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

F. J. Richards

Phil. Trans. R. Soc. Lond. B 1951 **235**, 509-564
doi: 10.1098/rstb.1951.0007

PHYLLOTAXIS: ITS QUANTITATIVE EXPRESSION AND RELATION TO GROWTH IN THE APEX

By F. J. RICHARDS
Research Institute of Plant Physiology, Imperial College of Science and Technology, London, S.W. 7

(*Communicated by F. G. Gregory, F.R.S.—Received* 14 *December* 1950)

CONTENTS

PART I

PART II

Current methods of classifying the phyllotaxis patterns found at stem apices are discussed, and it is concluded that the numerical measures employed do not characterize solely the arrangement or positioning of the primordia, but are partially determined also by primordial shape. A method of phyllotaxis assessment is proposed that is free from this ambiguity. For a complete description three parameters are necessary, namely, the angle of the cone tangential to the apex in the region under consideration, the divergence angle, and the plastochrone ratio, i.e. the ratio of the radial distances of two successive primordia from the central axis. For assessment of the transverse component of the system the two last parameters are alone required.

Of these three characteristics the plastochrone ratio is the most useful, and from it a 'phyllotaxis index' may be calculated that immediately conveys the most essential information relating to the primordial arrangement. Since this index is a continuously varying function, phyllotaxis assessment is no longer confined to a few discrete recognized systems, and it becomes possible to compare quantitatively with one another phyllotaxis arrangements of very diverse kinds. The relationship between the index and primordial pattern is presented for all important divergence angles, and also for those systems wherein more than one leaf appears at each node.

The phyllotaxis index is rigidly related to the ratio of the transverse components of two areas, that of the central apex and that of the newly initiated primordium; a simple extension enables a similar relationship to be determined on the actual apical surface, opening the way for a practical adaptation of the older theoretical concept of 'bulk ratio'.

Plastochrone ratio, moreover, is essentially a growth measurement, and in conjunction with the plastochrone period may be used to determine the radial growth rate of the apex; in favourable circumstances it provides all the necessary quantitative information to determine the rate of volume increase.

The practical application of these principles is fully considered, the methods being illustrated from measurements made on drawings of apical systems to be found in phyllotaxis literature. Tables are appended to facilitate the calculations involved when using the methods described.

PART I

1. The problem outlined

Assessment of phyllotaxis is a geometrical problem, and particularly so when it is concerned with the simple regular repetitive pattern of the primordia clustered round an apex. Like a crystal lattice, all such patterns lend themselves to definition in terms of a few numerical constants, and the attempt has long been made to define in this way the phyllotaxis systems found in growing plants. In the classical method of Schimper and Braun only one constant was considered, the so-called *divergence*. On an axis having single leaves at the nodes the divergence was defined as that fraction of the circumference which separates two successive leaves in a tangential direction; longitudinal separation along the axis was disregarded. In practice, by following the genetic spiral through the consecutive leaf-bases round a more or less elongated stem, two leaves were sought, such that the upper was superposed precisely over the lower; if the genetic spiral made t revolutions between the insertions of these two leaves, separated by n internodes, the divergence was evidently t/n. Extensive observations of this kind led to the belief that much the most frequent divergences are those that fall into the series $\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$, ..., in which either the numerators or the denominators of the fractions, considered alone, are the successive members of the well-known Fibonacci series.

An obvious practical objection to the method is the difficulty of determining whether any particular leaf is in fact exactly superposed by some other one; and even assuming that one such exists it is frequently impossible to decide which leaf fulfils this condition. In spiral phyllotaxis the few rational divergence angles solely recognized by Schimper and Braun fail completely to describe the true conditions at the plant apex, and presumably this is true also of elongated organs. They exist only where orthostichy lines can be found, i.e. where series of leaves or primordia occur alined along the axis of the stem instead of spiralling more or less steeply round it, and in spiral phyllotaxis no true orthostichies appear. Classification by divergence fails therefore because it is based on, and is entirely dependent upon, an incorrect assumption, namely, the presence of orthostichy lines. Moreover, it will readily be seen that even if orthostichy lines did exist at apices generally, divergences would supply only very incomplete information about the positions of the primordia there, i.e. the phyllotaxis, for this depends quite as much on radial as on tangential spacing.

For reasons such as these the estimation of divergence angles as a means of characterization was rejected completely by Church (1904). Instead, he pointed out that at the apex itself, so long as growth is uniform and the primordia arise along the genetic spiral at a constant angle, then a whole series of logarithmic spirals may be drawn connecting them. Two intersecting sets of these spirals, the *contact parastichies*, are usually conspicuous to the eye, owing to the fact that each primordium touches certain others; because of these contacts the eye tends to select these particular sets and to ignore the other spirals which traverse primordia not in contact with one another. Nevertheless, the inconspicuous curves have just as much, or just as little, objective reality as the conspicuous contact parastichies, which are simply a particular pair of sets from among the whole family of logarithmic spirals. These curves then are all *parastichies*.

The numbers of *contact* parastichies can readily be counted in a transverse section of an apex, and typically give an adjoining pair of numbers from the Fibonacci series, e.g. five curves running round the apex in one direction may intersect eight others spiralling in the opposite direction. Such arrangements Church classified by these numbers of intersecting contact parastichies; the example just given would be designated $(5+8)$, the numbers being connected by a plus sign and bracketed together.

Church claimed for this method of expressing phyllotaxis great advantages over that based on the idea of divergence, and, indeed, that it *completely defines* the transverse component of the ordered arrangement at the apex. It has been adopted by many subsequent workers, and apparently accepted as an adequate definition of the system, though sometimes the mean divergence angle also is appended. Nevertheless, the numbers of contact parastichies define the pattern completely only if Church's phyllotaxis theory holds, and if his particular method of constructing theoretical diagrams really reproduces the divergence angles associated in plants with the various systems. According to Church's theory, in the region of initiation one set of contact parastichies always intersects the other *orthogonally*, and each system, e.g. $(2+3)$, $(3+5)$, $(4+7)$, etc., conforms with a definite divergence angle peculiar to itself. Assuming the correctness of these assumptions, the numbers of orthogonal parastichies in both directions do indeed provide sufficient data from which to reconstruct the plan of the apex, i.e. the 'points of insertion' of the centres of all primordia. Moreover, for each such system may be calculated a numerical constant which expresses the size of a primordium relative to that of the meristem on which it arises. For this purpose Church used a purely conventional measure, the *bulk ratio*, based on the assumption that each primordium is circular (or '*quasi*-circular') in section and is in contact with each of its four nearest neighbours; bulk-ratio was defined as the sine of half the angle subtended by the approximately circular primordium at the apical centre (cf. figure 1*a*, primordia 11, 16, 19, 24). Every phyllotaxis system $(a+b)$ then is associated with a definite and calculable, though entirely conventional, bulk-ratio.

There is no evidence, however, that either of Church's postulates holds generally in apices; no support has been forthcoming for the thesis of universal orthogonal intersection, while the presentation by various workers of measurements of divergence angle together with contact parastichy numbers disposes of his second assumption. It follows that Church's description, far from defining completely the geometrical pattern at the apex, as he thought, provides little more information than that explicitly stated, viz. the numbers of contact parastichies. Discarding the principle of orthogonality involves also abandoning the relationship between contact parastichy numbers and the important measure bulk-ratio. Nothing can now be posited about radial spacing, though for any given pair of contact parastichy numbers limits may be set to the possible magnitude of the divergence angle; thus a modicum of extra information remains relative to tangential spacing. The purpose of Church's mode of approach to the problem fails then almost in its entirety, and for a very similar reason to that which invalidates the approach through divergences: it is grounded in an incorrect theory.

Since the usefulness of the method depends entirely on his theoretical assumptions, and these latter have not been accepted by other botanists, it is perhaps surprising that the method itself should have been adopted. Undoubtedly much of the reason for this is to be

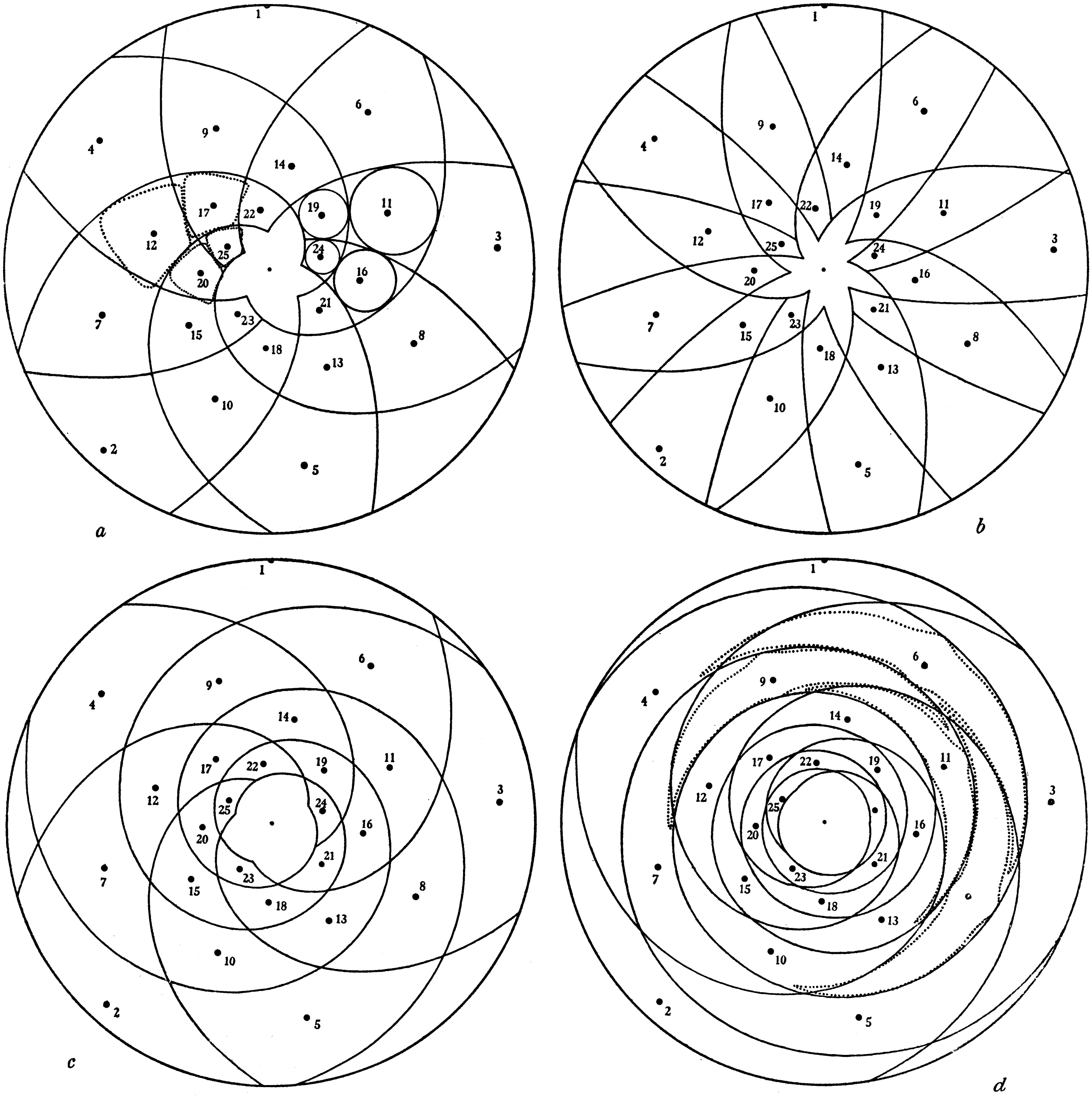

Figure 1, *a*–*d*. Ideal representation of the transverse components of four regular Fibonacci phyllotaxis arrangements in all of which the 5-parastichies intersect the 8-parastichies orthogonally. In terms of contact parastichies these arrangements are as follows: *a*, (5 + 8); *b*, (8 + 13); *c*, (3 + 5); and *d*, (2 + 3). Divergence = Fibonacci angle; plastochrone ratio = 1·07296.

found in its simplicity, and the ease with which an apex may be characterized in its terms. A further possible reason is the stress laid on primordial contacts, a theme which has been the corner-stone in the theories of several writers since the days of Schwendener.

Other writers on the geometry of phyllotaxis (e.g. Schwendener 1878; Van Iterson 1907; Schoute 1913) have of course recognized the importance to the pattern of bulk-ratio, or of some more or less equivalent measure, but those applied to and utilized in their theoretical constructions are again usually selected in accordance with the particular phyllotaxis theory proposed; they have not been adopted by other workers (and, indeed, could not well be adopted) in the purely practical problem of defining or of estimating the constants of the patterns actually found at plant apices—and yet estimation of this kind is the primary interest in any comparative study of meristems. Clearly for these purposes *measures are needed whose validity and usefulness do not depend on the assumptions of some particular phyllotaxis theory*; measures must be sought which are applicable to all, or the great majority, of apices, and which are equally valid regardless of the shapes of the primordia, and regardless also of whether or not those primordia are in contact one with another. Because of variability in these latter respects, direct comparisons, as between species, of the relative linear dimensions of primordia and the meristems bearing them are out of the question. The measurements adopted then must be of such a nature that they may be determined on actual apices, yet, nevertheless, should convey essential information relative to the apices themselves comparable with that given for purely formal theoretical schemes by bulk-ratio and similar concepts. As will be shown, these requirements are met quite simply by applying a geometrical analysis to the system of points marking the positions of the primordial centres (e.g. vascular strands), using polar co-ordinates in the manner suggested previously by the writer (Richards 1948).

A new theory

Before proceeding with the proposed solution it is perhaps necessary to refer to a recent theory of phyllotaxis due to Plantefol (1948), which has received favourable comment in some quarters (Philipson 1949). Plantefol places the entire emphasis in phyllotaxis on one only of the two sets of contact parastichies considered by Church. 'Leaf-generating centres' equal in number to these particular parastichies wind round the apex all in the same direction, and along the course of each arises a succession of leaf primordia; within the apex an organizer maintains uniformity between the activities of these generating centres. Hence on the shoot the leaf units come to lie along parallel 'foliar helices', one of which corresponds to each generating centre. The phyllotaxis of any shoot is characterized simply by the number of foliar helices.

Some defects in the theory have been pointed out by Snow (1948, 1949), and its inadequacy to define phyllotaxis systems on apices should be apparent, for if enumeration of two sets of intersecting parastichies fails to define the system without ambiguity it is evident that one set alone must fail to do so. In Church's theory the intersection points of the two sets of curves locate the leaf centres; in Plantefol's no indication is given as to these locations.

One of the striking facts of phyllotaxis is that in most spiral systems the mean divergence along the genetic spiral approximates closely to the Fibonacci angle; in other words, the series of leaves obtained by selecting, for instance, every thirteenth along the genetic spiral (where thirteen is a particular number taken from the higher terms of the Fibonacci series) will approach, though not in general precisely realize, the condition described as orthostichous, i.e. the fourteenth leaf will be nearly superposed longitudinally over the first. Plantefol stresses not only that the genetic spiral is an abstraction, a conclusion with which few would now disagree, but, much more debatably, accords it no part in practical discussions of phyllotaxis. Even if his theory be accepted, however, the simple facts of divergence, with the accompanying approximate leaf superpositions, cannot be disregarded altogether. In terms of this theory consideration of 'divergence' along the foliar helices should therefore replace that of divergence along the genetic spiral. Thus, where three foliar helices are recognized, in the large majority of spiral systems (cf. Plantefol 1948, figure 5) the selection of every seventh leaf along each helix will give a line which is nearly orthostichous, i.e. the mean 'divergence' along any one helix is about 52 to 53°; but where there are only two helices (cf. Plantefol 1948, figure 25) it is no longer every seventh, but every fourth or every seventeenth leaf which usually falls on a line nearly parallel with the axis, and there is a mean 'divergence' along each helix of roughly 85°. And so on with other numbers of foliar helices; the introduction of each new curve into an apical system radically alters the 'divergence' along those already in existence, although the divergence proper along the genetic spiral remains substantially unchanged. The concept of divergence cannot then be evaded by the introduction of foliar helices; it is, however, rendered much more abstruse. Before the views advanced can properly be regarded as constituting a theory of *phyllotaxis* it is just as necessary to explain the 'divergences' found along these helices, and their peculiar behaviour when phyllotaxis changes, as it is to account for the Fibonacci angle along the genetic spiral by any other approach. It is clearly insufficient to ascribe these phenomena to an apical 'organizer', with no indication of how the result may be brought about. Unless an explanation is forthcoming there must remain very strong reasons for regarding those parastichies now called 'foliar helices' as less likely even than the genetic spiral itself to indicate the course taken within the apex by certain fundamental entities responsible for leaf production. Valuable as Plantefol's observations may be in the study of the relations between leaf and stem, his views then do not elucidate the problem of leaf arrangement.

2. The primary solution

The kind of geometrical system that needs to be defined, and the inadequacy of the methods of classification in current use, may be illustrated from figure 1. In the four diagrams shown there the numbered points may be taken as representing the centres of primordia. In each figure they are inserted consecutively round the centre of the system at a constant divergence of approximately 137·5° (the Fibonacci angle), and radially at distances from the centre in geometrical progression, the ratio of the progression, working outwards, being 1·07296. Such a ratio between the transverse distance of a primordium from the centre relative to that of the next primordium to be produced has been termed (Richards 1948) a *plastochrone ratio*,* for in a uniform system it is the measure of the radial

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* As stated in the earlier communication, Van Iterson (1907) used the reciprocal of the plastochrone ratio in his constructions for plane systems of touching circles. Richards (1948), however, also stated that this particular constant used by Van Iterson was termed the 'relative radius'; this is incorrect. The term was applied to the 'factor *b*' in his constructions, whereas it is his 'factor *a*' which is the reciprocal of the plastochrone ratio.

expansion of the apex at this level during one plastochrone. Since it fixes the radial spacing of the primordia it is likewise a measure equivalent to the bulk-ratio of Church (as will be fully discussed in part II of this paper), but has two great advantages: it may be estimated from actual apices, being independent of the shapes of the primordia, and it provides information which is equally applicable whatever theory of phyllotaxis may ultimately be accepted. As pointed out in the previous communication, when the factors affecting phyllotaxis are constant the natural logarithm of the plastochrone ratio divided by the plastochrone period gives the *radial relative growth rate* of the apex in the region of initiation; hence for any given divergence angle the arrangement of the primordia, i.e. the phyllotaxis, may be regarded as a resultant of the relative velocities of two growth processes, rate of expansion of the apex and rate of production of primordia.

The actual plastochrone ratio used in all the four diagrams of figure 1, when combined with a divergence angle equal to the Fibonacci angle, results in exactly orthogonal intersection of those parastichies drawn through primordia differing in age by five and eight plastochrones respectively. Logarithmic spirals representing these parastichies have been drawn in figure 1*a*, but between the points instead of through them. Thus is produced a theoretical diagram nearly identical with the (5+8) system of Church. The area representing the apex is now divided up by spiral lines, crossing always at right angles, into a network, each mesh of which contains one of the numbered points. In every mesh it is possible to fit, to a high degree of accuracy, a circle, each such circle touching its four nearest neighbours, as in the construction of Church with its contact parastichies, e.g. points 11, 16, 19 and 24 in the diagram. Not only so, but, as is also shown in the figure, shapes representing the primordia may be drawn which approximate to the outlines of the spiral meshes and yet are also bilaterally symmetrical with respect to the radii of the system through the numbered points. The contacts of these areas are essentially the same as those of the circles.

But other systems of logarithmic spirals may equally be drawn between the numbered points. In figure 1*b* are shown eight curves intersecting thirteen others; figure 1*c* contains three spirals in one direction and five in the other, while figure 1*d* has only two in one direction and three in the other. Yet more extreme types could be constructed. In every case the meshwork isolates each numbered point from its neighbours, and every mesh contains one of them; also, as shown in figure 1*d*, it is just as possible in each diagram as it is in figure 1*a* to insert shapes representing primordia, bilaterally symmetrical with respect to radii of the system and approximating the outlines both of young leaves and also the spiral meshes. An apex similar in transverse section to figure 1*d* would be classified, according to the method generally in use, as (2+3), for these are the contact parastichies, while one similar to figure 1*a* would be termed (5+8), and these two would doubtless be regarded as differing greatly in their phyllotaxis.

Nevertheless, phyllotaxis is defined as leaf *arrangement* or *positioning*, and in these four diagrams this is identical, being determined by the numbered points representing the 'centres' of the primordia, which points are fixed absolutely by the two constants divergence angle and plastochrone ratio. Again, the positions of the spiral lines have been so adjusted that the areas of the meshes surrounding points similarly numbered (15 for instance) are identical in all diagrams. It is readily seen then that these diagrams represent apices

(1) displaying the same divergence angle, (2) whose growth during one plastochrone is the same, and (3) which allot the same proportion of the central meristem to each primordium at its initiation. In all essentials relating to manner of growth and to the geometrical arrangement of the primordia the four apices are exactly similar; the only difference between them lies in the *shapes of the primordia*, and phyllotaxis, by definition, is not concerned with these shapes whatever part they may play according to some theories in the production of the pattern, and however much they direct the eye along different spiral lines.

