from a contact to L_0 . The pitch of the foliar spiral is taken to be $\phi = \tan^{-1}(y_i/x_i)$, or the angle measured on the plane diagram.

Stem radius	Pitch of foliar spiral	Divergence angle	Contacts
1.0	15.01°	138.9°	1,2
1.3	6.59°	139.7°	2,3
2.0	3.72°	138.3°	3,5
2.6	2.24°	137.1°	5,8
4.0	0.75°	137.8°	8,13
6.4	0.24°	137.6°	13,21

T_m and T_n around L_m and L_n , respectively; these meet at L_{m+n} . Now, convexity means that if L_{m+n} lies outside T_0 , then T_n cannot meet T_0 , moving in the direction of increasing x (to the right in Fig. 5). This is because the tangent $t_n(x)$ to T_n at a given x is rotated away from the tangent to T_0 , $t_0(x)$, since T_n is a copy of T_0 displaced to the right. Thus the two curves are carried apart by increasing x ; so this part of T_0 lies within T_n and cannot meet any other leaf. Similar reasoning shows that the left-hand part of T_m does not meet T_0 if L_{m+n} lies outside T_0 . It follows that L_{m+n} is the next leaf to meet T_0 , and therefore the next contact in the series.

It is also important to consider the effect on the pattern of varying the steepness of the inhibitor gradient emanating from a leaf (or the apex). Unless this gradient is very steep we have no assurance that the new leaf L_0 will lie close to the intersection of threshold contours of its contacts, as all the previous analysis has required. The most critical situation is the transition, where L_{m+n} is about to replace L_m as a contact. If L_{m+n} lies on the "wrong" side of the y -axis—that is, on the same side as L_n —then the Fibonacci sequence breaks down. The minimum steepness necessary to prevent this can easily be estimated in a tractable case.

Suppose the inhibitor spreads isotropically, following an exponential law, so the concentration at distance r from a leaf (regarded as a point source) is $K\exp(-Ar)$, where K and A are positive constants. Suppose also that contributions from several sources can be summed. These are reasonable assumptions for an inhibitory gradient due to diffusion and linear destruction kinetics (21). The distance r is taken to be the (flat) distance on the cylinder diagram; this will be an acceptable approximation to the shortest distance in three dimensions if the stem diameter is large enough (or equivalently, m and n are large enough).

At the transition, suppose that only the

apex, L_m , L_n , and L_{m+n} contribute appreciably to determining the site of the new leaf L_0 . We require that L_0 lie at a minimum of the inhibitor landscape, at the threshold concentration; that is, L_0 is the first admissible site for a new leaf. This can be written formally as

$$I = \theta \quad (2)$$

$$\partial I / \partial y = 0 \quad (3)$$

$$\partial I / \partial x = 0 \quad (4)$$

where

$$I = \sum_{i=1}^4 K \exp(-Ar_i)$$

is the total inhibitor concentration at a point, with the sum taken over the four pertinent sources of inhibitor, and r_i is the distance from each. Here θ denotes the threshold and x , y are the usual coordinates.

Now, if m and n are large, $m/n \cong g$, the golden ratio (5). The coordinates of L_m , L_n , and L_{m+n} can therefore be written as (x_m, y_m) , $(x_n, y_n/g)$, and $(x_m + x_n, y_m/g^2)$, respectively. If these three leaves lie exactly on the contact circle about L_0 , normalized to have unit radius, the geometry dictates that $x_m \cong -0.962$, $x_n \cong 0.791$, and $y_m \cong 0.332$ (Fig. 3b). Choosing unit radius also specifies the ratio θ/K , and Eqs. 2 and 3 yield $\theta/K \cong 4.977$ (on eliminating r_4 , the distance from the apex to L_0). Now look for solutions of Eqs. 2 to 4 close to the contact circle conformation. Put

$$x_m = -0.962 + \epsilon$$

$$x_n = 0.791 + \eta$$

and calculate ϵ and η when y_m takes the preceding value, 0.332. Ignoring higher powers of ϵ and η , and using the approximations $\exp(A\epsilon) = (1 + A\epsilon)$ and so on, Eqs. 2 to 4 become