Nor must it be supposed that in a system defined as (3+5), for example, this definition in itself gives any information about the primordial shape; while it does so in the four diagrams of figure 1, this is solely because these have been constructed with the same plastochrone ratio. By varying this ratio, but without altering the divergence angle, 'primordia' of any of the forms shown (as regards their relative extensions in the radial and tangential directions) may readily be obtained displaying any desired contact parastichy numbers taken from the Fibonacci series. With a given divergence angle then the contact parastichies depend on two factors, both variable from apex to apex: plastochrone ratio and primordium shape, and as a means of defining a phyllotaxis system the contacts are clearly useless without further information. Phyllotaxis proper is uniquely defined by divergence angle and plastochrone ratio; if, *in addition*, contact parastichies are stated we have data from which also a very good notion of primordium shape may be inferred.

Precisely similar information, both as regards phyllotaxis and primordium shape, would be given by the presentation of divergence angle and number of contact parastichies together with the *angle of intersection* of the latter, for as may be seen from figure 1, the contact parastichies in each of the diagrams intersect isogonally and at a characteristic angle for each. The intersection angle is, however, difficult to estimate by direct measurement; nor is the information it provides in so convenient a form as when given via plastochrone ratio, as will be apparent later. Very full information of the geometry at the apex would again be available from divergence angle, plastochrone ratio and the angle subtended by a primordium at the centre; but an idea of primordium shape sufficiently good for most purposes is provided by the contact parastichies when considered in relation to divergence and plastochrone ratio, and as the contacts are very readily determined this presentation of the relevant data is recommended as a routine procedure.

Before leaving figure 1 it may be pointed out that the diagrams are in essence the equivalent of a simpler straight-line set of constructions, appropriate to mature cylindrical stems, presented by d'Arcy Thompson (1942, figure 452), though the idea goes back much further, at least to Schwendener. The present diagrams may be regarded as centric transformations of Thompson's; he did not, however, follow up the implications with regard to phyllotaxis classification and assessment.

From the above discussion it is evident that for a divergence equal to the Fibonacci angle a precise relation exists in the transverse plane between plastochrone ratio and the angle of intersection of the consecutive Fibonacci pairs of parastichies. A similar relation holds for other divergences and their appropriate parastichies, and may be calculated as follows:

If in a logarithmic spiral the lengths of two radii vectores be v_1 and v_2 and the angle between them be ψ, then

$$\frac{v_2}{v_1} = e^{\psi \cot \alpha},$$

where α is the (constant) angle between the radius and tangent through any point on the curve. This relation applies to all such parastichy lines as those drawn in figure 1; consider one passing through every ath primordium. The angle at the centre between two successive primordia along it (ψ_a) may be obtained by deducting the nearest multiple of 2π from a times the divergence angle. Expressed in radians this may be taken as ψ in the above equation. The corresponding value of v_2/v_1 is the ratio of the distances from the centre of the system of two successive primordia along the same parastichy i.e. r^a, where r is the plastochrone ratio. Substituting these in the equation and taking logarithms

$$a \log_e r = \psi_a \cot \alpha_a, \tag{1}$$

where α_a is the inclination of the tangent of this parastichy to the radius vector, and may now be calculated. Similarly for another parastichy passing through every bth primordium

$$b \log_e r = \psi_b \cot \alpha_b, \tag{2}$$

from which α_b may also be calculated. If these two parastichies run in opposite directions they interesect at the angle $(\alpha_a + \alpha_b)$, which angle may therefore be determined for any parastichy pair and any desired plastochrone ratio.

Should the plastochrone ratio be required at which the parastichy pair a and b intersect orthogonally, equation (1) may be divided by equation (2):

$$\frac{\cot \alpha_a}{\cot \alpha_b} = \frac{a}{b} \times \frac{\psi_b}{\psi_a}.$$

Since α_b now equals $(90^\circ - \alpha_a)$, the left-hand side equals $\cot^2 \alpha_a$. Hence

$$\cot \alpha_a = \sqrt{\left(\frac{a}{b} \times \frac{\psi_b}{\psi_a}\right)},$$

and $\cot \alpha_b$ equals its reciprocal. Substituting these values in (1) or (2)

$$\log_e r = \sqrt{\left(\frac{\psi_a \psi_b}{ab}\right)}. \tag{3}$$

When the divergence equals the Fibonacci angle, a and b may be taken as the nth and $(n+1)$th members of the Fibonacci series, 1, 1, 2, 3, 5, ... If $n = 1$, both a and b are 1; since in the parastichy system 1:1* the two curves travel in opposite directions, ψ_a becomes the Fibonacci angle proper, 222·49224°..., i.e. 3·883222 radians, and ψ_b the same angle, but measured in the opposite direction, i.e. 137·50776°, ... ψ_b thus equals $\psi_a \left(\frac{\sqrt{5}-1}{2}\right)$,

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* A symbolic method of expressing a quite general phyllotaxis system in terms of parastichy numbers must be introduced. In Church's nomenclature (adapted from the terminology of the brothers Bravais) the symbol $(a+b)$ implied a system in which the curves referred to were the contact parastichies, which also intersected orthogonally. In later usage this symbol refers to the contact relations only, and it is used in that sense throughout this paper (except, of course, when discussing Church's own views). On the other hand, phyllotaxis systems will frequently be defined in terms of parastichy numbers when the particular sets of curves indicated are not, or are not necessarily, contact parastichies. In these instances (except for figure 3) the symbol $a:b$ will be used. It might have been preferable to have adopted Church's symbol without the brackets, but unfortunately these are omitted by some authors even when contact parastichies are under discussion.

and it may readily be shown that, whatever the value of n, ψ_b always bears this same relation to ψ_a. Hence, for any value of n,

$$\psi_a = 3{\cdot}883222 \times \left(\frac{\sqrt{5}-1}{2}\right)^{n-1} \quad \text{and} \quad \psi_b = 3{\cdot}883222 \times \left(\frac{\sqrt{5}-1}{2}\right)^{n}.$$

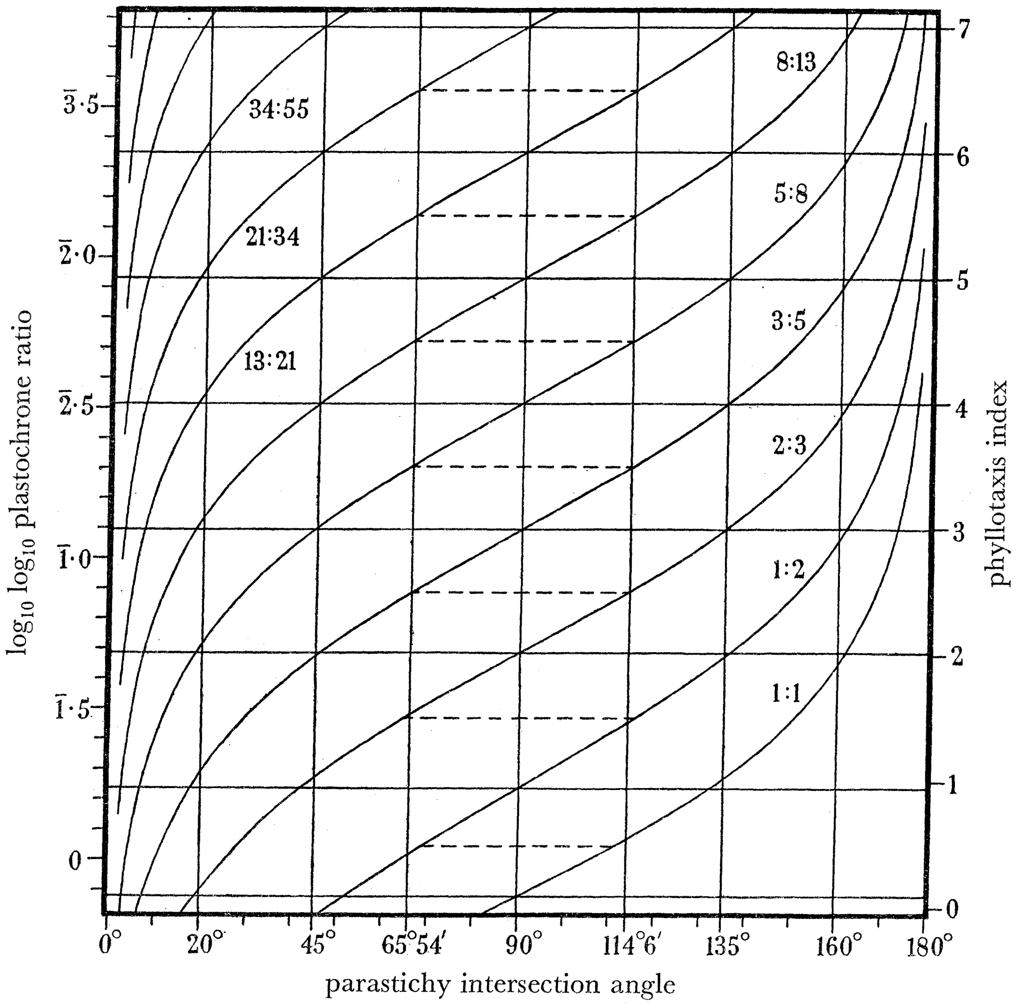

FIGURE 2. The relation, for a divergence equal to the Fibonacci angle, between the double logarithm of plastochrone ratio and the intersection angles of the successive parastichy pairs. Phyllotaxis indices are indicated on the right. Full horizontal lines are drawn to intersect the various curves at the orthogonal values, and broken lines to meet these curves at the positions at which two consecutive parastichy pairs depart equally from orthogonality.

Substituting these values in (3),

$$\log_e r = 3{\cdot}883222 \times \sqrt{\left(\frac{0{\cdot}618034^{2n-1}}{ab}\right)},$$

or, more accurately,

$$\log_{10} r = 1{\cdot}686461920 \times \sqrt{\left(\frac{0{\cdot}618033989^{2n-1}}{ab}\right)}. \qquad (4)$$

For a divergence equal to the Fibonacci angle the complete relation between plastochrone ratio and intersection angle of each parastichy pair was presented in diagrammatic form in a previous communication (Richards 1948); it is reproduced here with slight modification in figure 2. The parastichy intersection angles are plotted against the double logarithm of the ratio ($\log_{10} \log_{10} r$), since by so doing the curves representing the higher parastichy pairs become virtually parallel and equally spaced; hence the 13:21 curve (or even the 8:13) may represent equally any higher system simply by altering the $\log_{10} \log_{10}$ ratio scale by 0·41798 for each higher step. The full horizontal lines mark those plastochrone ratios at which the various parastichy pairs are orthogonal, while the short broken lines indicate the transitional values, i.e. systems in which two consecutive parastichy pairs depart equally from orthogonal intersection.

The relation between figures 1 and 2 will be obvious. The plastochrone ratio in the former is 1·07296, hence the possible Fibonacci parastichy relations are those defined by the points where the curved lines in figure 2 cross the fifth horizontal line. Each of the four parastichy systems shown in figure 1 is thus represented by a single point in figure 2, from which latter diagram their angles of intersection may be read, i.e. the $(5+8)$ system in figure 1 *a* is orthogonal, while the 8 and 13 parastichies in *b* intersect at 45° 10′, the parastichies 3 and 5 of *c* at 135° 9′, and finally the parastichies 2 and 3 of *d* intersect at 161° 36′. It will be equally clear from figure 2 that for any phyllotaxis system based upon the Fibonacci angle, plastochrone ratio (and therefore leaf position) is defined by a knowledge simply of the intersection angle of *any* one parastichy pair; as stated previously, by choosing the *contact* parastichies for this, extra information could be given concerning the shape of the primordia. For instance, the ratio between the tangential and radial dimensions of the primordia, assuming full contact between them and no intervening spaces, is approximately unity when the contact parastichies are orthogonal and rises continuously with their angle of intersection. At 135° the ratio of their dimensions becomes approximately 3 to 1, and at 160° about 8 to 1. However, an improved method of presenting the information supplied by plastochrone ratios is suggested in the following section and for nearly all purposes it is much preferable to take advantage of this, giving the contact parastichies where desired as additional data relating to primordial shape. Should more accurate information on this matter be required, other methods of conveying it will naturally be used.

3. A simplified descriptive method for Fibonacci systems

The primary requisites in defining a uniform phyllotaxis system, as seen at the apex by means of transverse sections, are then the two parameters divergence angle and plastochrone ratio. The first presents no difficulty; it has long been associated with phyllotaxis classification, and the fact that the genetic spiral and with it the divergence angle are recognized as abstractions from phyllotaxis theory (and therefore secondary phenomena) in no way detracts from its value as a constant for defining the various systems. Experimental evidence has accumulated (Snow & Snow 1931, 1933; Wardlaw 1949, etc.) indicating that the characteristic divergence angle must derive from the fact that a new primordium is in the main positioned tangentially by those primordia near to it in preceding cycles or whorls, in such a manner that the angle between the two main determining primordia tends to be divided in a particular and characteristic ratio. This is the primary phenomenon and parameters for purposes of definition might be derived directly from it. But in most phyllotaxis systems a single genetic spiral, with divergence angles scattered round a definite mean value, is a consequence of this method of positioning; the mean angle is thus a readily visualized, unequivocal and easily determined parameter providing all the information on tangential spacing needed to construct an idealized representation of the system.

The second parameter required, plastochrone ratio, lacks something of the immediate simplicity of divergence angle, and to this shortcoming may possibly be added its unfamiliarity as a botanical concept. It is, nevertheless, a most efficient measure and one which is well known as the complement to 'divergence angle' in many geometrical constructions (e.g. the logarithmic spiral) employing the method of polar co-ordinates. Again, phyllotaxis is largely dominated by Fibonacci systems; all classifications of these in the past have been based on Fibonacci numbers, and, indeed, for many purposes some such treatment is both natural and desirable. Since all these systems have very similar divergences they differ from one another practically only in their plastochrone ratios. But whereas the magnitude of the divergence angle, i.e. its proximity to 137·5°, immediately conveys the knowledge that a Fibonacci system is under consideration, the accompanying plastochrone ratio, in itself, does not with equal facility indicate to the mind the position of the system under consideration in the Fibonacci scale. In fact, of course, that position is fixed by it, and, as may be seen from figure 2 or from the first two columns of table 1, as the plastochrone ratio falls towards unity the parastichy system most nearly orthogonal changes, or rises, from one characterized by low Fibonacci numbers through those with higher and higher pairs of these numbers.

TABLE 1

orthogonal system	plastochrone ratio (r)	$\log_{10} \log_{10} r$	phyllotaxis index
1:2	3·79666	−0·2370	0·946
2:3	1·60969	−0·6846	2·017
3:5	1·20451	−1·0925	2·993
5:8	1·07296	−1·5145	4·002
8:13	1·02736	−1·9310	4·999
13:21	1·01035	−2·3495	6·000
21:34	1·003943	−2·7672	7·000
34:55	1·001504	−3·1853	8·000
55:89	1·000574	−3·6033	9·000
89:144	1·000219	−4·0213	10·000

A simple and useful transformation to bridge this mental gap is suggested by the almost uniform spacing of the curves drawn in figure 2. Since the double logarithms of the plastochrone ratios found in any two successive and high orthogonal Fibonacci systems differ by 0·41798, i.e. $\log_{10}\left(\frac{3+\surd 5}{2}\right)$,[*] multiplication of the entries in column 3 of table 1 by 2·3925, the reciprocal of 0·41798, must result in a series of numbers almost in arithmetical progression with a common difference of unity. If the negative signs are ignored and to each is now added 0·379, the numbers entered in column 4 of table 1 are obtained. These derivatives of the plastochrone ratios approximate very closely to the successive integers, and therefore provide immediate information as to position in the Fibonacci scale. For this reason they are more useful for descriptive and classificatory purposes than the original plastochrone ratios, yet are easily transformed back to them for growth studies or the construction of theoretical diagrams, etc. A number so determined from an actual apex may be called the *phyllotaxis index* of that apex.

[*] This is easily deduced from formula (4) on p. 518.

For practical purposes this index need be calculated to only one place of decimals, indeed, it will not infrequently be found that even this degree of precision is unattainable. This being so, all the necessary accuracy in computation is given by the formula

$$\text{phyllotaxis index} = 0{\cdot}38 - 2{\cdot}39 \log_{10} \log_{10} r.$$

To the first place of decimals all the orthogonal systems except the first, 1:2, are properly represented by the integers and the error in the remaining one is immaterial; nevertheless, true orthogonality here is found when the value is rather nearer 0·9 than 1·0. If measurements taken on an apex conforming to the Fibonacci angle lead to a phyllotaxis index of 3·0 it may be inferred immediately that the third Fibonacci parastichy system, 3:5, is exactly orthogonal; if the index obtained be 4·5, no parastichy pair intersects orthogonally, but the systems 5:8 and 8:13 are equally removed from orthogonality; again, 5·2 would indicate a phyllotaxis arrangement one-fifth of a unit removed from the 8:13 orthogonal system in the direction of the 13:21 orthogonal, and so on.

If desired, these fractional parts may be interpreted directly in terms of the intersection angles of particular parastichy pairs. As may be seen from figure 2 the angle between any pair bears a very nearly linear relationship to the double logarithm of the plastochrone ratio, and hence to the phyllotaxis index as well, over the range between the two transitional values 65° 54′ and 114° 6′. This range corresponds to one of a unit in phyllotaxis index, i.e. from $x-0{\cdot}5$ to $x+0{\cdot}5$, where x is some particular integer. Hence over this region one phyllotaxis unit corresponds to rather more than 48° change in the intersection angle of the most nearly orthogonal pair, or each one-tenth unit to about 5°. Outside this range the departure from rectilinearity in the relation begins to become evident, but it is useful to remember that a parastichy intersection of 45° represents one phyllotaxis unit below that for orthogonal intersection of the same parastichies, and one of 135° to one unit above that for orthogonality.

In the following six sections of this paper the relationships between phyllotaxis indices and parastichy intersection angles in Fibonacci systems will be considered more closely, both as seen in transverse section and on the actual apical surface; also the theoretical phyllotaxis indices appropriate to a variety of non-Fibonacci systems will be derived in order that any obtained from measurements on actual apices may be interpreted without the need for reconstructing the systems. If desired, these sections may be omitted on a first reading; the main conclusions reached in them are summarized on pp. 536–537 and in the appendix.

4. Effect of deviation of divergence angle from the Fibonacci angle

The above relations hold strictly only for a divergence equal to the Fibonacci angle, 137·50776°.... With the great majority of apices whose obvious parastichy numbers are a consecutive pair taken from the Fibonacci series, quite regardless of the precise divergence, there is nevertheless only a slight loss in precision if the phyllotaxis index be interpreted as regards parastichy intersection just as it is with the 'ideal' divergence. When, as usually happens, the actual divergence approximates to, but is not identical with, the Fibonacci angle, then only a certain number of the lowest of the parastichy systems are geometrically possible; the closer the approximation to the 'ideal' divergence, the greater is the number of possible Fibonacci systems. Thus on a centric diagram having a divergence of 135°, all the points representing primordial centres fall on eight radii inclined at 45° to one another, i.e. the 8-parastichies are radial or orthostichous. Similarly with the divergence angle 144°, the 5-parastichies are radial. With any divergence between these two limits the 5- and the 8-parastichies form two sets of spiral lines travelling outwards in opposite directions round the centre. But outside these limits, when the angle is either less than 135° or greater than 144°, both of the parastichy sets run in the same direction and no system 5:8, as usually understood, exists. This, however, does not preclude the existence of lower Fibonacci systems, for the corresponding limiting divergences in the 3:5 system are 120 and 144°, while in the 2:3 any angle greater than 120°, i.e. between 120 and 180°, is *geometrically* possible. The higher the parastichy system, the more restricted becomes the available range in divergence angle within which the two parastichy sets can run in opposite directions, the limits constituting the well-known fractional divergences of the botanical text-books.

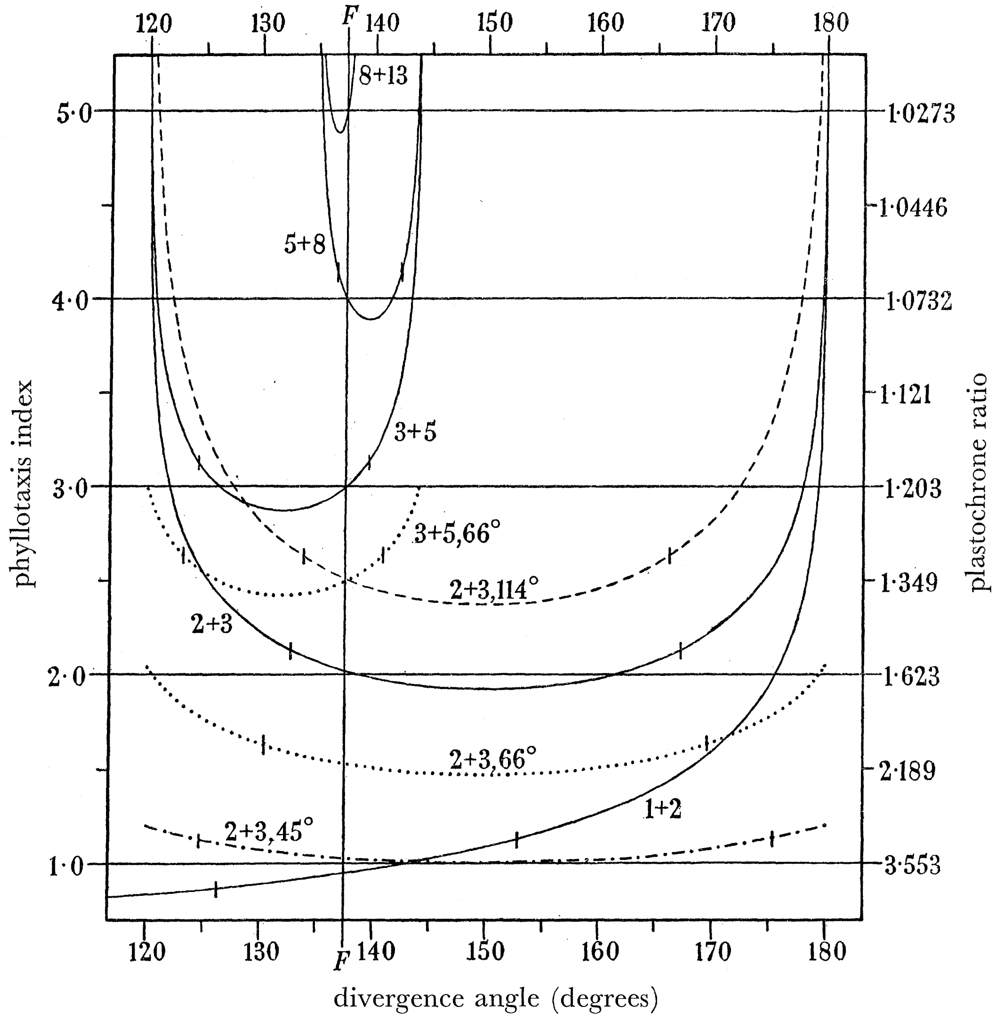

FIGURE 3. Modification of the relation between phyllotaxis index and parastichy intersection angle in Fibonacci systems due to changes in the divergence angle. For further explanation see text. The curves should be labelled 2:3, 3:5, etc., instead of 2 + 3, 3 + 5, etc.

For any given divergence angle and plastochrone ratio (or phyllotaxis index) the intersection angle of any parastichy pair may readily be determined by the method already given (p. 517). Figure 3 shows the relationship between phyllotaxis index, over the range 1–5, and divergence angle (between 120 and 180°) for orthogonal intersection of all possible Fibonacci pairs; in addition, curves are presented for 66° intersection of the 2:3 and the 3:5 parastichy pairs, and also for 45 and 114° intersection of the 2:3. The vertical line *F* represents a divergence equal to the Fibonacci angle.

Regarding first the full lines representing orthogonal intersections it will be seen that they all cross line *F* very nearly at integral phyllotaxis indices, and that the larger portions of the consecutive curves oscillate to right and left of it. Each curve is symmetrical about its own vertical axis, which is situated at the mean divergence angle between its geometrical limits; furthermore, they are all identical in form, so that a single one might be used to represent the whole family, provided the scale of phyllotaxis index be shifted the appropriate amount for each, and that of divergence angle be suitably expanded or contracted.

The form of the curves is best seen in that labelled 2 + 3; they are asymptotic to their divergence limits and are characteristically flat-bottomed. Consequently there is a wide range in divergence angle over which the phyllotaxis index deviates by only a small amount from the integral value found near where line *F* is intersected. Two points have been marked on each curve, and between them the true phyllotaxis index differs from the nearest integer by an amount not exceeding 0·13 of a unit—an arbitrary amount, but one which is of no great importance in practice. Deviations less than this amount are found over approximately 60 % of the possible range in divergence angle, but outside the marked limits deviation from the integral value increases rapidly.

The only real exception as regards these limits is found in the 1:2 orthogonal curve. This is of the same form as the others and is symmetrical round its mean value 90°, but it is situated low, crossing the *F* line appreciably below the phyllotaxis index 1·0; consequently the central region of the curve as well as the outer branches falls ouside the chosen permissible deviation. The limiting divergence angles shown for departures of less than 0·13 are about 126 and 153°, but there is another similar range on the other branch of the curve, between about 27 and 54°. This need not be considered, for although geometrically possible, phyllotaxis systems with divergence angles below 90° would certainly not be regarded as Fibonacci systems; indeed, they do not exist as 1:2 orthogonal arrangements.

Two other curves show the similar relations for intersection angles of 66 and 114° between the 2- and 3-parastichies; in all but the very lowest systems conforming exactly with the Fibonacci divergence these intersection angles are only a few minutes of arc removed from the precise points of transition between two consecutive orthogonal arrangements, as may be seen from figure 2. The curves drawn in figure 3 represent the largest deviations from this condition which it is necessary to consider, yet it is apparent that even these cross the *F* line at phyllotaxis indices very close to 1·5 and 2·5 respectively. For a smaller deviation than 0·13 unit from the value 1·5, the 66° curve has a wider latitude of divergence angle than has the 2:3 orthogonal for the same deviation from 2·0. At lower intersection angles still (cf. curve for 2:3 at 45°) the latitude increases rapidly, but as the angle of parastichy intersection increases to 114° the permissible divergence range, for this same departure from the phyllotaxis index found at the *F* line, narrows somewhat compared with the range at orthogonality. Finally, the 3:5 intersection at 66° is also shown in the diagram; this again is of precisely similar form to the 2:3, 66° line. These particular curves are shown as if they ended abruptly at their orthostichous values; they may, however, be continued beyond these divergences, but soon turn upwards towards infinity like the other curves. Outside the range shown, of course, the two parastichy sets run round the apex in the same direction, and Fibonacci systems in the usual sense no longer exist. The curves representing orthogonal systems run up to infinity (or to a plastochrone ratio of 1·0) at their theoretical limiting divergence angles; here the parastichies in one direction reduce to a set of points and those in the other to a circle.

In order to illustrate the change in form of the curves drawn in figure 3 with alteration of the intersection angle of the parastichy pairs, the pair 2:3 has been selected because it is the lowest that need be considered in this connexion in phyllotaxis systems, and because in this case the conditions are the most stringent for the present purpose, namely, to demonstrate that only a comparatively minor error is involved if a phyllotaxis index, derived from an apex conforming with a divergence somewhat different from the 'ideal' angle, is interpreted in regard to the parastichy relations as though (with this same phyllotaxis index) the divergence were in fact exactly equal to the Fibonacci angle. In higher systems the proportion of the total range in divergence angle having an error not exceeding 0·13 unit is somewhat greater than in the 2:3 curves shown.

TABLE 2

orthogonal system	divergence ranges (degrees) for error $< 6\frac{1}{4}°$
1:2	126·3 –152·9
2:3	132·7 –167·3
3:5	124·5 –139·5
5:8	136·7 –142·3
8:13	135·69 –137·77
13:21	137·41 –138·20
21:34	137·244–137·546

It is seen in figure 3 that the ranges of divergence angle, over which a uniform relation between phyllotaxis index and parastichy intersection angle may reasonably be assumed to hold, are very unsymmetrically divided at the Fibonacci angle itself, and that the portion having the greater latitude alternates above and below this angle with the successive parastichy pairs. The approximate divergence ranges for the first few orthogonal systems are tabulated in table 2, allowing a maximum error just exceeding 6° (the equivalent of 0·13 phyllotaxis unit) in the intersection angle as immediately deduced from the phyllotaxis index.

The range on that side of the Fibonacci angle which has the greater latitude is far wider than is likely to be encountered in any actual Fibonacci phyllotaxis system, but that on the other side may possibly be exceeded in very aberrant apices. However, in such a case a limiting orthostichous condition is rapidly approached that will be evident on the plant from the leaves tending to be arranged in 'parallel spires', and in transverse section at the apex by the primordia lying along only slightly curved radial lines. Nevertheless, the very large majority of apices exhibiting anything that may be called Fibonacci phyllotaxis display divergence angles falling well within the prescribed limits, and only slight errors will be involved if the parastichy intersections are assumed to be related to phyllotaxis index just as they are when the divergence is exactly the Fibonacci angle.

5. Parastichy relations on the apical surface

The knowledge gained from the phyllotaxis index is confined to the curve system as seen in transverse section, since both plastochrone ratio and phyllotaxis index are defined in terms of the transverse component; and in the absence of further data comparatively little is known of the curve system as it exists on the surface of the apex. In some connexions this knowledge is unnecessary, but for others is important. In these latter circumstances an adjusted phyllotaxis index may be used to supply the required information, the adjustment being obtained very simply from an angular measurement made on a central longitudinal section of the apex.

A typical apical surface is often described as approaching a paraboloidal form; over a small region, such as that where the youngest primordia are situated, it may be regarded to a first approximation as conical. The angle at the apex of the cone that most nearly fits the region wherein interest is centred may readily be determined from a longitudinal section, and is sufficient to enable the required adjustment to the phyllotaxis index to be calculated, as the following considerations show.

A conical surface has the advantage that it may be unrolled to a plane; if a Fibonacci curve system be drawn on a cone which is then unrolled, the angles of intersection of the curves are unaltered and the plane displays the same parastichy relations as did the conical surface. Figure 4 in its entirety represents a 'bijugate' Fibonacci system, and will be considered as such subsequently, but if it be cut along any diameter, say AB, then each half may be rolled in such a way that A is brought into proximity with B; two cones whose apices coincide with the centre of the bijugate system might thus be produced from the diagram. In figure 4 the curve system is symmetrical on the two sides of any diameter; the halves are identical in pattern, hence on each of the derived cones the curves will be continuous across the line of junction. Each numbered point in the figure formally represents the centre of a primordium, and in interpreting the diagram as two unrolled cones the outer of the two numbers associated with each parastichy intersection point should alone be considered; the inner set of numbers applies when the diagram is regarded as representing a plane bijugate system. Using the outer numbers then, in the figure the angle at the centre between points 1 and 2 for instance, or between 3 and 4, has been made equal to one-half the Fibonacci angle; similarly, the angle between point 2 and A, and that between B and point 3 also sum to the same angle. By rolling a semicircle into a cone all angular measurements are doubled, hence each of the derived cones will display a 2:3 parastichy system whose divergence is exactly the Fibonacci angle.

In a very similar manner a cone having any desired apical angle and displaying any Fibonacci system may be constructed by drawing this curve system on a sector of a circle of the appropriate size. For a cone of apical angle 2θ a sector must be taken whose angular size bears to the whole circle the ratio $\sin\theta$. In figure 4 this ratio is 0·5, or sin 30°, so that the two derived cones would have apical angles of 60°.

If then a cone (apical angle 2θ) is to be constructed, on whose surface is drawn, for example, a particular orthogonal Fibonacci system $a:b$, it is now obvious that the divergence angle on the plane drawing must be $\sin\theta$ times the divergence required on the cone. All other derivative angles in the system are similarly affected, e.g. ψ_a, ψ_b, etc. (see p. 517) become on the unrolled cone $\psi_a \sin\theta$, $\psi_b \sin\theta$, etc. Instead of the relation (3) on p. 517 we now have

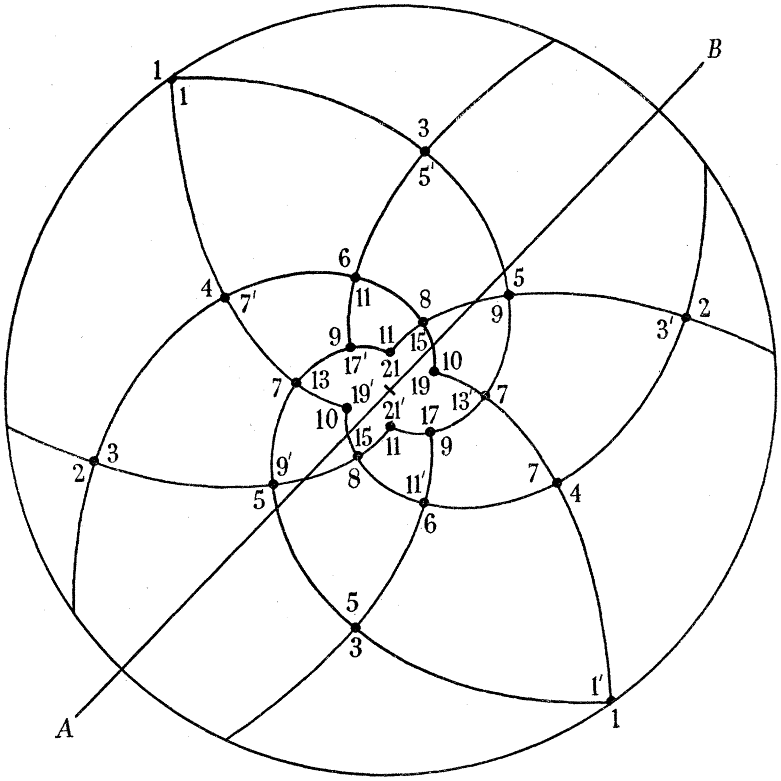

FIGURE 4. Ideal representation of the transverse component of the bijugate orthogonal system 4:6. Any diameter cuts the figure into two identical halves, each of which may be rolled into a 60° cone exhibiting on its surface a 2:3 Fibonacci orthogonal system. The inner numbers are appropriate to the plane bijugate figure, the outer to the conical systems.

$$\log_e r = \sin\theta \sqrt{\left(\frac{\psi_a \psi_b}{ab}\right)},$$

which gives the plastochrone ratio to be used on the plane drawing.

Let X and Y (figure 5) represent two successive points on the cone surface, and X', Y' their projections on the base; then r in the above relation is the ratio of AX to AY. By rotating the section $AXX'O$ round AO through the divergence angle, X may be made to fall along AY produced and X' along OY' produced, and evidently $OX'/OY' = AX/AY = r$. But OX'/OY', and therefore r also, is the true plastochrone ratio as measured on transverse sections of the cone, which, together with the divergence angle, defines the system as seen there, or in projection.

By hypothesis, however, on the cone surface the Fibonacci system $a:b$ is orthogonal. For orthogonality in this same system on a full circular plane diagram, as was shown on p. 517,

$$\log_e r' = \sqrt{\left(\frac{\psi_a \psi_b}{ab}\right)}.$$

Therefore log r' equals log $r/\sin\theta$, whatever the base of the logarithms, and if r corresponds to a phyllotaxis index of n (where $n = 0{\cdot}38 - 2{\cdot}39 \log_{10}\log_{10} r$), r' will be equivalent to one of $n + 2{\cdot}39 \log_{10}\sin\theta$. Since $\log_{10}\sin\theta$ is always a negative quantity, n is lowered numerically by the adjusting term.

In this expression n is the true phyllotaxis index, as previously defined, and is obtained in practice solely from measurements taken in the usual way from transverse sections; the adjustment, $2{\cdot}39 \log_{10}\sin\theta$, is obtained from the angle 2θ as measured on a longitudinal section. The adjusted index may be termed the *equivalent phyllotaxis index* for the surface, and its sole purpose is to define the curve system existing there, as distinct from its appearance in section. It is the phyllotaxis index which in a plane construction has the same parastichy relations as those displayed on the apical surface, which may therefore be immediately stated.

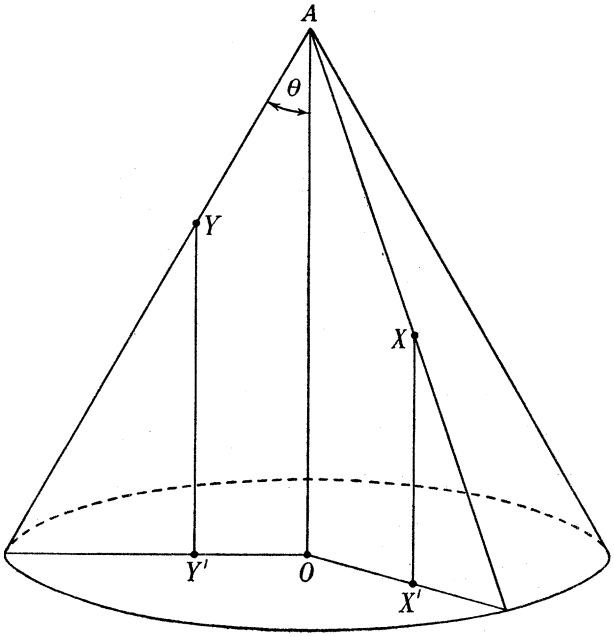

FIGURE 5. Diagram illustrating the relation between the constants of a phyllotaxis system on a conical surface and those of the same system projected on to a transverse plane. See text.

In illustration of the above method, either semicircle in figure 4 may again be considered. If this were rolled into a cone, and the numbered points projected on to the base (cf. figure 5), this plane would correspond to the transverse section of an apex, and the plastochrone ratio as determined on that base would equal that actually occurring in figure 4. This ratio (r) is 1·26875. $\mathrm{Log}_{10} r$ equals 0·103376, and $\log_{10}\log_{10} r$ is $\bar{1}{\cdot}0144$, or $-0{\cdot}9856$. Hence n (phyllotaxis index) equals $0{\cdot}38 + (2{\cdot}39 \times 0{\cdot}9856)$, or 2·74, i.e. as seen in section the parastichy system intersecting most nearly orthogonally is the 3:5, the actual intersection angle being approximately 77°. Now the apical angle of the cone is 60°, hence the correction factor is $2{\cdot}39 \log_{10}\sin 30$, which equals $-0{\cdot}72$. Adding this to n gives 2·02 for the equivalent phyllotaxis index, which is to be interpreted as if obtained from a plane figure; it indicates then that on the cone surface (or as drawn in figure 4) the 2:3 system is exactly orthogonal (cf. table 1).

Values of $\log_{10} \sin\theta$ are frequently presented directly in tables of the trigonometrical functions. Ignoring their negative signs a few are given here in table 3 for cones of apical angle 2θ, together with the corresponding differences between equivalent phyllotaxis index and phyllotaxis index proper; while for practical work the necessary adjustment for any cone may be read from table 3 in the appendix.

Table 3

2θ (degrees)	$-\log_{10} \sin\theta$	adjustment in phyllotaxis index
180 (i.e. plane)	0·0	0·0
120	0·0625	0·150
90	0·1505	0·360
60	0·3010	0·720
45	0·4172	0·998
30	0·5870	1·404
15	0·8843	2·116
0 (i.e. cylinder)	∞	∞

It is seen from table 3 that for moderately flat apices the adjustment is not great, amounting even at $2\theta = 90°$ to little more than a third of a phyllotaxis unit, and the apical angle needs to be narrowed to 45° before a difference of a whole unit is found. It follows that over a wide range of apical angle this need be determined with no great precision, for the estimation of phyllotaxis index itself is not profitably attempted closer than to the nearest one-tenth unit. It is apparent also that the fitting of a cone to a part of the apex that is not strictly conical can lead to no serious error, for the change in angle of the 'cone' over the region considered will only be small and the effect on the adjustment trifling. But with apices that taper gradually the possibility of serious error increases, and in the limiting case of a cylinder the method breaks down altogether, since there is here no growth in the transverse direction; plastochrone ratio sinks to its limit at 1·0, and phyllotaxis index rises indefinitely, as also does the adjustment for equivalent phyllotaxis index. This is perhaps unfortunate, since an important group of plants, the Gramineae, is largely characterized by just such apices; these systems can be investigated by the present method only in the region where the axis is expanding laterally, some distance below the zone of primordial initiation.

In more normal apices, however, the investigation could if desired be extended over the whole expanding portion from the apex itself where the primordia arise to the region where transverse growth of the axis ceases. As zones further and further removed from the apex are examined the plastochrone ratio is likely to fall; at the same time the angle of the cone appropriate to the successive zones will narrow, and the resultant estimates of equivalent phyllotaxis index will show whether and how the parastichy relations on the axis surface are changing.

Finally, it should be emphasized that although this discussion of the parastichy relations on the actual surface has been confined to Fibonacci phyllotaxis, the method is equally applicable without modification to all those other phyllotaxis systems whose transverse components are alone considered in the following pages.

6. Bijugate and multijugate systems

The relation between phyllotaxis index and parastichy intersection angles examined in the preceding sections applies to the large majority of spiral apices. Nevertheless, not infrequently apices are found which display truly spiral arrangements but have divergences differing widely from the Fibonacci angle and associated with numbers of conspicuous parastichies not taken from the Fibonacci series. In all these the phyllotaxis index supplies information as to the parastichy relations only a little less readily than in the more usual systems.