$$(0.644A - 1.356)\eta - (1.125 - 0.876A)\epsilon + 0.270 = 0 \quad (5)$$

$$(0.350 + 1.006A)\eta - (0.483 + 1.544A)\epsilon = 0 \quad (6)$$

Or, even more approximately, when A is large

$$\epsilon = -0.144/A; \eta = -0.222/A \quad (7)$$

These last equations give support to the intuition that the leaf L_n must shift toward L_0 (and L_m away from L_0) to balance circumferential components of inhibition at L_0 . The important point is that L_{m+n} does not stray across the y -axis through L_0 as A decreases; in fact, it is displaced in the opposite direction. This remains true, using the more exact values from Eqs. 5 and

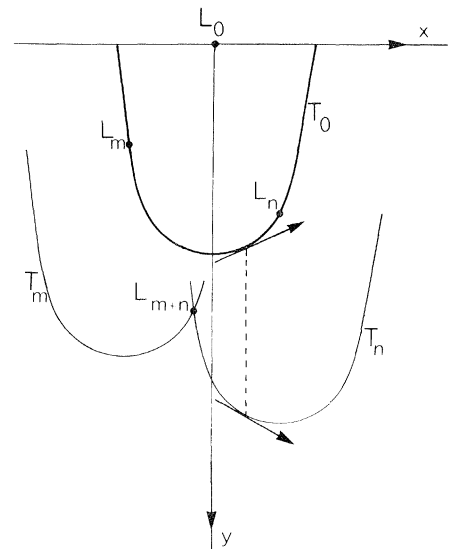


Fig. 5. It is convenient to draw an inverted θ contour round L_0 , with L_m and L_n lying on it, rather than putting L_0 at the intersection of the θ contours belonging to these leaves. Here T_0 denotes the (inverted) θ contour around L_0 , and T_m , T_n those around L_m and L_n , respectively. Tangents to T_0 and T_n are shown at a particular x (dotted line).

6, until A falls to about 4. Here the assumptions become invalid, for other leaves, such as L_{n-m} , make an appreciable inhibitor contribution (> 10 percent) at L_0 . This value of A corresponds to a gradient which falls about 50- to 100-fold from L_m or L_n to L_0 .

Experimental evidence suggests that leaves other than the contacts do not influence the position of L_0 . Thus, in Wardlaw's experiments on fern apices (16), the isolation of a primordium only influenced the position of the two subsequent leaves for which the isolated primordium would have been a contact. But a small effect on other leaves can not be ruled out, and it is reasonable to ask what happens when inhibitor gradients are shallow. Analytical treatment becomes difficult when many sources have to be taken into account. Accordingly, I have simulated a growing apex on a computer (22).

As before, I assume a regular lattice, and require that Eqs. 2 to 4 hold. But now the sum $I = \sum K \exp(-Ar_i)$ is taken over all leaves L_i , $i \geq 1$. The stem is represented by a solid cylinder, while the distance r is now the shortest distance in space (this being perhaps a more realistic measure when the stem diameter is small). Beginning with 1,2 contacts, the stem diameter is increased in small steps, with the parameters of the lattice being adjusted at each step so as to satisfy Eqs. 2 to 4 (23).

I find that Fibonacci phyllotaxis is generated for all values of A tested, even when the gradient falls twofold or less from a contact to L_0 . The correct se-

quence of contacts occurs, with a consequent convergence to golden angle divergence (24), while the pitch of the foliar spiral decreases smoothly (Table 1). This conclusion appears to be robust; for example, a different choice of diffusion function, such as $K \exp(-Ar)/r$, yields very similar results.

Summary

The principal conclusion is that Fibonacci phyllotaxis follows as a mathematical necessity from the combination of an expanding apex and a suitable spacing mechanism for positioning new leaves. I have considered an inhibitory spacing mechanism at some length, as it is a plausible candidate. However, the same treatment would apply equally well to depletion of, or competition for, a compound by developing leaves, and could no doubt accommodate other ingredients.

The mathematical principles involved are clear when it is assumed that only two leaves (the contacts) position a new leaf. There is some experimental evidence for this assumption. Nonetheless, it is not a precondition for Fibonacci phyllotaxis, since a computer model shows that this pattern is generated even when many leaves contribute to inhibition at a given point. Indeed, the Fibonacci pattern seems to be a robust and stable mathematical phenomenon, a finding which goes some way to explaining its widespread occurrence throughout the plant kingdom.