In the first place, apices may be considered whose parastichy numbers are double those found in Fibonacci patterns. Figure 4 gives a formal representation of the 4:6 orthogonal system, a duplicated version of the 2:3 orthogonal Fibonacci arrangement. Systems of this nature are known as *bijugate*, or are described as being composed of twisted whorls of two members; for at every node two opposite leaves are produced, but those at any one node, instead of alternating exactly with the previous pair, arise at a constant angle to them differing from 90°. No single genetic spiral can be put through all the leaves, but two such, situated 180° apart, may conventionally be inserted. The numbering in figure 4 illustrates this (inner of the two numbers associated with each point); the points representing the oldest leaves are labelled 1 and 1′ respectively, the next pair 3 and 3′, etc. One 'genetic spiral' passes through points 1, 3, 5, 7, ..., and the other through 1′, 3′, 5′, 7′, ... These systems tend towards an ideal divergence angle along each 'genetic spiral' of 68·75388°..., one-half the Fibonacci angle, and in figure 4 the divergence is of this magnitude. From the point of view of phyllotaxis definition, the presence of two 'genetic spirals' needs to be indicated with the other defining constants; for this purpose the divergence in figure 4 might be given as 2 × 68·75°, where the 2 refers to the bijugate condition, and the product indicates the closeness of approach to the primary ideal angle.

The assessment of the phyllotaxis index appropriate to the plane curve system figured may be inferred from what has previously been said of the diagram. The curve pattern is identical with that of the orthogonal 2:3 Fibonacci arrangement on a 60° cone, the sole difference being that there is twice as much of it, two primordia being initiated in each 'plastochrone'. As with the conical construction, a 'plastochrone' ratio may be estimated from the ratio of the distances from the centre of the successive points of foliar insertion, i.e. the distance of point 1 to that of point 3, or of 1′ to that of 3′, etc. Since every 'plastochrone' is double, ratios measured in this way may be supposed to alternate with ratios of exactly 1·0. When comparison is to be made with the plastochrone ratio of unijugate systems therefore, the ratio as measured needs modifying, one part of the appropriate correction evidently being to take its square root; for by so doing the growth made during each double plastochrone is divided into two equal steps, each formally corresponding to the production of one primordium. Hence $\log r$ (observed) needs dividing by two, and $\log_{10}\log_{10} r$ (observed) to be reduced by $\log_{10} 2$.

This correction needs to be applied to the value of $\log_{10}\log_{10} r$ appropriate to the semi-circle in figure 4 representing the unrolled 60° cone. This latter has been shown to be derivable from that for the plane orthogonal Fibonacci 2:3 system by adding $\log_{10}\sin 30° = -\log_{10} 2$ (cf. p. 527). Hence, starting from the $\log_{10}\log_{10} r$ value for the plane 2:3 system, the total correction to apply in order to obtain a corresponding value for the plane 4:6 system is a reduction of $2\log_{10}2$, or $\log_{10}4$, i.e. the fourth root of r in any plane Fibonacci system supplies the r value appropriate to the corresponding bijugate system,* for the above argument would hold precisely whatever bijugate system were taken for illustration. Since $\log_{10}\log_{10}r$ is negative, deducting from it $\log_{10}4$ increases the numerical value, and phyllotaxis index will be increased by $2{\cdot}3925\log_{10}4$, or 1·440 units, twice the correction appropriate to a 60° cone. In any plane system then, a doubling of the parastichy numbers in both directions, without altering their intersection angle, leads to an increase in phyllotaxis index of 1·44 units.

Since the plane 2:3 orthogonal system has a phyllotaxis index of 2·02, that of the plane 4:6 orthogonal will be 3·46; similarly, the plane 1:2 orthogonal is indicated by 0·95, and the corresponding 2:4 by 2·39. Higher Fibonacci bijugate systems are orthogonal when the fractional part of the phyllotaxis index is 0·44, e.g. 6:10 system = 4·43; 10:16 = 5·44; 16:26 = 6·44, etc. The point of exact transition between one orthogonal system and the next is marked by a phyllotaxis index terminating in ·94, and so on. The parastichy relations then may be stated directly from these numbers just as in the Fibonacci systems, but the values at orthogonality are no longer the integers.

The correction factor of 1·44 units has been used in deriving the orthogonal values theoretically from those of Fibonacci systems, but it should be made quite clear that in calculating the phyllotaxis index of a bijugate apex from measurements taken on transverse sections, the correction factor to add is only one-half this, i.e. 0·72 of a unit, which allows for the fact that two leaves appear during each 'plastochrone'; or the correction may be applied earlier in the calculation by dividing $\log_{10}r$ (observed) by 2—this will automatically be done in the calculation of r if the primordia present are numbered in the manner shown in figure 4.

A plane trijugate system, whose parastichy numbers are Fibonacci terms multiplied by three, may be treated in a similar manner to the bijugate; it may be divided by any three equally inclined radii into sectors, each of which may be rolled into a cone that then displays a Fibonacci system and whose apical angle is twice $\sin^{-1}\frac{1}{3}$. This gives $\log_{10}3$ for the difference between the $\log_{10}\log_{10}r$ (observed) of one-third of the plane trijugate system and that of its full circular Fibonacci counterpart. But in the trijugate system r (observed) refers to a triple plastochrone, and the appropriate correction for this is to take its cube root; so, as before, $\log_{10}\log_{10}r$ (observed), a negative number, needs to be reduced by a further $\log_{10}3$ before converting into the corresponding phyllotaxis index. Hence the difference in phyllotaxis index between a plane Fibonacci construction and one with three times the number of

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* That this is the appropriate correction to apply may perhaps be seen more readily by regarding the bijugate arrangement in figure 4 as composed of two superimposed Fibonacci 2:3 *curve* systems; these two might be dissected apart by selection of alternate parastichy curves in both directions. Such a superposition of similar curve systems introduces new points of parastichy intersection, for each set of curves in either original system now intersects not only the complementary set of its own, but also that of the other system. Since there are two Fibonacci *curve* systems in figure 4, each with its appropriate set of intersection points, the total *points* in the diagram constitute those of *four* similar interlaced Fibonacci 2:3 systems, i.e. points 1, 5, 9, 13, ..., points 3, 7, 11, 15, ..., points 1′, 5′, 9′, 13′, ... and points 3′, 7′, 11′, 15′, ... There are now two genetic spirals, and since the divergence along each is reduced to one-half the Fibonacci angle, each of these spirals maps out two Fibonacci systems in terms of primordia. It appears then that in some ways *bi*jugy might better have been termed *quadri*jugy, and x-jugy generally, x^2-jugy.

parastichies is 2·3925 $\log_{10} 9$, i.e. 2·283 units, and indices ending in ·28 imply orthogonal parastichy intersection in plane Fibonacci trijugate systems generally.

It will now be apparent that the phyllotaxis index of any plane x-jugate system is 2·3925 $\log_{10} x^2$, or 4·785 $\log_{10} x$, units greater than that of the corresponding plane isogonal Fibonacci system; and also, that the appropriate correction to apply, in calculating the phyllotaxis index of any such apex from measurements taken on transverse sections, is either a final addition of one-half this value, 2·39 $\log_{10} x$, or else a division of $\log_{10} r$ (observed) by x.

7. Other spiral systems

Sometimes primordia are produced singly in other spiral patterns than Fibonacci arrangements. In these cases the divergence angle most frequently approximates to $\frac{1}{5}\pi(5-\sqrt{5})$, i.e. 99·50155° ..., and the parastichy numbers are two successive terms of the 'first accessory' series 3, 4, 7, 11, 18, ..., a series built up from the first pair of terms in the same way as is the Fibonacci series. In a system of this kind the intersection angle of any pair of parastichies associated with a particular plastochrone ratio, or phyllotaxis index, may be determined in precisely the same manner as was done for the Fibonacci patterns. It may readily be shown that for orthogonal intersection in the system $a:b$

$$\log_{10} r = 0{\cdot}754208699 \times \sqrt{\left(\frac{0{\cdot}618033989^{2n-1}}{ab}\right)},$$

where a and b are the nth and $(n+1)$th terms in the series beginning 1, 3, 4, 7, 11, ... The theoretical orthogonal values for all the systems likely to be found are given in table 4.

Table 4

orthogonal system	plastochrone ratio (r)	$\log_{10} \log_{10} r$	phyllotaxis index
3:4	1·2758	−0·9756	2·713
4:7	1·10357	−1·3686	3·653
7:11	1·03741	−1·7972	4·679
11:18	1·014256	−2·2113	5·670
18:29	1·005403	−2·6308	6·673
29:47	1·002063	−3·0482	7·672
47:76	1·000787	−3·4664	8·672
76:123	1·000301	−3·8843	9·672

Just as in Fibonacci and multijugate arrangements, the difference in $\log_{10} \log_{10} r$ between two consecutive systems rapidly approaches the constant value 0·4180. Hence their phyllotaxis indices again differ by one unit. The values at orthogonal intersection approximate to numbers whose fractional part is ·672; and in every case, to the nearest one-tenth unit, this fraction is ·7. Otherwise indices actually found are to be interpreted exactly as in the Fibonacci systems. Small departures of the divergence angle from its 'ideal' value have similar effects on the relation between phyllotaxis index and parastichy intersection angle to those already described for Fibonacci arrangements.

Occasionally the divergence assumes yet other irrational angles, each of which has its own characteristic set of parastichy numbers. One of these may very briefly be referred to, i.e. $\frac{1}{11}\pi(7-\sqrt{5})$. This angle, 77·95525° ..., leads to parastichy numbers from the Fibonacci-like 'second accessory' series: 4, 5, 9, 14, 23, ... The indices at the successive orthogonal intersections again differ by one phyllotaxis unit, those of the higher systems having values whose fractional part is ·179. The two systems deviating most from this rule are the lowest, 4:5 with an index of 3·232 and 5:9 with one of 4·153. Every system therefore has a phyllotaxis index that, to the nearest one-tenth unit, is 0·2 greater than an integer, and indeed from 14:23 upwards, one that to the nearest one-hundredth unit is 0·18 greater than an integer. Similarly with other 'ideal' angles and their accessory series, data for two of which ($\frac{1}{19}\pi[9-\surd 5]$ and $\frac{1}{11}\pi[7+\surd 5]$) are included in the appendix.

In exceptional instances bijugate and even multijugate versions of any of these arrangements may be found. Evidently their theoretical phyllotaxis indices may be obtained by adding the appropriate constants to the values representing the corresponding unijugate systems, just as for the multiple Fibonacci arrangements already considered. An x-jugate system is always $4\cdot785 \log_{10} x$ units higher than its unijugate counterpart.

8. THE ALTERNATING SYSTEMS

All systems considered hitherto are characterized by irrational divergence angles, or at least by divergences approximating to certain 'ideal' irrational angles. In them all, if phyllotaxis rises (or plastochrone ratio falls) the nearly orthogonal parastichy pairs close up, or increase their angles of intersection; as they do so higher parastichy pairs open out until they become orthogonal, further rise resulting in a similar process being repeated, so that higher and higher parastichy systems pass through orthogonality. The parameter proposed here under the name 'phyllotaxis index' is adjusted to the rhythm common to the systems produced by any of these irrational angles, and especially so to the most frequent set of all, those associated with the Fibonacci angle itself.

Several important phyllotaxis arrangements exist (alternate, opposite decussate, alternating whorls) in which any change of plastochrone ratio cannot lead to the replacement of one set of parastichies by another as the most nearly orthogonal pair, and in these arrangements therefore phyllotaxis index loses something of its significance. It nevertheless remains a valuable parameter, for in terms of it these systems may still be quantitatively compared with spiral systems, and, indeed, quantitative differences may be established even between apices which are usually regarded as displaying the same phyllotaxis, e.g. there is no reason to suppose that all opposite decussate apices have the same plastochrone ratio or phyllotaxis index, and a comparative study within this group might well prove of interest. Rising phyllotaxis will not be reflected here in a change in the number of conspicuous parastichies, but it will *alter the angle of intersection* in the 2:2 spiral system. The relation between this angle and phyllotaxis index is not entirely without interest, and will be elucidated in the following paragraphs, especially as its inclusion completes the survey undertaken in earlier sections.

These various systems from which 'rising' phyllotaxis (in the usually accepted sense) is excluded, all derive geometrically from the fact that a new primordium always appears in a position bisecting angles between the primordia of the preceding whorl; even in the alternate arrangement the new member may be regarded as bisecting the 360° angle round the whole apex terminated in either direction by the centre of the preceding primordium. It follows that the leaves produced at any node are orthostichous with those separated from them by two, four, etc., internodes. All these phyllotaxis systems are then essentially similar, the sole difference residing in the numbers of leaves occurring at the nodes, one in the alternate, two in the opposite decussate, x in alternating whorls of x. Hence in the opposite decussate arrangement we are dealing simply with a *bijugate* version of the alternate system, and in alternating whorls of x with an x-jugate version of the same system. If the relation between parastichy intersection angle and phyllotaxis index is known for alternate phyllotaxis it may be immediately obtained for these other arrangements by adding the appropriate constants. Such constants have already been determined in the consideration of multijugate Fibonacci systems, and the same corrections are applicable here. That this is so may readily be appreciated from the fact that a plane centric diagram of an opposite decussate arrangement could be bisected along any diameter, and either half rolled into a 60° cone displaying an alternate arrangement having the same parastichy intersection angle; similarly with a plane diagram of any system of alternating whorls.

In the alternate system only two parastichies wind round the apex, and these in opposite directions, each passing through every primordium; the system may thus be designated 1:1. Starting from relations (1) and (2) on p. 517

$$a \log_e r = \psi_a \cot \alpha_a \quad \text{and} \quad b \log_e r = \psi_b \cot \alpha_b,$$

it is seen that in this system $a = b = 1$; $\psi_a = \psi_b = \pi$ radians; and $\alpha_a = \alpha_b =$ one-half the intersection angle of the two parastichies. Therefore

$$\log_e r = \pi \cot \alpha.$$

For orthogonal intersection α is 45°; $\cot \alpha = 1$ and $\log_e r = \pi$, or $r = e^{\pi}$, an interesting conjunction of the two great incommensurable quantities of mathematics. Hence for orthogonality in the transverse plane the plastochrone ratio equals 23·14 and the corresponding phyllotaxis index is 0·057. So high a plastochrone ratio presumably never occurs at plant apices; in any event it is scarcely to be expected that growth would continue uniform over so large an area of the apex as it presupposes, and thus the fitting of logarithmic spiral parastichy lines can only be of formal interest here.

In Fibonacci phyllotaxis, at the point of exact transition between two orthogonal systems, the pair of parastichies representing one of these intersect at about 114° 6′. A similar intersection angle of the parastichies in alternate systems occurs theoretically with a plastochrone ratio of 7·662, or phyllotaxis index of 0·507, i.e. a number whose fractional part is almost exactly ·5, as in the Fibonacci systems whose parastichies intersect at this angle. Further, when any pair of parastichies in a Fibonacci system intersect at 135° the next higher pair is orthogonal, and the phyllotaxis index is almost exactly integral; similarly for intersection at 135° in the alternate arrangement $r = 3{\cdot}674$ and phyllotaxis index equals 0·972, or to the nearest one-tenth unit 1·0. In fine, the theoretical relation between the parastichy intersection angle and phyllotaxis index in the 1:1 alternate system is almost identical with that drawn in figure 2 for the 1:1 Fibonacci curve, i.e. when the divergence is the Fibonacci angle instead of 180°. It is, however, displaced very slightly downwards, by an amount that is scarcely larger than the error of drawing. This displacement, when measured in terms of phyllotaxis index, amounts at orthogonality to only 0·03 of a unit, and even at 179° to little more than double this quantity. Hence in the alternate arrangement phyllotaxis index could be interpreted formally in terms of parastichy intersection angle, to a very close approximation, exactly as it may be for any one pair of parastichies in Fibonacci systems.*

Since this is so for the alternate system it holds also for its multijugate counterparts, and in these, in consequence of their lower plastochrone ratios, the interpretation ceases to be merely formal. The only extra knowledge required is that of the phyllotaxis indices at orthogonality in these systems, obtainable by adding the constants already determined to 0·057, the value in the alternate system. Hence for the opposite decussate (bijugate) and other alternating whorled arrangements orthogonality coincides with the following indices:

orthogonal system	1:1	2:2	3:3	4:4	5:5	6:6
phyllotaxis index	0·057	1·497	2·340	2·938	3·402	3·780

With indices 0·5 of a unit higher than these values, intersection occurs at about 114° (each one-tenth unit accounting as before for approximately 5° increase in the angle over this range), and with indices 1·0 unit higher the intersection angles are increased to 135°, etc. Phyllotaxis indices lower than the orthogonal values listed are unlikely to be found, but if found could be interpreted in an analogous manner.

9. Relation between phyllotaxis index and total parastichies

From the general expression for $\log_{10} r$ in orthogonal Fibonacci systems (equation (4), p. 518), together with the definition of phyllotaxis index as $0{\cdot}379-2{\cdot}3925 \log_{10}\log_{10} r$, it may be shown that in these systems

$$\text{phyllotaxis index} = \tfrac{1}{2}n + 1{\cdot}19625 \log_{10} ab - 0{\cdot}414.$$

In this expression, as n increases by steps of unity ab increases nearly geometrically, hence among the various orthogonal Fibonacci systems a nearly linear relation exists between phyllotaxis index and the logarithm of the product of the numbers of parastichies in the two directions. Similarly, in orthogonal systems with parastichy numbers from the first accessory series, for instance,

$$\text{phyllotaxis index} = \tfrac{1}{2}n + 1{\cdot}19625 \log_{10} ab + 0{\cdot}422.$$

An even closer rectilinear relation exists between phyllotaxis index and the logarithm of the *sum* of the parastichies in the two directions. This is illustrated in figure 6 for all the various orthogonal arrangements discussed previously whose phyllotaxis indices do not exceed 5·0, including multijugate forms up to 5-jugy. Thus examples from a very wide range of phyllotaxis types appear in the diagram, and the closeness with which all the points cluster round a mean straight line is most striking.

In general, however, any three points are not exactly collinear, though certain groups are so. These are the points representing the various multijugate derivatives from each parent system; for example, the Fibonacci derivatives 1:2, 2:4, 3:6, 4:8, ... lie on one straight line, the systems 2:3, 4:6, 6:9, ... on another, and the alternating systems 1:1, 2:2, 3:3, ... on a third, and so on. These lines all have the same slope, which may easily be

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* This result is not surprising, for we are really dealing with a particular application of the curves shown in figure 3. In 1:1 'Fibonacci' systems the permissible variation in the divergence angle, for a given small error in phyllotaxis index, is very great, so that when this angle deviates to 180° the relation between the index and parastichy intersection angle is scarcely altered, even though a very different leaf arrangement is produced.

determined. The difference between the phyllotaxis indices of any x-jugate system and its parent system was shown on p. 531 to equal $2{\cdot}3925 \times 2 \log_{10} x$, where 2·3925 is the multiplier used in calculating the indices and is the reciprocal of $\log_{10}\left(\frac{\sqrt{5}+3}{2}\right)$. As this last equals $2 \log_{10}\left(\frac{\sqrt{5}+1}{2}\right)$ the above expression may be written $\frac{\log x}{\log(\sqrt{5}+1)-\log 2}$. Again, the total

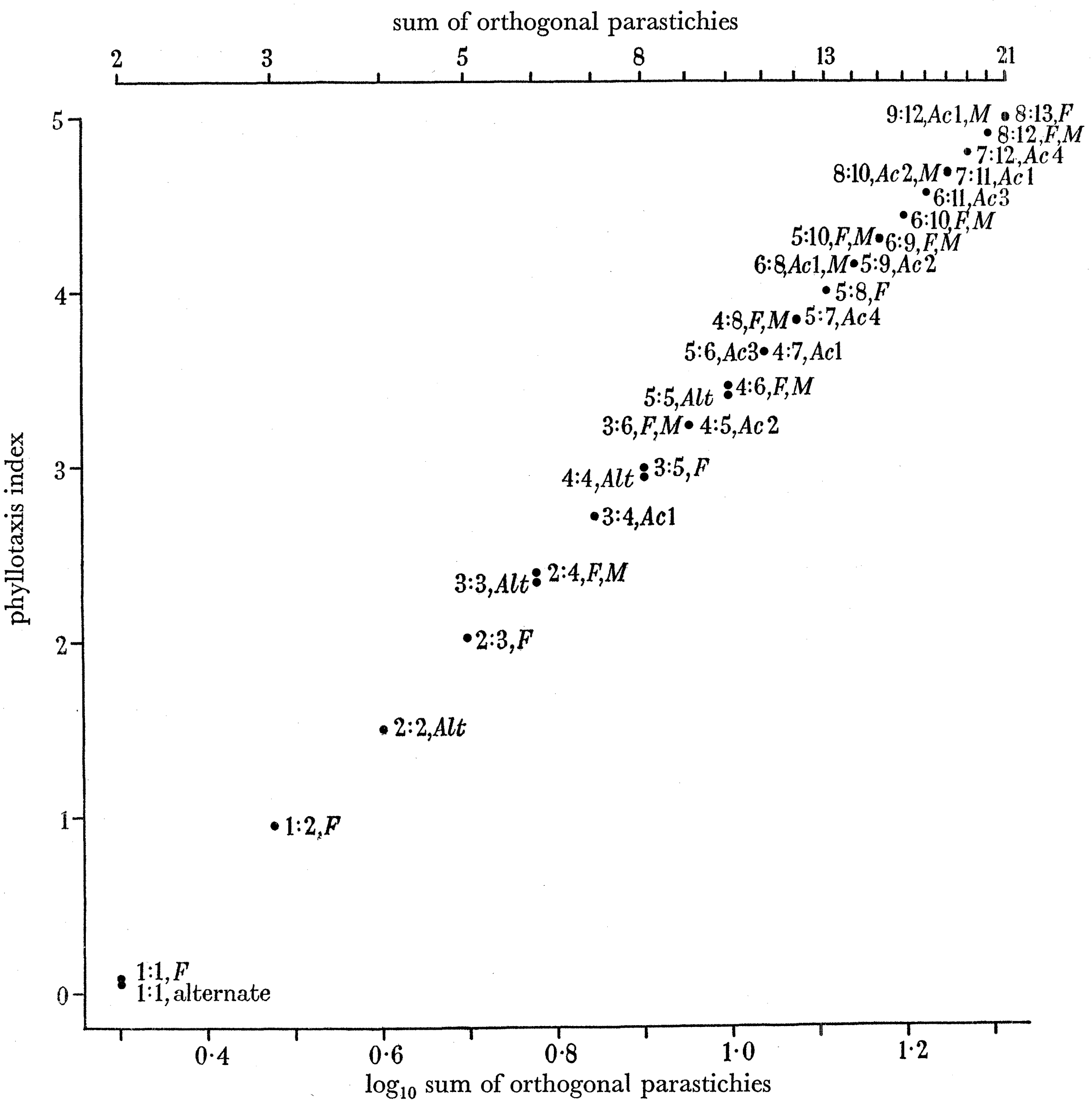

FIGURE 6. Relation between phyllotaxis index and the logarithm of the sum of the numbers of parastichies in a wide variety of orthogonal phyllotaxis systems.

F, Fibonacci, ∠ = 137·50776° . . . ;
Ac 1, first accessory, ∠ = 99·50155° . . . ;
Ac 2, second accessory, ∠ = 77·95525° . . . ;
Ac 3, third accessory, ∠ = 64·07936° . . . ;
Ac 4, fourth accessory, ∠ = 151·13566° . . . ;
Alt, alternating whorls;
M, multijugate variant.

parastichy number in the x-jugate system is by definition x times that in the parent system, hence the difference between the logarithms of the total parastichies in the two is $\log x$. The slope of any multijugate line in figure 6 is therefore $\tan^{-1}\dfrac{1}{\log(\sqrt{5}+1)-\log 2}$, or $\tan^{-1} 4{\cdot}785$.

Again, the slope of the line that fits best the points representing the successive orthogonal Fibonacci systems, together with those having parastichy numbers taken from any of the accessory series,* may also be calculated. For among both high Fibonacci and accessory systems, if the phyllotaxis index increases by one unit the sum of the parastichies becomes $\dfrac{\sqrt{5}+1}{2}$ times as great as previously. The slope of this line therefore is also

$$\tan^{-1}\frac{1}{\log(\sqrt{5}+1)-\log 2}.$$

That is to say, the best line through the starting points (the unijugate spiral systems) of the various parallel lines representing the several sets of multijugate systems is itself parallel to these same lines, and the whole system of points becomes nearly rectilinear. The only starting point not included in the above generalization is that of the alternating series, the point representing the alternate series itself, but, as has been shown, the phyllotaxis index for the orthogonal form of this arrangement is very close indeed to that for the orthogonal 1 : 1 Fibonacci, and so the point comes to lie very near to the line of best fit in figure 6.

Thus for all these systems phyllotaxis index appears to be only another way of expressing the total number of parastichies. This is of course not generally true. In the first place, only orthogonal systems are plotted in the diagram. A similar system of points could be inserted for any other constant parastichy intersection angle, yielding another composite line parallel to that shown but displaced in the vertical direction. For instance, if the intersection angle of 114° 6′ were chosen, the point representing any system would be raised by approximately one-half a phyllotaxis unit. Secondly, each spiral orthogonal system shown has been assumed to be conforming with its appropriate 'ideal' angle, and considerable deviation from this condition might lead to a large vertical displacement. But speaking generally, in the spiral systems found in plants phyllotaxis index may be expected to be quite closely related to the logarithm of the sum of the parastichy numbers in the two sets that intersect most nearly orthogonally. In the alternating systems this correlation will presumably not be so close, for in them only one set of parastichies is possible and these may intersect at angles very different from a right angle. Calling the sum of the most nearly orthogonal parastichies N, and assuming equal deviations on both sides of the line, the regression may be expected to be

$$\text{phyllotaxis index} = 4{\cdot}785 \log_{10} N - 1{\cdot}328.$$

10. Recapitulation of results

The salient points brought out in §§ 4 to 9 may be summarized as follows:

(1) The relation between phyllotaxis index and parastichy intersection angle is not seriously affected by such deviations of the divergence from the Fibonacci angle (or other 'ideal' angle) as are usually found in apices. Suggested permissible limits of divergence

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* It is unnecessary to present here a formal proof that the best fitting line for the Fibonacci systems not only has the same slope but is identical with that for each of the sets of accessory systems.

angle for the first few Fibonacci parastichy pairs, when each is the most nearly orthogonal pair in any system, are shown in table 2; within these limits phyllotaxis index may be interpreted unhesitatingly as though the divergence were exactly the Fibonacci angle, any error in the parastichy intersection angle deduced being not greater than about 6°. Should the limits given be appreciably exceeded orthostichy is approached in one of the two most nearly orthogonal parastichy sets and will become evident in the resulting 'spired' pattern.

(2) The parastichy curve system on the apical *surface* may be determined from a knowledge of phyllotaxis index together with the inclination of opposite sides of the apex to one another in the region of primordium initiation—or in any older part of the apex if so desired. In table A3 of the appendix are listed correction terms to be subtracted from the phyllotaxis index for various inclination angles of the apex. By this operation the 'equivalent phyllotaxis index' of the surface is obtained; this indicates that the parastichy relations on the actual apical surface are identical with those obtaining in a plane construction having a phyllotaxis index equal to it. They may therefore be immediately stated.

(3) 'Ideal' angles other than the Fibonacci lead to different numbers of prominent parastichies. Phyllotaxis index is related to these in a precisely similar way as to the parastichies in Fibonacci systems. A change in phyllotaxis index of one unit always indicates a step of exactly one system, so that intersection of the parastichies in the new system remains at the same angle as in the old. The Fibonacci systems are unique in that orthogonal conditions correspond with integral phyllotaxis indices; the orthogonal relations for four other divergence angles are given in table A1 of the appendix, thus enabling the index to be interpreted directly in any of these systems.

(4) Multijugate systems again are related to phyllotaxis index in just the same way. The production of more than one primordium at each node entails a slight complication in the estimation of the index; the necessary adjustment may be made either by adding a constant to the index as directly calculated from measurements on the apex, or by dividing the logarithm of the 'plastochrone ratio' as measured by the number of leaves produced at each node, as explained in the appendix. In the same place are also given the data for determining the indices for orthogonality in any multijugate system. The opposite decussate is a bijugate development of the alternate system, and alternating whorls of x members provide an x-jugate representation of the same arrangement; these can all be dealt with by the methods described.

(5) A close rectilinear relation exists among the parastichy systems belonging to all these various phyllotaxis types between phyllotaxis index and the logarithm of the sum of the numbers of parastichies in the two most nearly orthogonal sets at the apex. The relation is illustrated in figure 6.

In bringing the theoretical section of this part of the paper to a close, the main advantages of the methods proposed may very briefly be re-stated. It is evident that the phyllotaxis index presents all the information relevant to the radial spacing of the primordia at any stem apex. Together with divergence angle, the measure of tangential spacing, it completely defines the transverse phyllotaxis system, and defines it in such a way that in any spiral arrangement the parastichy relations involved are immediately apparent. It provides a criterion whereby any phyllotaxis system may be directly compared with any other in terms of an essential quantitative characteristic, however unlike the primordial patterns of the two systems may appear. In conjunction with a simple angular measurement taken from a longitudinal section of the apex it enables the curve system as it exists on the actual apical surface to be accurately described, just as readily as is that of the transverse component. Furthermore, its counterpart, the plastochrone ratio (into which it is easily transformed), when considered in relation to the plastochrone period, will frequently give valuable information concerning growth rates within the apex. Finally, the methods, being based entirely on strict analysis, provide data with which any theory of leaf-positioning must be in harmony. The failure of past classificatory systems has been due to their derivation from some particular, and false, phyllotaxis theory, so that the data collected have little more permanent value than the theory itself; indeed, by a regrettable inversion, the facts of phyllotaxis have frequently been falsified in order to conform with the postulates.

In § 12 some applications of the methods advocated are illustrated, using published data, but prior to this certain practical points relating to the collection of data are considered in the following paragraphs.

11. Some practical considerations

In the practical determination of plastochrone ratio and phyllotaxis index it is occasionally possible to take the necessary measurements directly from a plan of the apex. This is eminently true of many fern apices, for which camera lucida drawings of the region are sufficient. In ferns practical difficulties are minimized in a second way, for the apical cell defines the centre of the system, and the distances of the primordia from this centre may be determined with relative ease.

Most phanerogamous apices cannot be treated in this way and transverse sections become necessary. On a section taken at the level of the younger primordia the positions of the primordial 'centres' are often well defined by the vascular strands, but the determination of the centre of the whole system is a more difficult matter, and the best position can be located only by trial. That position must be deemed best from which the distances of the successive primordia fall into the most uniform progression.

There is, however, an objection, sometimes serious, to the use of a single transverse section when determining the required distances. The leaf primordia are cut at different levels above their insertions on the apex, and unless their bundles all follow a course parallel to the stem axis, measurements of their relative distances from the centre may not reflect sufficiently exactly the transverse growth of the apex in successive plastochrones. Serial sections circumvent this difficulty, for then each leaf may be measured at a comparable level close to its insertion. The chief objection to this procedure is that the centre of the axis needs determining afresh on each section used, and the several estimates will not exactly correspond. Nevertheless, there seems no doubt that it is generally preferable to employ serial sections.

It is possible to avoid the determination of the axial centre altogether, for in a system growing uniformly the plastochrone ratio (r) will appear in ratios of other distances on the sections, e.g. numbering the primordia inversely as their ages, r will be given by the distance of the centre of 3 from that of 2 divided by the distance of 2 from 1. This fact does not generally provide the basis of a good method, for measurements so obtained are affected by inequalities in divergence angle as well as in plastochrone ratio, but on occasion it may be useful; a similar method is always useful in bijugate systems (including the opposite decussate), where the distance across the apex between the members of any leaf pair is very easily determined. Again, it is possible that in some plants the ratio of the diameters of consecutive primordia may give a good estimate of r, but usually the primordia do not grow uniformly with the apex, and also change their form in the transverse plane during their first few plastochrones.

A simple and easily made measuring device, consisting of a fairly large number of concentric circles with radii in arithmetical progression, is useful in helping to locate the best position for the centre of the system and to speed up the measurements. The circles, except for every fifth, which may be heavier, should be thinly drawn in Indian ink on paper and reduced by photography to such a size that they are separated by distances of 1 mm. or more, depending on the sizes of the drawings to be measured; care must, however, be taken that the photography does not distort the circles into ellipses. The whole is printed rather faintly as a 'ghost' transparency and applied, unbound and gelatine side downwards to avoid parallax, to the drawings to be measured; such an arrangement will neither conceal and confuse the drawings nor unduly dazzle the eye. The circles first enable the position of the plate to be adjusted so that the primordia under examination are spaced outwards from their centre as uniformly as possible, and then provide the scale to measure the primordial distances from this point. It appears probable that a similar method could be used to measure the sections directly through the microscope; for this purpose the photographic reduction would need to be considerably greater, to a size suitable for an eyepiece graticule; the circles might be printed on film and this mounted between cover-slips.

When determining plastochrone ratios oblique sections should be avoided as far as possible. Single determinations of r (e.g. derived from the distances from the centre of primordia 1 and 2, or of 2 and 3) are subject to considerable error, owing largely to the fact that the primordia compared are situated in very different azimuths; one region of an apex may differ slightly from another in its growth and irregularities persist sufficiently long to be reflected in the phyllotaxis pattern; obliquity of the sections would produce a similar effect. Hence measurements in radial directions inclined to one another at only small angles are preferable. In Fibonacci phyllotaxis this means that primordia differing in age by 2, or better by 3, 5, 8, etc., plastochrones should be compared, according to the height of the system. If now the radial distances of two primordia differing by three plastochrones be measured, the plastochrone ratio is given by the cube root of the ratio of the measurements.

A better estimate could be obtained by finding log r as given by each of the pairs of primordia 1 and 4, 2 and 5, 3 and 6, and taking the mean of the three derived estimates before converting to phyllotaxis index. Finally, in order to achieve the greatest accuracy a slightly more laborious method may be used, and particularly so if the change in phyllotaxis index or plastochrone ratio is to be followed as the primordia recede farther and farther from the apex. The distances of all the primordia over the required range may then be recorded and their logarithms taken; provided there is no appreciable evidence of the increment in these distances decreasing with increasing plastochrone number, a straight-line regression may be fitted, relating log distance to age in plastochrones. The slope of this regression provides the best estimate of log r. The arithmetic is simple, an example being worked out later (p. 541). Should the increment decrease with distance from the centre a curved regression will enable the best value at any plastochrone age to be determined (see p. 560).

In order to obtain knowledge of the curve system on the apical surface the phyllotaxis index obtained as above may be converted into the equivalent phyllotaxis index for that surface. The angle of inclination towards one another of opposite sides of the apex in the region under consideration is then required (2θ), and may be obtained easily from a longitudinal radial section. This method, however, involves collecting the two sets of required data from different apices, and to this extent is unsatisfactory. If the measurements for phyllotaxis index are made on serial transverse sections of known thickness, the latter may also be used for determining the angle of inclination required. Thus if d_1 is the radial distance of one primordium at its insertion level and d_2 is that of another, and the higher measurement is made on the nth section above the lower, each section having a thickness of h, then $\tan\theta = \frac{d_1 - d_2}{nh}$. From either 2θ or $\tan\theta$ the appropriate amount to be subtracted from the phyllotaxis index may be read from table A3 in the appendix. It is, however, especially important to note that if transverse sections alone are used, oblique cutting must be scrupulously avoided.

12. ILLUSTRATIONS OF THE METHOD

A few illustrations follow of the application of the above methods to certain published phyllotaxis data, though it should be borne in mind that these data were not collected for the purpose and so do not provide ideal material.

(a) *Dryopteris aristata*

As a first example may be taken the apex of the fern *Dryopteris aristata*, which presents a dilemma when classification is attempted by the method in general use, i.e. the numbers of contact parastichies in the two directions. The primordia are in fact very far from being in contact one with another, each being separated from its neighbours by an expanse of bare apical surface. It has already been pointed out (Richards 1948) that methods involving the use of plastochrone ratios provide the sole means of classifying and assessing such systems. Wardlaw (1949, p. 171), however, writes concerning his own text-figures 5 and 6 'it would be more accurate to describe [primordium] I_1 as originating between [primordia] P_3 and P_5, rather than between P_2 and P_3, although the latter description is not incorrect'; and again, on p. 188 concerning his text-figure 44, 'In a phyllotactic system of this kind some investigators would no doubt regard P_2 and P_3 as the "contact" primordia. But direct observation of fern apices indicates that the primordia immediately adjacent to I_1 are P_3 and P_5.' Clearly such a position is unsatisfactory; for in dicotyledonous apices there is no guarantee that the contact system of primordia is the same as the system of *nearest* primordia, when distances are measured from their central regions; that this is not always so is readily seen from figures 1*c* and *d*. Some other method of assessing phyllotaxis is essential if comparison is to be made between the apices of leptosporangiate ferns and those of flowering plants.

In Wardlaw's figure 4, five primordia are represented together with the position of the apical cell. Measurements on the drawing give relative distances from the centres of these primordia to the apical cell as shown in column 2 below, and the logarithms of these distances are given in column 3. In order to determine plastochrone ratio and phyllotaxis index the extreme values might be chosen, relating to primordia 1 and 5. The difference of their log distances divided by the difference of their ages in plastochrones gives the mean $\log_{10} r$, i.e. $\frac{1}{4}(0{\cdot}702-0{\cdot}589)=0{\cdot}02825$. Hence the estimate of plastochrone ratio becomes 1·0672; the corresponding phyllotaxis index is 4·08. Table A4 in the appendix may be used for converting the estimated $\log_{10} r$ into phyllotaxis index, giving 4·1.

primordium (P)	relative distance	$\log_{10}$ distance (L)	P^2	$P \times L$
1	3·88	0·589	1	0·589
2	4·11	0·614	4	1·228
3	4·50	0·653	9	1·959
4	5·10	0·708	16	2·832
5	5·03	0·702	25	3·510
total 15		3·266	55	10·118
mean 3			45	9·798
			10	0·320

$$\log_{10} r = \frac{0{\cdot}320}{10} = 0{\cdot}0320$$

The $\log_{10}$ distances in column 3 show that although the mean increment is 0·02825, individual increments differ rather widely from this value; indeed, primordium 4 is situated slightly farther from the apical cell than is number 5, which is presumed older. When irregularity is as great as here, it is advisable to fit a regression to the data, as by this means equal weight is given to the evidence provided by each primordium. The arithmetic, worked out above, is particularly simple, for the independent variate, primordium number, consists of the successive integers. The best estimate of $\log_{10} r$ derivable from the data is given by the ratio of the numbers derived in the last two columns, in this instance 0·0320. Hence phyllotaxis index becomes 3·95 and plastochrone ratio 1·0765.

The general level of the index indicated in the above example is confirmed by measurements taken from other apices figured by Wardlaw (1949). Thus by applying the regression method to measurements relating to the last eight primordia shown in his figure 1, an estimate of 3·80 has been obtained; similarly, from the last ten primordia of the apex drawn in his figure 5 an index of 3·87 has been derived.

The statistical error of $\log_{10} r$ in each of these estimates may of course be calculated, and from it the limits of phyllotaxis index within which the 'true' value for the apex may be assumed to lie with a given level of probability. The example worked out above, which was chosen largely because of the aberrant positioning shown by some of the primordia, has an unusually low precision, and for a probability level of 0·05 the fiducial limits of the index are 3·5 and 4·7; for a probability of only 0·2 the range becomes restricted to 3·71–4·27. The other two apices mentioned have considerably lower errors, the index range for 0·05 probability being 3·63–4·00 in Wardlaw's figure 1, and 3·66–4·14 in his figure 5. The results from these apices thus reinforce one another, and it may be assumed with some confidence that the best value lies between 3·8 and 3·9, or only very slightly outside these limits.

Wardlaw's figure 6 presents an 'idealized phyllotactic system' for comparison with the real apex of his figure 5. In this diagram, however, only the divergence angles have been equalized, for the increments in log apical distance between the first ten primordia vary irregularly over the approximate range 0·025 to 0·08. The regression method yields a phyllotaxis index for the diagram of 3·51, and indicates a distinctly lower system than that of the real apex it illustrates, the best value lying outside the probable range given in the previous paragraph for the real apex; indeed, the difference between the two drawings in this respect is appreciable to the eye. A further 'ideal' arrangement of primordia is presented in his figure 40, and from this an index slightly above 3·9 has been obtained, which may perhaps be considered as confirmatory evidence of the general level in these apices.

Phyllotaxis indices of 3·8 to 3·9 then are indicated by the drawings, and it follows that as seen from above the 5:8 system of parastichies in these apices is much more nearly orthogonal than the 3:5, their intersection angle being over 80°. In the same article Wardlaw (1949, figure 2) presents a semi-diagrammatic drawing of a median longitudinal section. The apical cone, on whose lower flanks the primordia are produced, is comparatively broad, having an angle of 98°, so that $2{\cdot}39 \log_{10} \sin 49°$, or 0·29, gives the amount to be deducted from the phyllotaxis index proper in order to obtain the equivalent phyllotaxis index of the surface towards the base of the apical cone (from table A3 in the appendix the correction may be read as 0·3). The equivalent phyllotaxis index thus becomes 3·5 to 3·6; that is to say, on the surface in the region of initiation the parastichy systems 3:5 and 5:8 are almost equally removed from orthogonality, though probably the higher system is a little nearer orthogonality than the lower. In choosing the system 3:5 rather than 2:3 Wardlaw has not therefore overstepped the evidence provided by the apices; on the contrary, any argument that might exist lies between the claims of 3:5 and 5:8. But the statement that the equivalent phyllotaxis index is 3·5 to 3·6 leaves little room for uncertainty, and the intersection angle of either parastichy pair on an idealized apex may be stated with only a narrow margin of error.