References and Notes

1. F. J. Richards, *Symp. Soc. Exp. Biol.* **2**, 217 (1948).
2. I. Adler, *J. Theor. Biol.* **45**, 1 (1974).
3. A. H. Church, *On the Relation of Phyllotaxis to Mechanical Laws* (London, 1904).
4. G. Van Iterson, *Studien über Blattstellungen* (Jena, 1907). F. J. Richards [*Philos. Trans. R. Soc. London Ser. B* **235**, 509 (1951)] shows how contacts may change with leaf shape. I assume contacts are nearest neighbors on the stem surface; my arguments are easily modified for other leaf geometries.
5. I note first some properties of the Fibonacci series. If F_n is the n th term of the series, then the ratio F_n/F_{n+1} tends to a limit g given by $1 + g = 1/g$; that is, $g = (\sqrt{5} - 1)/2$. This is the golden ratio, considered by the Greeks to define the ideal proportions of a rectangle. The golden angle ϕ is defined by $\phi/(2\pi - \phi) = (2\pi - \phi)/2\pi$; the ratio of these sectors is in fact the golden ratio (hence the name), and $g = \phi/(2\pi - \phi)$ implies $\phi = 2\pi(1 - g) = 2\pi g^2$ radians or 137.5° , approximately. The connection between contacts and the golden angle is proved by using the lattice of leaves, with coordinates relative to L_0 ; x measuring the circumference of the cylinder. It is convenient to use a more general concept than that of a contact: A point of close return (2) (abbreviated to POCR) is a leaf L_n which comes nearer to L_0 circumferentially than any preceding leaf; that is, $|x_p| > |x_n|$ for all $p < n$. A contact is a POCR. Suppose now that $m < n$ are successive Fibonacci terms, and L_m, L_n are POCR's on opposite sides of the y -axis (with $x_n > 0$, say). Then L_{n-m} is a POCR. The proof is simple. If $|x_n| < |x_{n-m}|$ with $p < n - m$, and if $x_p > 0$, look at L_{n-m-p} .

$x_p > x_n$ since L_n is a POCR, so $0 < x_{n-m-p} = x_n - x_m - x_p < -x_m$ (which is impossible since L_m is a POCR). If $x_p < 0$, look at L_{m-p} . In both cases there is a contradiction, so there can be no such x_p . This can be applied inductively to show that all leaves numbered $n, m, n - m, 2m - n, \dots, 2, 1$ —that is, the whole Fibonacci series from n back—are POCR's. Now let $D = |x_n|$, the circumferential distance between adjacent leaves of the genetic spiral. Let $C =$ stem circumference, so that the divergence angle $d = 2\pi D/C$. Clearly $C = 2|x_n| + |x_m|$. From this beginning, induction on successive terms of the Fibonacci series shows that

$$C = m|x_n| + n|x_m| \quad (8)$$

At each inductive step the property of being a POCR ensured that $|x_{n+m}| = |x_n| - |x_m|$, since the signs must alternate. Similarly, induction shows that

$$D = (n - m)|x_n| + (2m - n)|x_m| \quad (9)$$

Since $0 \leq |x_n| \leq |x_m|$ the ratio D/C is bounded by $(n - m)/n$ for $x_n = 0$ and $m/(m + n)$ for $|x_n| = |x_m|$. These are successive convergents of the series, which tend to the limit g^2 ; therefore $d = 2\pi D/C$ is bounded by ever narrower limits around the golden angle $2\pi g^2$. The first few bounds beginning with $n = 1$ are $180^\circ, 120^\circ, 144^\circ, 135^\circ, 138.5^\circ, \dots$. This means, for instance, that with 2,3 POCR's $10^\circ \leq d \leq 144^\circ$.