This method of dealing with phyllotaxis carries with it also interesting implications regarding growth rate within the apical cone. Provided the apex remains constant in size, or nearly so, i.e. that the successive primordia are initiated at the same distance from the apical cell (and there is no reason to suppose this is not substantially correct in the present instance), then the natural logarithm of the plastochrone ratio is the transverse linear relative growth rate of the lower part of the apical cone, time being measured in plastochrones. Twice this value gives the corresponding growth rate of the transverse area. Again, the maintenance of a given conical form at an apex implies very strongly that in any frustum the longitudinal growth rate equals the linear transverse rate. For if the longitudinal rate is higher than the transverse the form of the frustum will change and the apex as a whole may be expected to deviate towards the shape usually described as paraboloidal, the flanks becoming convex in the longitudinal direction; while if the longitudinal rate is lower than the transverse the flanks will become concave in this direction. Hence in the apical cone of *Dryopteris* it may legitimately be assumed that the growth rates in all directions are approximately equal, and that the volume relative growth rate per plastochrone is roughly $3 \log_e r$. Since for a phyllotaxis index of 3·8 to 3·9, $\log_e r$ equals 0·082 approximately (appendix, table A4), this indicates the relative rate of radial increase per plastochrone, and the corresponding volume increase is 0·246. As $\log_e 2 = 0{\cdot}693$, the time taken for a given frustum of the lower part of the apical cone to double its volume is 0·693/0·246, or 2·82 plastochrones approximately. Since Wardlaw (1949, p. 171) states that his specimens 'formed new primordia at the rate of about one per week', this implies a period of about 19 to 20 days. On the data presented then it appears that the *minimum* period that must be assumed to elapse between two consecutive divisions of the same cell towards the base of the apical cone (i.e. in the event of there being no growth by cell enlargement) is on the average nearly three weeks; the average cell in the interior of the cone remains quiescent while about three primordia are being produced at the surface.

(*b*) *Lupinus albus*

A second illustration may be taken from the experiments of Snow & Snow (1931, 1933) on *Lupinus albus*. On p. 4 of the first of these papers it is stated that the 'contact parastichies of *L. albus* form a 2+3 system. The leaves have stipules which extend round the axis, so that the stipules of successive leaves are in contact with each other. If the stipular contacts are included, the contact parastichy system becomes 1+2+3 .... The primordia arise as circular humps, with the stipules forming tapering horizontal projections on either side. The whole primordium is thus roughly oval in shape with its longer diameter lying transversely to the axis of the shoot.' Even in dicotyledons then, with the leaf members making close contact everywhere, the correct position in the binomial classificatory system may be doubtful. Moreover, the drawings of transverse sections presented, and also the diagrams showing the contact relations as seen in surface view, indicate clearly that while the central parts of the primordia are in contact along the 3-parastichies, they are far from being so along the 2-parastichies. Hence if the system be described as (2+3), one of the contacts referred to is made by the central parts of the primordia only, while the other involves a stipular contact. For this reason it might perhaps seem preferable to regard the system as (1+2), these being the overall stipular contacts, rather than (2+3). However, for purposes of classification and assessment at least, it is advisable to avoid the difficulty altogether and to use a system leading to an unambiguous conclusion. This is not to say that information regarding the actual contacts is either valueless or superfluous—indeed, for some purposes it may be important—but that it is information which by itself gives no clear idea of *phyllotaxis* proper; in conjunction with such a measure as phyllotaxis index it provides very full data indeed as to the geometry at the apex.

Estimates of phyllotaxis index may be obtained from several of the sectional drawings of apices presented by Snow & Snow; the methods used are similar to those adopted when assessing the *Dryopteris* apices of Wardlaw, but owing to the fact that transverse sections now replace the plan of the apex, for reasons given above (p. 538) it is necessary to confine the measurements to a smaller number of the youngest primordia. At least this is so when, owing to the fact that only a few isolated sections from any apex are presented, the measurements must be confined to a single section. This may well increase the error of determination, although in fact the *Lupinus* apex appears to be more regular than that of *Dryopteris*. A number of determinations on single sections have led to phyllotaxis indices ranging from 2·8 to 3·3, and usually a little higher than 3·0.

For a few of the apices depicted, however, it is possible to obtain estimates derived from two sections, using two selected primordia each measured at the particular level where it is just breaking completely free from the axis. Such an estimate may be compared with a similar one derived from the same two primordia, but in this case taken from a single section, the upper one of the two previously used. The estimate derived from two sections appears to be a little higher than that derived from a single one:

	phyllotaxis indices from four apices			
single section	3·30	3·26	2·99	2·83
two sections	3·39	3·61	3·17	3·04

The mean difference is 0·2 of a unit. Accepting this value and applying it as a correction to the more numerous estimates based on single sections, it appears that the phyllotaxis index of a typical *Lupinus* apex as used by Snow & Snow is about 3·2 to 3·3; in plan the 3:5 system of parastichies intersects at 100 to 105°.

A few longitudinal sections of *Lupinus* apices are presented by Snow & Snow, and others are given by Pilkington (1929); from them estimates are obtainable of the apical angle of the cone that best fits the region of primordial initiation. Unfortunately for the present purpose these apices had usually been mutilated some time before sectioning, a fact that may possibly account for a rather high variability among the estimates derived from them. The angles measured are respectively 48, 48, 52, 56, 58, 59, 60, 63 and 78°, with a mean of 58°. Hence the equivalent phyllotaxis index of an average apex is about $3·25-0·75$, or 2·5, and on the apical surface the phyllotaxis is almost exactly midway between the 2:3 and 3:5 orthogonal systems. The fact that the stipular contact parastichies are expressed by appreciably lower Fibonacci numbers, i.e. $(1+2)$, indicates the considerable tangential elongation of the primordia in this species.

The result throws an interesting sidelight on certain diagrammatic representations of the primordial arrangement on the apical surface, reconstructed from careful observation of the primordial sizes and contacts (Snow & Snow 1931, figures 9, 12, 13; and 1933, figures 4, 10, 17). In these diagrams the apical surface is represented in a cylindrical transformation. In the 1931 reconstructions the resulting intersection angle of the 2- and 3-parastichies, measured on the diagrams, is 105°, and that of the 3- and 5-parastichies 61°; as the assumed divergence angle is 136°, it may be deduced from the present figure 3 that the equivalent phyllotaxis index represented by these diagrams is 2·36. Certain modifications were made in the 1933 reconstructions, and the angles of intersection of the same two parastichy pairs become 114 and 70° respectively, corresponding to an equivalent phyllotaxis index of 2·54. These numbers, especially the second, agree very closely with the value 2·5 deduced by measurement and calculation from the sections presented, and indicate the essential accuracy of the positioning of the primordia in the reconstructions of Snow & Snow, in spite of the doubts expressed by these authors as to their exactness.

A final point deducible from these data refers to the rate of increase in volume of the internal apical mass in the region of initiation. Calculation similar to that used in the case of *Dryopteris* leads to the conclusion that a given section in an apex having a phyllotaxis index of 3·25 will double its volume in about 1·6 plastochrones; since the plastochrone is apparently about three days, the average cell may be expected to divide every five days or rather more frequently, about four times for every division in the apical cone of *Dryopteris* in Wardlaw's experiments. The assumptions underlying this result (constancy of apical size, equality of longitudinal and transverse growth rates, and absence of cell enlargement) are possibly less likely to be strictly true than in the apical cone of the fern, yet it is unlikely that any of them will lead to serious error. Clearly departures from all these assumptions could be observed and some allowance made for them.

(*c*) *Epilobium hirsutum*

One last illustration of a rather different kind may be given, again from the writings of Snow & Snow (1935). It concerns the data from an experiment in which the opposite decussate apices of *Epilobium hirsutum* were split into two by vertical diagonal cuts. The majority of the regenerated half-apices subsequently developed spiral phyllotaxis, though a few either remained decussate or returned to this arrangement after a few primordia had appeared. There is little resemblance between the apical patterns of opposite decussate and spiral systems; not only are their angular relations entirely different, but one of them is bijugate and orthostichous while in the other only one leaf is produced at a time and orthostichies are absent. It becomes of considerable interest therefore to determine in what manner, if at all, radial spacing was affected in those apices that became spiral, and whether the relationship usually existing between the rate of growth within the *Epilobium* apex and the rate of production of primordia was modified with the pattern of the system.

Drawings of one particular split apex are presented by Snow & Snow (1935, figure 11) which are of special interest from this point of view; both halves regenerated and grew well, one of them becoming spiral (Fibonacci), while the other quickly re-established the opposite decussate arrangement; at the time of sectioning the spiral apex had produced ten primordia, the other eleven. Relative distances of the last six promordia from the centre in the spiral system are as follows: 0·47, 0·51, 0·59, 0·78, 0·87, 1·15. By the regression method a phyllotaxis index of 3·02 is obtained. This estimate is quite unchanged if the distance of the seventh leaf (1·31) also be included in the calculation, but is slightly raised (to 3·11) if either the sixth alone, or the fifth and sixth, be omitted. The corresponding distances of the three youngest pairs of primordia in the opposite decussate apex are respectively 0·44, 0·63 and 0·91, and their logarithms $\bar{1}{\cdot}643$, $\bar{1}{\cdot}799$ and $\bar{1}{\cdot}959$. With only three values the best estimate of the log increment, i.e. that provided by the regression method, is given also from the first and third values alone. Their difference, 0·316, needs to be divided by 4 in order to obtain $\log_{10} r$, for each of the two actual increments is a double one in the sense that it represents the production of two leaves. Hence $\log_{10} r$ equals 0·079 and the phyllotaxis index becomes 3·01, almost identical with that obtained from the spiral partner when the same number of leaves, six, is used in each calculation. If the oldest pair of leaves be omitted the resulting index is 3·05, comparing with 3·11 derived from the innermost four leaves of the spiral apex. There is therefore no indication here that the phyllotaxis index was altered when the transition from an opposite decussate to Fibonacci phyllotaxis took place.

This result is confirmed by other apices figured by Snow & Snow. Thus the index derived from the normal decussate apex of their figure 2 is 2·96, and those of two other apices which after cutting returned to decussation 2·94 (figure 9*a*) and 2·86 (figure 10*a*) respectively. Corresponding indices from other split apices that became spiral are 3·00 (figure 4*a*, *A*), 2·98 (figure 5*a*, *A*), 2·85 (figure 7*a*, *A*), 2·74 (figure 4*a*, *B*) and 2·72 (figure 3*a*, *A*). The last two are a little low; this may be a matter of apical size, i.e. of the amount of tissue regenerating. Thus two of the specimens (figure 4*a*, *A* and *B*) were derived from a single split apex; the one with the lower index had produced only five leaves since regeneration, whereas the other had produced seven.

The general relation between phyllotaxis index and apical size may be illustrated from these same data, for in their figure 16 are presented sections of young spiral axillary buds which arose on some of the split apices when the main portion did not regenerate. The index derived from figure 16*a* is 2·68, and that from figure 16*c* is 2·29, both appreciably below the usual level in regenerated apices. Again, one axillary bud (Snow & Snow 1935, figure 17), presumably smaller than the others, produced four primordia in a distichous (alternate) arrangement; the phyllotaxis index estimated from the youngest three is 1·81. So far as the evidence goes then it appears that the transition from the alternate to the spiral system (when it occurs in these buds) may take place within the index range 1·8 to 2·3.

Returning to the full-sized regenerated apices in these experiments, the above analysis amply confirms the belief that the change from opposite decussate phyllotaxis to a spiral system has occurred without any appreciable alteration in the fundamental growth phenomena, though full confirmation perhaps requires the determination of the angle of the apical 'cone' in both types. The actual pattern on apices of the same size is to a large extent incidental. This result recalls the observation of Schüepp (1916) that the plastochrone in decussate specimens of *Helianthus annuus*, as measured between the successive leaf pairs, is double that of similar plants with spiral phyllotaxis, the plastochrone in the latter being measured in the usual way.

13. Conclusion

The primary object in the first part of this article has been to point out the inexactitude and ambiguity underlying current methods of classifying phyllotaxis patterns and to propose a new system which rigidly defines the positions of the primordia in the region of initiation by means of a numerical index (the *phyllotaxis index*) derived by simple calculation from measurements easily carried out on sectioned material. Tables also are provided in an appendix by whose use much of the calculation may be avoided.

So long as phyllotaxis at an apex is steady the measurements taken are essentially growth measurements, and these, together with the divergence angle, relate the transverse phyllotaxis pattern to the radial growth rate of the apex and to the rate at which it produces primordia; under some circumstances valuable deductions may be drawn about the rate of volume increase of the apical tissues. In spiral systems the phyllotaxis index, calculated from measurements on transverse sections, conveys information about the parastichy relations in the transverse plane much more exactly and almost as readily as does the usual method of quoting the contact parastichies of the system. For Fibonacci systems, much the most frequent of all spiral forms, these relations are immediately apparent from the index itself, for others slight extra information is required, and this also is tabulated in the appendix.

The determination of an angle on a longitudinal section, in addition to the measurements on transverse sections, further enables the phyllotaxis index to be reduced by such an amount that it now indicates the parastichy relations existing on the actual apical surface in just the same way as the original index defines those of the transverse component.

By these means phyllotaxis becomes a continuously varying function, not one which, being confined to a few discrete recognized systems, is characteristically discontinuous. Phyllotaxis indices enable an important feature of all the widely different types of primordial arrangements to be quantitatively compared, with the exception of those alternate systems that arise on cylindrical apices.

The application of the methods advocated to some published data and drawings illustrates something of their scope, but more complete analyses than these might be possible on data collected specifically for the purpose, and it is hoped that the present contribution may stimulate investigations along these lines.

PART II

14. Effect on phyllotaxis of changing apical size; 'area ratio'

The relationship between phyllotaxis index and the transverse growth characteristics of the apex may be stated with greater precision than hitherto. In the transverse system let

x = radial distance of a particular primordium at the time of its first appearance (time 0).
y = radial distance of the next primordium at the time of its first appearance (time t).
z = radial distance of the first primordium at time t.
r = plastochrone ratio.
c = radial relative growth rate of the apex.

In the general case x need not equal y, for the central region of the apex which does not bear primordia may itself be either increasing or diminishing in size quite apart from the periodic fluctuations associated with primordium production.* During the plastochrone (t) the radius x expands to z, hence

$$c=\frac{1}{t}\log_e\frac{z}{x}.$$

Also

$$r=\frac{z}{y}=\frac{z}{x}\div\frac{y}{x}.$$

Hence

$$\log_e r=ct-\log_e\frac{y}{x},$$

or

$$\log_{10}r=\frac{ct}{2\cdot3026}-\log_{10}\frac{y}{x}.$$

$$\begin{aligned}\text{Phyllotaxis index}&=0\cdot379-2\cdot3925\log_{10}\log_{10}r\\&=0\cdot379-2\cdot3925\,[\log_{10}(ct-2\cdot3026\log_{10}y/x)-\log_{10}2\cdot3026]\\&=1\cdot246-2\cdot3925\log_{10}(ct-2\cdot3026\log_{10}y/x).\end{aligned}$$

In this relation, phyllotaxis index is expressed in terms of the radial growth rate of the apex as a whole, the change in size of the bare central portion during one plastochrone, and the plastochrone itself. For the practical determination of the mean change in size of the bare portion per plastochrone, and hence also c, observations of the same apex would be necessary at intervals, or alternatively it might be possible to use a sampling method; thus,

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* That large changes in apical size may sometimes occur during development is well illustrated in *Cyathea* (Wardlaw 1948), where a well-grown apex may have linear dimensions 7 to 10 times as great as those of a young apex.

when the bare apex is changing in size, growth data can be obtained only from growth measurements repeated at intervals over a period of time, although a precise relation still exists between the growth characteristics and the phyllotaxis pattern. But where the bare central apex may be assumed to remain constant in size, or its growth per plastochrone to be slight relative to the plastrochrone ratio, $\log y/x$ approaches zero and the relation reduces to

$$\text{phyllotaxis index} = 1{\cdot}246 - 2{\cdot}3925\,(\log_{10} t + \log_{10} c).$$

The radial relative growth rate c, may then be deduced from phyllotaxis measurements taken on an apex on one occasion only, provided the plastochrone is also known.

For phyllotaxis to remain constant while the bare portion of the apex is growing, $ct - 2{\cdot}3026 \log_{10} y/x$ must also remain constant. If neither the plastochrone nor the relative growth rate of the apex as a whole (c) changes, then y/x must also be invariable from one plastochrone to another. In this event the bare region expands exponentially (apart from its periodic fluctuation in each plastochrone), and calling its radial relative growth rate c',

$$\text{phyllotaxis index} = 1{\cdot}246 - 2{\cdot}3925\,[\log_{10} t + \log_{10}(c - c')].$$

It is probable, however, that the bare apical portion will increase in size more nearly linearly, so that y/x, and therefore c', decreases with time. Under these conditions phyllotaxis index also decreases. If both the growth rate of an apex as a whole and the plastochrone remain constant, while the central bare area increases from a previously fixed size until it reaches another at which it again becomes stable, the phyllotaxis index during the change must first rise from its initial value to a higher one and finally fall again to the original value. The change in size of the apex will have had a temporary effect on phyllotaxis (while it was occurring), but no permanent effect. In fact, however, the height of phyllotaxis is known usually to be correlated with size of apex, hence it appears inevitable that, when the bare portion increases in diameter, either the growth rate of the apex as a whole, or else the plastochrone, must normally diminish. Presumably the dominant effect is on the plastochrone, and indeed such a change may almost be regarded as automatic, as the following considerations show.

Whatever may be the immediate causes of the *absolute* distancing of the primordia from one another at initiation, assume that they do not change while the radius of the bare portion of the apex producing them increases from R_1 to R_2; provided that full contact is maintained among the primordia, this is tantamount to the assumption that their absolute size at initiation does not alter with that of the bare region of the apex. Assume further that the relative growth rate of the whole apex, c, does not alter. Primordia are produced, both before and after the change in apical size, as rapidly as space becomes available, through growth of the system, beyond the limit defined by the circle of radius R_1 (or R_2). The rate of liberation of space beyond such a circle depends on (1) the circumference of the circle and (2) the rate of recession of the newly formed primordia from its vicinity, due to apical growth. Since the apex is assumed always to expand exponentially at the rate c, each of these factors is proportional to R, and when the bare apex changes its radius from R_1 to R_2 the rate of liberation of space available for primordium production becomes $(R_2/R_1)^2$ times the original rate. Hence the plastochrone changes in the inverse ratio.

Since phyllotaxis index equals $1{\cdot}246 - 2{\cdot}3925\,(\log_{10} t + \log_{10} c)$, it must decrease by $2{\cdot}3925 \log_{10} (R_1/R_2)^2$, i.e. increase by $4{\cdot}785 \log_{10} R_2/R_1$. If then no changes occur in the magnitudes of the factors concerned in the distancing from one another of the primordia at initiation, and the diameter of the bare apex doubles, phyllotaxis index automatically increases by $4{\cdot}785 \log_{10} 2$, or 1·44 units; for a rise of one unit due to this cause the apical diameter must increase to 1·618..., i.e. $\frac{\sqrt{5}+1}{2}$ times its original length, or its area to 2·618... or $\frac{\sqrt{5}+3}{2}$ times the initial size.

The concept of phyllotaxis index as a resultant of the transverse apical growth rate and of the plastochrone thus leads easily to another, equivalent to that of 'bulk-ratio', i.e. the relative sizes of apex and primordium in relation to phyllotaxis level. In the present terms the relation is particularly simple, for it is evident that although the method of approach has been to postulate a constant primordial size, or rather spacing, and varying apical size, yet it is the ratio of the two that determines the phyllotaxis index; the absolute sizes of apex and primordium are immaterial, and provided their ratio is constant phyllotaxis also is fixed. Hence, as regards the transverse component of the system, a change of 2·618... times in the ratio of bare apical area to the area associated with a newly initiated primordium leads always to a change of one unit in the phyllotaxis index, regardless of whether the change occurs in apical size alone, primordial size alone, or in both simultaneously.

The solution of the problem of 'bulk-ratio' given here is, moreover, a practical one, being in a form in which it may easily be applied to the plant. This is so because elements have been chosen that are unaffected by the idiosyncrasies of particular apices; e.g. the shapes of primordia are not considered. It should be emphasized also that it is not necessarily the transverse area of the newly initiated primordium that is referred to, but the projection on a transverse plane of the portion of apical surface associated with a single primordium, whether or not the whole of that area is actually occupied; it is the maximal possible transverse size of a primordium that can exist without compression in the particular phyllotaxis pattern. This definition of 'primordial area' should be borne in mind throughout the following pages.

A practical illustration may help to clarify one manner in which the relationships between apical size, primordial spacing and phyllotaxis may be investigated. Church (1904, figures 40 and 41) presents drawings depicting transverse sections of four apices of *Araucaria excelsa*, these differing in their phyllotaxis systems and apical diameters. A similar set of drawings from four apices of *Podocarpus japonica* is presented in his figure 42, and a third set from four apices of *Lycopodium Selago* in his figures 78 and 79. The drawings for any one species are to the same scale of magnification, but this evidently does not hold between the different species, though the actual scales are not stated. The phyllotaxis types are widely divergent; according to Church's method of classifying them, three of the *Araucaria* apices show Fibonacci systems: (3+5), (5+8) and (8+13), the fourth being of the first accessory type, (7+11). In *Podocarpus* two are Fibonacci, (3+5) and (5+8), one first accessory, (3+4), and the fourth Fibonacci bijugate, (6+10); while in *Lycopodium* there are two systems of alternating whorls, (4+4) and (5+5), and one from each of the second and third accessory types, i.e. (4+5) and (5+6).

From measurements made on any one of these drawings, and involving only a few of the innermost primordia, the phyllotaxis index may be calculated, using the regression method (see p. 541) on the logs of the radial distances of the successive primordial centres P_1, P_2,

P_3, ... Thus from the (8+13) *Araucaria* apex has been obtained the regression equation $Y = 0{\cdot}01085P + 0{\cdot}844$, where P is the number given to any primordium and Y is the predicted value for the logarithm of its radial distance (in mm., as measured on the drawing); 0·01085 is $\log_{10} r$, and from it the phyllotaxis index is calculated as 5·08. If now the 'bare apex' is defined as that region on which primordial *centres* do not arise (the distances of the primordia being measured to these centres), the best estimate of the logarithm of its radius is obtained from the value of Y in the regression equation when P is made equal to 0·5, i.e. 0·849. The reason for this is that in the drawings of Church the stage in the plastochrone is quite unknown; one can only assume a random distribution of the stage among them and that on the average the mean will be the mid-plastochrone. The position of P_1 one-half a plastochrone earlier than appears in the drawing is thus required, and is obtained by putting $P = 0{\cdot}5$.

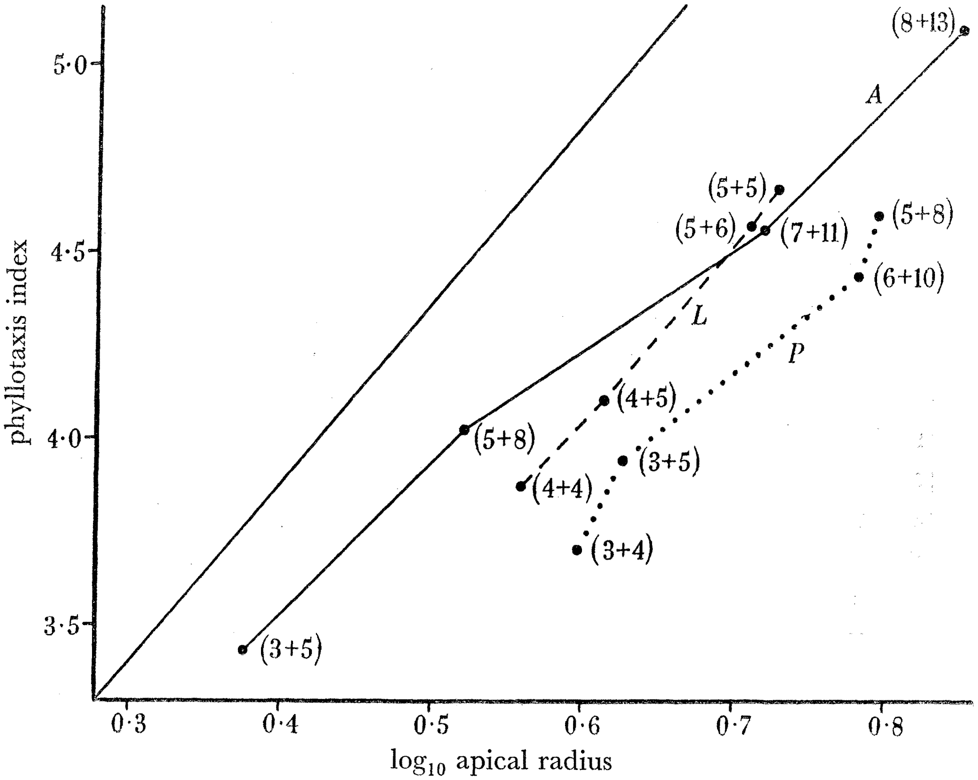

FIGURE 7. Relation between phyllotaxis index and the logarithm of the radius of the bare apex. Primary data taken from Church (1904): *A*, *Araucaria excelsa*; *L*, *Lycopodium Selago*; *P*, *Podocarpus japonica*. The straight line shows the slope of the relationship if primordial size is constant.

In figure 7 the two calculated quantities, phyllotaxis index and log apical radius, are plotted against one another, both for this apex and also for the other three of *Araucaria* depicted by Church. The four points are connected by straight lines (*A*). The similar relation between the four *Podocarpus* apices is also shown (*P*), together with that in *Lycopodium* (*L*).

Some difficulty arises in the treatment of the two whorled apices of *Lycopodium*; in the (5+5), for instance, five primordia are produced together. The procedure adopted here is to determine the mean log radial distances in each of the youngest two whorls, 0·768 and

0·849 respectively. $\text{Log}_{10}r$ (corrected) is obtained by dividing the difference between these two quantities by five, giving 0·0162, and hence a phyllotaxis index of 4·66. The mean of the log distances in the two whorls is also required, i.e. 0·808, together with the mean 'primordium number'. Calling those in the youngest whorl 1, 2, 3, 4 and 5 respectively, and those in the next whorl 6–10, the mean number becomes 5·5. A conventionalized regression equation may now be set up: $Y-0{\cdot}808=0{\cdot}0162\,(P-5{\cdot}5)$, or $Y=0{\cdot}0162P+0{\cdot}719$. Putting $P=0{\cdot}5$ again gives the best estimate of log apical radius (0·727), and this value is plotted in figure 7.

By these means the apex is treated as if it were unijugate, producing the ten primordia one at a time in uniform succession instead of in two whorls. Putting $P=3$ in the regression equation reproduces the actual mean log distance in the innnermost whorl, while if $P=8$ that in the second whorl is produced. When $P=-2$ an estimate of the actual present radial distance of the centres of the next whorl to be produced ($P=0$, -1, -2, -3 and -4) is obtained. According to the convention of unijugy therefore it is known that primordium 3 has already appeared and that primordium -2 has not yet done so; nothing is known of the conventional presence or absence of the four intermediate primordia, but in a number of such apices on the average numbers 2 and 1 would have appeared but not numbers 0 and -1, the mean stage being again 'mid-plastochrone' between numbers 0 and 1. Hence to obtain the estimate of log apical radius comparable with that from the truly unijugate apices, P in the equation is taken equal to 0·5. The average error may be larger than in unijugy, but is unbiased; the actual agreement in figure 7 between the points representing the two whorled apices of *Lycopodium* and those calculated in a more standard manner from spiral apices is strikingly good.

Since all the drawings for any one species are to the same scale, if the absolute spacing of the primordia in them is similar then a line through the four points plotted will represent simply the effect of varying apical size on phyllotaxis, as discussed above. The line must then have a slope equal to the reciprocal of $\log_{10} 1{\cdot}6180$, or 4·785 (i.e. the same slope as the best line through the points in figure 6). If the slope has a different magnitude the departure indicates a change in primordial spacing (or in the linear dimensions of the primordia if full contact be assumed) accompanying the known difference in apical size. A line of the theoretical slope has been drawn in figure 7, and it may be seen at once that the data derived from the *Lycopodium* apices agree remarkably well with it; those for *Podocarpus*, though a little irregular, possibly indicate a slightly different slope. The data of *Araucaria* display a slope which appears to be probably different, though not very greatly so, from that to be expected if apical size were its sole determinant. If lines of theoretical slope were drawn through the two extreme points in this species, representing the largest and smallest apices, they would be separated horizontally by a distance equivalent to $\log_{10} 0{\cdot}129$. If this is accepted as real it implies that the assumption of uniform primordial spacing does not hold, but that the primordia in the $(8+13)$ contact system are about 1·35 times as far apart at initiation as those in the $(3+5)$ system, and probably therefore that the larger apex produced primordia which from the start were larger than those on the smaller apex. This difference in size, however, is not very great compared with that between the bare apices, whose diameters are in the approximate ratio 3:1. Needless to say, it is quite impossible to determine directly from the original drawings whether or not the size of the ill-defined youngest primordium varies with apical diameter, and owing to very different amounts of growth per plastochrone in the various phyllotaxis systems older primordia cannot be directly compared.

The relation between phyllotaxis index and the ratio of the transverse area of the bare apex to the maximum possible transverse primordial area at initiation may readily be expressed in a more concrete form. In discussing this relation the assumption will again be made that any change in size of the bare apex from one plastochrone to another is sufficiently small to be negligible. When it is not so, plastochrone ratio and phyllotaxis are likely to be changing rapidly and conditions are then unsuited to any simple practical analysis. In the first place it should be stated that in the transverse component of a constant phyllotaxis system the outline of the bare portion of an apex is not circular and may be complex in form; the apex nevertheless has a shape that is maintained. It may be regarded as expanding uniformly during the plastochrone to its maximum size and then surrendering a certain amount of its area, again of definite form, to a primordium. The bare apex is now at its minimum size, but it has precisely the same shape as before,* the new figure being orientated differently from the original; in a Fibonacci system it is rotated through the Fibonacci angle, etc. Hence the piece of apex associated with the primordium is in the nature of a geometrical gnomon to the bare apex. A figure of a certain shape, and having a particular linear dimension of unity, say, expands uniformly until the corresponding measurement is r (the plastochrone ratio); it then parts with a gnomon, leaving its shape unaltered but reducing it to the original dimensions. The maximum and minimum figures, being geometrically similar, have areas proportional to the squares of equivalent dimensions, i.e. $\frac{\text{minimum area}}{\text{maximum area}}=\frac{1}{r^2}$. The ratio of the maximum apical area to the area of the primordium at initiation is $\frac{r^2}{r^2-1}$, and that of the minimum apical area to the primordial area $\frac{1}{r^2-1}$.

Every value of r corresponds to a particular phyllotaxis index, hence the relation between this index and the ratio of either maximum or minimum apical area to primordial area may readily be calculated. The two relations are shown respectively in *A* and *B*, figure 8, but phyllotaxis index is plotted there against the logarithms of the ratios to base 10. At low indices the two curves diverge widely, but as phyllotaxis rises they rapidly approach the same straight line, for here the fluctuations in apical size are very small and it becomes immaterial at what stage in the plastochrone the area is considered. The actual values for the ratio of maximum apical size to primordial size in the various orthogonal Fibonacci systems have been tabulated in an earlier paper (Richards 1948) in the form $\frac{100\,(r^2-1)}{r^2}$, i.e. the percentage of the cross-sectional area of the enlarged smooth apex associated with a single primordium at initiation.

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* This may not always be true, and the bare apex, in the above sense of the term (as distinct from the visibly bare apex) may actually change its form during the plastochrone. It may readily be shown, however, that even so all the area relations deduced in the following paragraphs remain unchanged for all practical purposes, though the *precise* mathematical form and position of the lines *C* and *D* in figure 8 become theoretically uncertain.

Curve C in figure 8 gives the phyllotaxis index in relation to the ratio of apical size at mid-plastochrone to primordial area at initiation; it is more nearly linear than the other two. At this time any dimension of the apex has a magnitude equal to the geometric mean between its extreme values, hence the curve plotted is the log of $\frac{r}{r^2-1}$. Finally, the straight

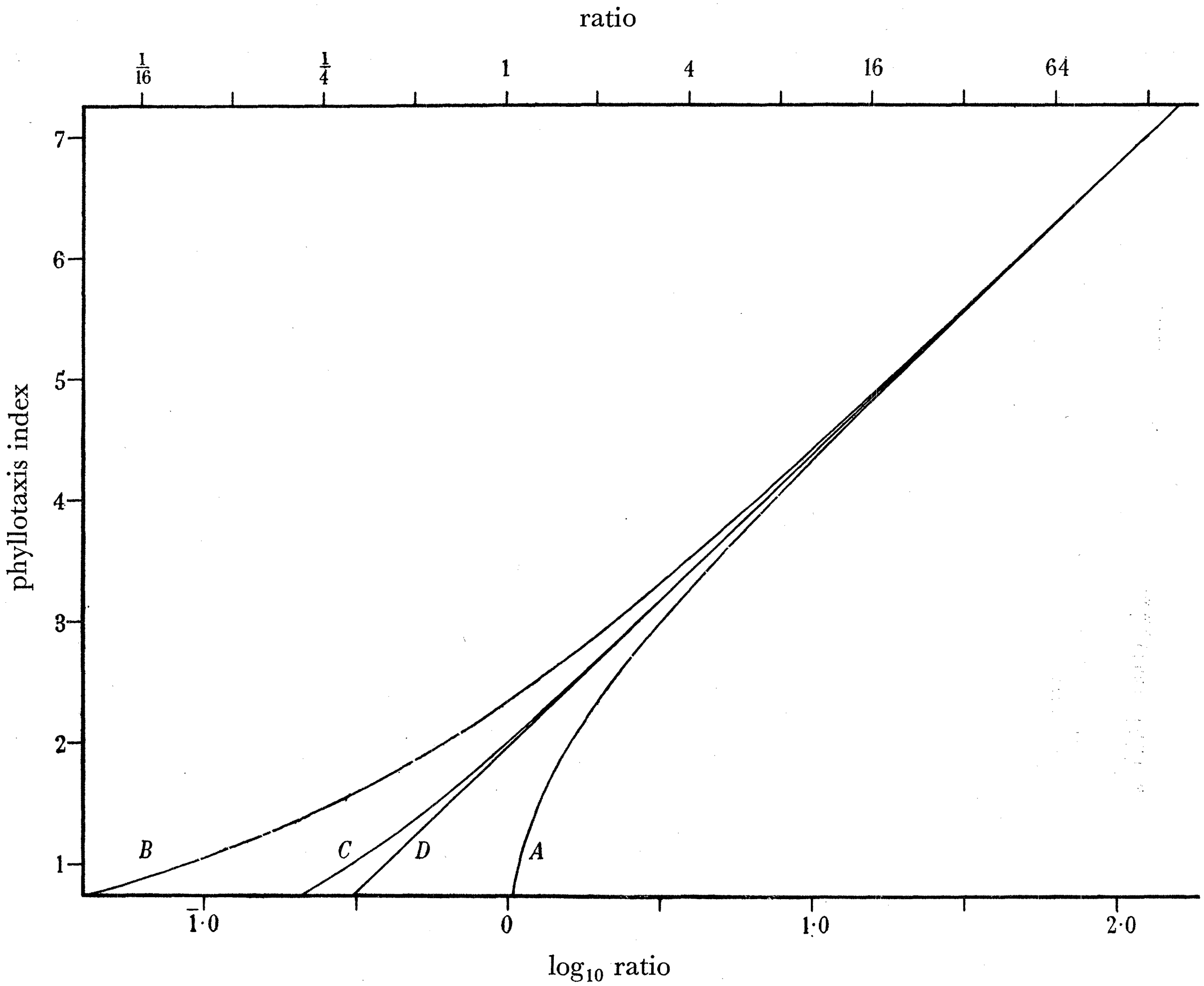

FIGURE 8. Relation between phyllotaxis index and the logarithm of the ratio of bare apical transverse area to the transverse area associated with a single primordium: A, the relationship when maximum apical area is considered; B, that for minimal apical area; C, that for apical area at mid-plastochrone; and D, that for mean apical area, i.e. the 'area ratio'.

line D on the diagram gives the corresponding relation when the apical area considered is the true mean area. For in a system expanding exponentially from radius $=1$ to radius $=r$, the mean area is given by the ratio of the difference between the extreme areas to the difference between their natural logarithms, i.e. mean apical area is proportional to

$$\frac{r^2-1}{\log_e r^2-\log_e 1}=\frac{r^2-1}{2\log_e r}.$$

Since primordial area is similarly proportional to r^2-1, the ratio of mean apical area to primordial area $=\frac{1}{2\log_e r}$. In any phyllotaxis system, this quantity $\frac{1}{2\log_e r}$ will be termed the *area ratio*; it will be seen to be the reciprocal of the relative growth rate in transverse area of the apex when time is measured in plastochrones. In D, figure 8, therefore, phyllotaxis index is plotted against the logarithm to base 10 of the reciprocal of $2\log_e r$, or $\log_{10}\left(\frac{0\cdot21715}{\log_{10} r}\right) = -0\cdot6632 - \log_{10}\log_{10} r$. Since phyllotaxis index $= 0\cdot379 - 2\cdot3925 \log_{10}\log_{10} r$ the relation plotted is rectilinear, with the slope $2\cdot3925$ (straight line D).

This slope is one-half that of the theoretical line on the previous figure, and as the latter gives a relation in terms of linear dimensions and the former in terms of area, the two clearly refer to the same conditions; that is to say, the apical radius appropriate to the theoretical line in figure 7, derived from considerations of rate of availability of space for primordium formation, is the radius corresponding to the mean area during the plastochrone. Figure 8 shows that for phyllotaxis indices of the magnitudes actually investigated, 3·4 and upwards, the particular time in the plastochrone at which the apex is measured is not of great moment, since the curves for both maximum and minimum apical size depart relatively little from that for mean size; but, as will be readily appreciated from the diagram, investigations of this nature involving apices having much lower phyllotaxis indices would need to have special attention paid to this aspect. Again, at the level of phyllotaxis index under investigation the line on figure 8 representing the relation with apical area at mid-plastochrone is indistinguishable from the straight line representing the relation with mean apical area; this latter is the theoretical comparison line actually used in figure 7, but strictly the mid-plastochrone relationship should have been used.

So far, in dealing with the figures of Church, estimates have been obtained of the transverse size of that portion of the apex on which primordial centres do not arise (or of the radial distance at which these centres arise), and of the relative initial sizes of the primordia in the several specimens from one species. Estimates of the absolute sizes of these primordia at the time of their initiation, as defined on p. 549, may also be made from figure 7, for the theoretical line there has been drawn to correspond with that of D, figure 8, not only in slope but also in position, the horizontal reading at any phyllotaxis index in the former being numerically one-half that in the latter. Hence, assuming the primordial area to be replaced by an equal circle (of radius R_p), for any phyllotaxis index the line drawn in figure 7 gives $\log_{10}\left(\frac{\text{apical radius}}{R_p}\right)$, i.e. $\log_{10}$ apical radius $-\log_{10} R_p$. Since the point calculated from any particular apex gives $\log_{10}$ apical radius, the horizontal distance between the point and the line must represent $\log_{10} R_p$, the logarithm of the radius of the circle equal to the area on the original section associated with a primordium at initiation, measured in the same units as the bare apex, in this case mm. on Church's drawing. The actual transverse area associated with a primordium at initiation may thus be obtained, as represented on the original drawing.

Applying this to the points in the diagram representing the $(8+13)$ and $(3+5)$ apices of *Araucaria*, horizontal distances of 0·198 and 0·069 respectively are found, leading to estimates of the primordial areas of 7·8 and 4·3 sq.mm. Similar calculations starting from the values for $\log_{10}$ apical radius on the graph, or in the primary regression equations, lead to mean apical areas of 156 and 17·7 sq.mm. respectively. Consequently the ratios of these areas, i.e. the 'area ratios', in the two apices are 20·0 and 4·12; their logarithms are

1·301 and 0·615, which when plotted in figure 8 against the phyllotaxis indices of the apices, 5·08 and 3·43 respectively, fall on the theoretical straight line there.

The implications involved in such calculations should be carefully considered, since the values obtained depend on the postulates inherent in the methods used for their evaluation. In the present example the radial distances of the primordia were originally measured from their geometrical centres, and the regression calculation employed led to the determination of two numerical constants, one of them being the plastochrone ratio. From these constants the radial distance of the primordial centres at the time of their first appearance was estimated; by so doing it was implied solely that the apex may be supposed continually to be expanding past the circumference of a *fixed* circle, which serves merely to indicate at any time the region where new primordial centres appear.

In using this same circle as one of the two parameters from which primordial size at initiation is to be estimated, however, it is regarded in a very different manner, as representing the *mean area* of an apex pulsating rhythmically in the period of the plastochrone. Underlying the method lies the conventional postulate that the bare apex expands exponentially; when a certain maximum size is attained a primordium is instantaneously 'initiated', reducing the bare apex once more to its minimum size. One may define how one pleases the size of the circle to represent the mean area of the apex, but once this is defined the 'primordial area' is automatically defined also, for in the analysis it is completely determined by the mean apical area and the phyllotaxis index. In the present case the area taken to represent the 'bare' apex at its mean size is that circle on whose circumference the geometrical centres of the primordia make their first appearance, so that when the apex is regarded as pulsating in size the circumference of an equal fluctuating circle may be supposed to lie inside the line of appearance of primordial centres at the beginning of the plastochrone and outside it at the end, while its position when the apex is at its mean size defines the line. The annulus between the limiting positions has then, to a reasonable approximation, the same area as that associated with each primordium at the time of its appearance, whether the primordia are actually annular or of any other form; the chief practical difficulty lies in the precise location of the primordial 'centres' in any particular case, so that the measurements taken may conform to the demands of the theory.