6. D. W. Thompson, *On Growth and Form* (Cambridge Univ. Press, London, 1942).
7. The Right Hon. Lubbock (Bart), *The Growth of Seedlings* (London, 1896).
8. R. Buvat, *Ann. Biol.* **31**, 595 (1955).
9. F. A. L. Clowes, *Apical Meristems* (Blackwell, Oxford, 1961).
10. When the POCR's L_m, L_n are circular contacts the bounds on the divergence angle for a given m, n are narrower than the previously calculated extrema of $d = 2\pi D/C$ (5). This is because the ratio $|x_n/x_m|$ does not cover the whole range 0 to 1. The maximum occurs at the transition to $n, m + n$ contacts. From Fig. 4b

$$x_m^2 + (my_1)^2 = x_n^2 + (ny_1)^2 = (x_n + x_m)^2 + [(m + n)y_1]^2 \quad (10)$$

which gives $|x_n/x_m| = (n + 2m)/(m + 2n)$. Using this ratio in the formula for D/C gives the bounds on the divergence. The first few are now $180^\circ, 128.5^\circ, 142.1^\circ, 135.9^\circ, 138.1^\circ, \dots$. Thus with 2,3 contacts $128.5^\circ \leq d \leq 142.1^\circ$.

11. The ratio of C from one mode to the next follows from Eqs. 8 and 10. For example, if $C_2 = C$ at the transition to a 1,2 spiral, and $C_3 = C$ when 2,3 begins, then $C_3/C_2 = 1.53$. The next ratio is $C_4/C_3 = 1.65$. These rapidly tend to the limit $1/g = 1.618$.
12. M. Snow and R. Snow, *Philos. Trans. R. Soc. Lond. Ser. B* **244**, 483 (1962).
13. Consider the case of 1,2 contacts. Suppose that the leaf lattice was initially regular at leaf N and has subsequently been subjected to a slow, linear increase in stem circumference. If c_n denotes the circumference at L_n , this latter assumption implies that $\delta = (c_{n-1} - c_n)$ is a small constant. Let d_n and h_n denote the divergence angle and vertical separation, respectively, between L_{n+1} and L_n . If R denotes the radius of the contact circle, the geometry of contacts implies

$$(c_n - d_n - d_{n-1})^2 + (h_n + h_{n-1})^2 = R^2$$

$$h_n^2 + d_n^2 = R^2$$

Suppose $(d_{n-1} - d_n)$ and $(h_{n-1} - h_n)$ are small, so that their quadratic and higher-order terms can be ignored. Then

$$d_n + d_{n-1} = c_n/2 + 3R^2/2c_n$$

From this difference equation

$$(d_{n-1} - d_n) = \delta[1/4 - 3R^2/4c_n^2 + (-1)^n(1/4 - 3R^2/4c_n^2)]$$

This approximate solution is valid when δ is small. It shows that the irregularity of the lattice, measured by $(d_{n-1} - d_n)$, can be made as small as desired by making δ sufficiently small. Higher-order contacts are treated similarly.

14. P. H. Helliendoorn and A. Lindenmayer, *Acta Bot. Neerl.* **23**, 473 (1975).
15. M. Snow and R. Snow, *Philos. Trans. R. Soc. Lond. Ser. B* **221**, 1 (1931).
16. C. W. Wardlaw, *Growth (Suppl.)* **13**, 93 (1949).
17. J. C. Schoute, *Recl. Trav. Bot. Neerl.* **10**, 153 (1913).
18. S. Schwenender, *Mechanische Theorie der Blattstellungen* (Leipzig, 1878).

19. W. W. Schwabe, *Symp. Soc. Exp. Biol.* **25**, 319 (1971).
20. The equation for combined diffusion, axial polar transport (in the y -direction), and linear destruction kinetics of the inhibitor is

$$D\nabla^2 I + P\partial I/\partial y - KI = \partial I/\partial t$$

where D is the diffusion constant, P the transport rate, and K the first-order rate constant. This being a linear equation, the effect of two or more sources at a point will simply be the sum of their individual contributions. Now, the time between successive leaves appearing is typically about 1 day, while the distance between L_0 and its contacts is typically about 1 mm. It may therefore be assumed that equilibrium conditions are reached; that is $\partial I/\partial t = 0$ [F. H. C. Crick, *Nature (London)* **225**, 420 (1970)]. The solution of $\partial I/\partial t = 0$ for a point source in an infinite three-dimensional volume is

$$I(r) = A \exp(-\alpha r - \beta y)/r$$

where A measures the source strength, $\beta = P/2D$, $\alpha^2 = P^2/4D^2 + K/D$, and r is the distance from the source. Note that $\alpha^2 \geq \beta^2$ if $K \geq 0$. Ignoring effects of curvature of the stem surface, the same solution holds for the semi-infinite volume bounded by the stem surface, with a leaf treated as a source on its surface. The contour T is the curve $I = \text{constant}$ (see text). Expressing this as a function $x = f(y)$ (coordinates about L_0 as in Fig. 3) and differentiating gives $f' = -(y + \beta r^2)/(1 + \alpha r) \leq 0$ and $f'' = (r^2/y)(\beta^2 - 3\alpha^2) - (\text{further positive terms}) \leq 0$ since $\alpha^2 \geq \beta^2$. Now $f' \leq 0$, $f'' \leq 0$ implies that f is convex. Note that a logarithmic transform of this curve leaves it convex, since $\log(f)' = f'/f \leq 0$, and $\log(f)'' = f''/f - (f')^2/f^2 \leq 0$. Thus exponential growth of the stem still gives a convex contour after transforming to make a regular lattice.

21. With isotropic diffusion through the whole plant body, and ignoring curvature of the stem, the equilibrium distribution of inhibitor is $I(r) = K \exp(-Ar)/r$ (20). If diffusion takes place predominantly through surface layers and can be treated as planar, then $I(r) \cong K_0(Ar)$ is appropriate. In either case, when Ar is large and r remains near the contact circle, $K \exp(-Ar)$ is a good approximation.
22. The computer simulations in (14) are similar to those I describe. However, they were aimed at reproducing the characteristic patterns in *Bryophyllum tubiflorum*, where spiral phyllotaxis is commonly disrupted, occurring as an intermediate stage between decussate and tricusate phyllotaxis.
23. A Modular One computer (Computer Technology Ltd.) was used. With the initial radius of the stem taken as 1, and choosing values of A and y_1 , the computer searches for values of the divergence d which satisfy Eq. 4 together with the condition for a minimum, $\partial^2 I/\partial x^2 > 0$. When y_1 is large enough (≥ 0.1) there is only one solution, with 1,2 contacts. [When y_1 is smaller, there may be many solutions (24)]. Next, θ/K is calculated from Eqs. 2 and 3, which give

$$\theta/K = \sum_{i=1}^3 \exp(-Ar_i)(y_i/r_i + 1) \quad (11)$$

the sum being taken over L_m, L_n , and L_{m+n} . Differentiating Eqs. 4 and 11 allows δy_1 and δd to be calculated for an increase δC in the stem circumference. In this way a path is traced through the (y_1, d) -plane as C increases, which approximates at every point to a solution of Eqs. 4 and 11. The accuracy of this approximation is checked by showing (i) that convergence is achieved through reducing step size, and (ii) that Eqs. 4 and 11 are satisfied to sufficient accuracy after every few steps along the path.

24. J. H. M. Thornley, *Ann. Bot.* **39**, 491 (1975). Thornley's computer calculations show that certain divergence angles allow the origin to be a minimum for a sum of exponential gradients, similar to the function I have used. These divergence angles include approximations to the golden angle, even for very flat gradients. I find similar ranges of admissible divergences; for example, with $A = 1.0$ and $y_1 = 0.02$, d can take the values $\dots, 78.1^\circ, 82.1^\circ, 99.7^\circ, 106.2^\circ, 108.2^\circ, 109.1^\circ, 132.8^\circ, 137.8^\circ, 150.8^\circ, 157.7^\circ, 162.0^\circ, \dots$ and so on. Of these, only 137.8° is actually generated by an expanding apex. Thornley did not analyze the effect of apical growth.
25. I thank A. T. Winfree for awakening my interest in phyllotaxis and for a critical reading of the manuscript; F. H. C. Crick and W. W. Schwabe for helpful comments; and J. White for generous assistance with computing.

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References and Notes

⁴ **Phyllotaxis: Its Quantitative Expression and Relation to Growth in the Apex**

F. J. Richards

Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, Vol. 235, No. 629. (Oct. 25, 1951), pp. 509-564.

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