Approached in this way, the time of 'initiation' of the primordium, as well as the apical area associated with it at this time, is conventional, being governed by the definition of size we choose to give to the 'bare' apex. If, however, the time of initiation be defined by other criteria (such as the time of leaf 'determination' in the sense of the word as used by Snow & Snow (1931) measured in plastochrones before the appearance of the hummock; or the time of the first periclinal divisions), then the corresponding apical radius would be obtained by substituting the appropriate value, instead of 0·5, for P in the regression equation on p. 550. The absolute area associated with the primordium at this defined initiation time could then be evaluated. The estimate of the ratio of mean apical area to primordial area is of course unaffected by the particular definition given to either the time of primordial initiation or the 'bare' apical area, since it depends solely on the phyllotaxis index.

Before leaving figure 7 attention may once again be drawn to the classification of the apices by Church according to the numbers of contact parastichies. In general, as would be expected, phyllotaxis index rises with the numbers of contact parastichies, but there are notable exceptions. In *Podocarpus*, for instance, a (5+8) apex appears above a (6+10); or again, the (7+11) *Araucaria* apex has the same index as the (5+6) *Lycopodium* apex, and apparently a lower one than even the (5+5). These discrepancies arise, of course, from the fact that the contact parastichies in the various apices intersect at very different angles, and hence do not really indicate the 'bulk-ratios', as Church assumed. The area ratio on the other hand is a direct measure of precisely this kind and its logarithm is linearly related to the phyllotaxis index, when the transverse component of the system is alone under consideration, i.e.

$$\log_{10} \text{area ratio} = \frac{\text{phyllotaxis index} - 1{\cdot}9660}{2{\cdot}3925}.$$

With the aid of a table of natural logarithms it may be obtained even more simply from the plastochrone ratio, as the reciprocal of $2 \log_e r$.*

15. Area relations involving the apical surface

Theoretical measures such as bulk ratio, which depend for their validity on some defined and simple primordium shape, fail when the attempt is made to apply them to actual apices, where the primordia are of differing and uncertain forms. They also fail in fern apices, at least, for another reason, that the primordia do not nearly fully occupy the apical space they control. The area ratio on the contrary may readily be estimated on an apex and provides information of precisely the kind sought, quite regardless of the actual primordium size and shape.

But while the information derivable from the relationship between phyllotaxis and the area ratio applies only to the transverse component of the system, it may be desired to extend an investigation of a similar nature to the whole three-dimensional system. For this purpose an equation is required relating the equivalent phyllotaxis index to the actual primordial area on the apical surface and some determinable area characteristic of the bare apex (by 'primordial area' is meant here, and in what follows, the *apical* surface area associated with a single primordium at initiation, not the surface area of the primordium).

It would be possible to deduce such a relationship using the bare apical surface area as the third of these variables, provided the apex was assumed always to conform to some specified shape, a paraboloid for instance. This procedure, however, would immediately be open to a similar criticism to that just raised against the concept bulk-ratio, for the form of apices is unknown and very variable, and serious errors might be involved in the attempt to apply the resulting relationship to actual phyllotaxis systems. No similar objection arises if the transverse area of the bare apex, in the region of primordial initiation, be substituted in the relation for the apical surface area: that is to say, the same area that has already been

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* The area ratio calculated in this way for a multijugate apex is no more conventional in character than that derived from a unijugate apex. For in an x-jugate system let r_a be the actual ratio of the radial distances of the primordia in two successive whorls, and r the conventional plastochrone ratio as used above, so that $\log r_a = x \log r$. The actual maximum apical area is proportional to r_a^2, and the actual minimal area to 1, hence the actual mean apical area is $\frac{r_a^2-1}{2\log_e r_a}$. The area given over to x equal primordia at initiation is similarly proportional to r_a^2-1, hence that of each primordium is $\frac{r_a^2-1}{x}$. The actual ratio of mean apical area to primordial area is therefore $\frac{x}{2\log_e r_a} = \frac{x}{2x\log_e r} = \frac{1}{2\log_e r}$.

considered in the area ratio. Moreover, it will be clear from the sequel that the only way in which the shape of the whole apex affects geometrically the height of phyllotaxis is through this transverse area in the region of leaf initiation. Hence in what follows the equivalent phyllotaxis index will be related to the ratio between the transverse apical area and the actual primordial area on the apical surface.

For this purpose the relation between the actual primordial area on the apex and its transverse component is required. A closely approximate solution to this problem may be arrived at by again imagining a cone to be fitted tangentially to the apex in the region of initiation of primordial centres, the cone having an angle of 2θ. The outline of the area representing a primordium on the apical surface may then be projected on to the conical surface. Since in the region of primordial initiation the cone and apex are almost in contact at all relevant points, the area of the projection on the cone will reproduce with considerable accuracy that of the primordium on the apex. If now this area on the cone be itself projected orthogonally on to a transverse plane, the area of the transverse projection is $\sin\theta$ times that of the projection on the cone; it therefore closely approximates $\sin\theta$ times the actual primordial area.

This relation is, of course, not strictly accurate, since it again is affected slightly by the form of the apex; nevertheless it is evident that the error involved in accepting it will be inappreciable practically, except possibly in extremely low phyllotaxis systems wherein the primordial area is large relative to the apex.

The relation given on p. 556 between phyllotaxis index and area ratio may be expressed:

$$\text{phyllotaxis index} = 1{\cdot}966 + 2{\cdot}3925\,(\log_{10}\text{transverse apical area} - \log_{10}\text{transverse primordial area}).$$

Now, equivalent phyllotaxis index = phyllotaxis index $+ 2{\cdot}3925 \log_{10} \sin\theta$.

Therefore

$$\text{equivalent phyllotaxis index} = 1{\cdot}966 + 2{\cdot}3925\,(\log_{10}\text{transverse apical area} - \log_{10}\text{transverse primordial area} + \log_{10}\sin\theta).$$

But

$$\text{transverse primordial area} = \text{actual primordial area on apex} \times \sin\theta,$$

or

$$\log_{10}\text{transverse primordial area} = \log_{10}\text{actual primordial area} + \log_{10}\sin\theta.$$

Therefore

$$\text{equivalent phyllotaxis index} = 1{\cdot}966 + 2{\cdot}3925\,(\log_{10}\text{transverse apical area} - \log_{10}\text{actual primordial area}),$$

and

$$\text{phyllotaxis index} = 1{\cdot}966 + 2{\cdot}3925\,(\log_{10}\text{transverse apical area} - \log_{10}\text{actual primordial area} - \log_{10}\sin\theta).$$

The first of these two final relations is similar to that on p. 556 between area ratio and phyllotaxis index, but it is now the *equivalent* phyllotaxis index and the primordial area *on the apex* that are referred to. The range of applicability of figure 8 may therefore be extended to include the more general relation. An analysis of the immediate causes of changing phyllotaxis on the surface of growing shoot apices, for example, could thus be made, using only measurements easily taken from transverse and longitudinal sections. At each growth stage investigated the regression method as used in the analysis of Church's drawings would enable the estimates of $\log_{10}R$ (apical radius), $\log_{10}r$ and phyllotaxis index to be obtained from a transverse section; θ may be directly measured on a longitudinal section and by its use the index converted into equivalent phyllotaxis index. Log_{10} apical transverse area is given by $2\log_{10}R+0{\cdot}4971$, and $\log_{10}$ primordial area may then be obtained from the equation, or alternatively from the formula:* $1{\cdot}1604+2\log_{10}R+\log_{10}\log_{10}r-\log_{10}\sin\theta$. Hence any modification occurring with age, etc., in the equivalent phyllotaxis index might be interpreted as the resultant of two numerically defined changes due to the alterations which have occurred respectively in the absolute distancing of the primordial centres from one another on the apical surface and in the transverse size of the apex in the region of initiation. Any modification of the phyllotaxis index is a resultant of these same two changes plus a third due to alteration in the form of the apex in the same region (the angle θ).

It is noteworthy that for any given transverse apical area and primordial area the equivalent phyllotaxis index is independent of the angle θ and apical shape; for any given divergence angle the parastichy intersection angles near the region of initiation on the surfaces of all apices, whether elongated or flat, are identical provided the ratio of primordial area to mean apical transverse area is the same. As a point of theoretical interest, since the curve system is independent of the angle θ, the above relation holds even for cylindrical structures such as are found in many Gramineous apices. The application of the equation also to the phyllotaxis curves seen in many mature structures, where flowers or fruits are crowded together round an axis which is a surface of revolution, will be apparent; here the phyllotaxis curves in any region are determined solely by the divergence angle, the area occupied by a single fruit and the transverse area of the whole structure in that region: the actual shapes of the fruits are immaterial to the parastichy systems, though they will of course help to determine which of these curves represent the *contact* system.

16. RECAPITULATION AND GENERAL VALIDITY OF THE PROPOSED METHODS

In the preceding pages phyllotaxis index has been expressed in very different ways. It was originally defined as a simple transformation of the plastochrone ratio, a measure that may readily be obtained from a transverse section of the apex, for the purpose of defining the radial component of phyllotaxis in a manner which, given also a knowledge of divergence angle, supplies immediate information as to the parastichy relations to be seen in the section. Plastochrone ratio, while easily measured and readily understood in relation to

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* This is derived as follows:

$$\frac{\text{mean transverse apical area}}{\text{primordial area in transverse projection}}=\text{area ratio}=\frac{1}{2\log_e r}.$$

Therefore

$$\frac{\text{mean transverse apical area}}{\text{primordial area on apical surface}}=\frac{\sin\theta}{2\log_e r}.$$

Denoting the apical radius, when the apex is at its mean transverse area, by R, it follows immediately that the actual primordial area equals $\frac{2\pi R^2\log_e r}{\sin\theta}$ or $14{\cdot}47\,R^2\log_{10}r\operatorname{cosec}\theta$, whose logarithm appears above. In a flat apex, or in the transverse component of any apex, $\operatorname{cosec}\theta=1$, and the resulting formula thus allows the primordial areas in the sections already considered, from Church, to be calculated directly from the two constants in the fitted regression equation.

a section across the apex, is not necessarily a simple concept when considered in relation to the processes of growth and differentiation in the apex. It may be compounded of the rates of three simultaneously occurring processes: rate of production of primordia, overall rate of transverse growth of the apex in the region of the youngest primordia, and rate of change in transverse size of that apical region inside the zone of primordial initiation. Change in any one of these three rates is reflected in a corresponding alteration of the phyllotaxis index; the relation of the latter to the three processes is given on pp. 547–548. Phyllotaxis index may then be expressed entirely in terms of rates of change within the apex, and, if desired, even calculated from these, i.e. from dynamical physiological considerations only.

As a result of the various growth processes the ratio between the sizes, in the transverse direction, of the apex itself and the portion of it associated with a single primordium at initiation attains a particular magnitude in a certain time. Provided the various rates are so correlated that the area ratio remains substantially constant for a period, the parastichy curves also remain constant in form, and the phyllotaxis index is rigidly and simply related to the ratio, i.e. the index is now expressed entirely in static morphological terms (p. 556). Even if the areas considered are changing differentially in time the phyllotaxis index corresponding to any particular plastochrone may, theoretically at least, be determined (see later, p. 560), but it can no longer be regarded as a constant and phyllotaxis is variable. Phyllotaxis index and plastochrone ratio therefore are concepts related equally to the morphology of the shoot apex and to certain rates of growth and differentiation within it.

By a slight extension of the morphological analysis the height of phyllotaxis on the apical surface itself may be shown to be completely defined by the ratio of apical cross-sectional area to the amount of apical surface associated with a single primordium, in just the same way as the phyllotaxis in the transverse component is defined by the area ratio (p. 557).

The questions discussed in the foregoing pages, and the validity of the analytical methods developed, are not directly concerned with those aspects of phyllotaxis theory that relate to the immediate physiological causes underlying the emergence of a primordium at a particular place on the apical dome. Only the well-known regularities in both tangential and radial spacing due to these causes have been accepted as facts of observation, and certain relationships which must necessarily follow have been investigated. Theories of the underlying causes of phyllotaxis, if they are to account for all the factors recognized here as contributing to the geometrical pattern produced, must explain (1) the absolute distancing of the primordial centres from one another, usually regarded as a consequence of the influence of existing primordia in determining the position of the next one to appear, and (2) the absence of primordia from the central apical dome and the factors determining its transverse size in the region of initiation. Since the phenomena of phyllotaxis may be discussed also in terms of growth rates within the apex, an ideal theory would be capable, under clause (2), of accounting for the plastochrone in relation to these rates. The reasons for the appearance of the various 'ideal angles' in apices will be answered implicitly under clause (1) above, but a full understanding of radial spacing and phyllotaxis index requires the explanation of both groups of phenomena. A few aspects of phyllotaxis may fall under neither of these headings, e.g. the tendency of some apices to maintain or establish whorled constructions under apparently adverse conditions (cf. Schoute 1922, 1925, 1936, 1938; Snow 1942).

Whatever the ultimate solution of these problems may be, the applicability of the analytical methods proposed will remain unaffected. At first sight they appear to rest on two assumptions: uniformity of tangential primordial spacing and constancy of plastochrone ratio as measured on sections from the successive pairs of primordia. Only if both these are true will the parastichies as seen in transverse projection be logarithmic spirals, and these curves have been used in the establishment of the theoretical relation between parastichy intersection angle and plastochrone ratio, and hence also phyllotaxis index.

The approximate regularity in tangential spacing, and the apparently extraordinary exactness with which the mean divergence angle may approach particular irrational values, have long been recognized as facts, at least in the vast majority of plants, and studies in leaf arrangement from the first have been stimulated by these phenomena, and largely confined to them. The second assumption, constancy of the plastochrone ratio, might on the contrary legitimately be questioned, and with it therefore the description of the parastichies as *logarithmic* spirals. As d'Arcy Thompson (1942, p. 918) states, 'the curves resemble, and sometimes closely resemble, the logarithmic spiral; but that they are, strictly speaking, logarithmic is neither proved nor capable of proof'; and again (p. 914), 'They doubtless resemble the logarithmic or equiangular spiral, but different spirals may look much alike; and these are ill-suited to the careful admeasurement and rigorous verification which Moseley gave to the spirals of his molluscan shells.'

In the first place, when estimates are made of the transverse distances of the successive primordia from the apical centre, the logarithms of these distances are never exactly in arithmetical progression; the ratio between each pair of successive distances fluctuates, so that there is a greater or lesser amount of 'random' error in the radial positioning. In order to obtain the best estimate of the increment in log distance corresponding to a single plastochrone a regression must be fitted to the data. If the observed log distances are reproduced adequately by a rectilinear relation, there being no statistical evidence that a curved regression will fit them appreciably better, then the original assumption is justified and the smoothed or idealized parastichy lines may be taken as logarithmic spirals within the limits of accuracy set by the random fluctuations. So long as measurements are confined to only a few of the inner primordial cycles on an apex these conditions are usually found to apply, and the subsequent calculations then clearly give the correct relation between phyllotaxis index and parastichy intersection angle.

But when older zones of primordia are included in the investigation the assumption of a constant proportional increase in axis diameter with primordium number is no longer found to hold, and a curved regression fits the log distances better than any straight line. Sometimes evidence of curvature in the relationship may be found even in the inner zones. In such circumstances the assumption of logarithmic spiral parastichy lines is certainly unjustified; nevertheless from an appropriate curved regression estimates of the plastochrone ratios (no longer constant) may be obtained corresponding to any particular zones of primordia on the apex, and from these the changes in phyllotaxis index followed from the centre outwards. If for instance the regression is put in the form $Y = a + bP + cP^2$, where Y is the estimated log distance of primordium number P, and a, b and c are constants, the slope of the regression is $b + 2cP$; by putting in this expression $P = 5$, for example, the estimate of $\log r$ is obtained for a narrow annulus on the apex containing the fifth primordium.

Phyllotaxis is thus changing with distance from the apical centre, but the phyllotaxis index for a particular zone, as calculated from the curved regression, still indicates the parastichy intersection angle in that region. For the short segments of the parastichy lines in each zone may be regarded in essence as having been replaced by closely fitting bits of logarithmic spirals, and the complete parastichies as built up of a large number of segments taken from different logarithmic spirals. The intersection angles of these theoretical curves will therefore agree everywhere with those of the actual parastichies within the limits of accuracy permitted by the random irregularities of the latter, and are correctly indicated at any position by the calculated phyllotaxis index. Hence, so far as the analytical methods are concerned, the precise form of the spiral parastichies is of no moment.

The survey of methods for defining the positions of primordia near the apex, as developed in these pages, has shown increasingly the significance attaching to their radial and longitudinal positioning; in many ways the tangential spacing is of less immediate interest and usefulness, yet it is this latter aspect that has engaged almost exclusively the attention of botanists. This *lacuna*, which phyllotaxis index is designed to fill, was noted by d'Arcy Thompson (1942, p. 917) who, in focusing attention on the importance of longitudinal spacing in phyllotaxis patterns, wrote 'But this matter botanical students have not concerned themselves with; in other words, their studies have been limited (or mainly limited) to the relation of the leaves to one another in *azimuth*—in other words, to the angle ϕ [the divergence] and its multiples.' A paper like the present, intimately concerned with questions of the interrelationships between form and growth, cannot end more fittingly than with this reproof from so eminent an exponent of many such problems.

APPENDIX

A 1. *Phyllotaxis indices at orthogonal intersection in the successive systems for various 'ideal' divergence angles*

angle	137·50776° . . .		99·50155° . . .		77·95525° . . .		64·07936° . . .		151·13566° . . .	
	system	index	system	index	system	index	system	index	system	index
	1:2	0·95	3:4	2·71	4:5	3·23	5:6	3·65	5:7	3·84
	2:3	2·02	4:7	3·65	5:9	4·15	6:11	4·56	7:12	4·79
	3:5	2·99	7:11	4·68	9:14	5·19	11:17	5·60	12:19	5·81
	5:8	4·00	11:18	5·67	14:23	6·18	17:28	6·58	19:31	6·80
higher systems		x·00		x·67		x·18		x·59		x·80

A 2. *Multijugate systems*

The index for orthogonal intersection in the x-jugate system $xa:xb$, where x is the common factor and a and b are mutually prime, may be obtained by adding $4{\cdot}785 \log_{10}x$ to the corresponding value in the system $a:b$. For values of x from 2 to 6 these quantities are as follows:

x	2	3	4	5	6
$4{\cdot}785 \log_{10}x$	1·44	2·28	2·88	3·34	3·72

In calculating the phyllotaxis index of an x-jugate apex from measurements taken on transverse sections, the primordia should be numbered so that x of them (those of the same age) receive the same number, e.g. in the trijugate the first nine receive respectively: 1, 1, 1; 4, 4, 4; 7, 7, 7; and so on. If these numbers are interpreted as ages in 'plastochrones' all the necessary adjustment in calculating phyllotaxis index will appear automatically in the determination of $\log_{10}r$. The opposite decussate system should be numbered: 1, 1; 3, 3; 5, 5; . . . .

A 3. *Equivalent phyllotaxis index*

Equivalent phyllotaxis index = phyllotaxis index + $2{\cdot}3925 \log_{10}\sin\theta$, where θ is the inclination of the apical region under consideration to the axis of the shoot. The angle 2θ may be determined from a longitudinal section as the inclination of two opposite sides of the apex to one another. Alternatively $\tan\theta$ may be obtained from measurements on serial transverse sections (see p. 540). Below are tabulated, in steps of one-tenth of a unit, the appropriate amounts to be *subtracted* from the phyllotaxis index for the various ranges of 2θ and $\tan\theta$.

2θ (degrees)	$\tan\theta$	correction	2θ (degrees)	$\tan\theta$	correction
180	∞	0·0	47·3	0·437	1·0
144·7	3·147	0·1	42·7	0·391	1·1
119·9	1·729	0·2	38·6	0·350	1·2
103·7	1·272	0·3	35·0	0·315	1·3
91·1	1·020	0·4	31·7	0·283	1·4
80·9	0·852	0·5	28·7	0·256	1·5
72·2	0·729	0·6	26·0	0·231	1·6
64·7	0·633	0·7	23·6	0·209	1·7
58·1	0·556	0·8	21·4	0·189	1·8
52·4	0·492	0·9	19·4	0·171	1·9
47·3	0·437		17·6	0·155	2·0
			16·0	0·140	

A 4. *Conversion table*

In order to avoid the necessity of calculating a phyllotaxis index for every apex measured the following table has been compiled. From the measurements taken will be obtained either plastochrone ratio (r) or $\log_{10} r$. The table gives the range of these two quantities corresponding to each one-tenth phyllotaxis unit. Thus an index of 2·3 will be assigned to any apex whose plastochrone ratio lies between 1·4127 and 1·4629, or in which $\log_{10} r$ lies between 0·1501 and 0·1652. In growth studies $\log_e r$ may be required, and this also is tabulated; intermediate values sufficiently accurate for most purposes may be obtained by interpolation.

r	$\log_{10} r$	$\log_e r$	phyllotaxis index
32·47	1·5114	3·4802	0·0
23·59	1·3727	3·1609	0·1
17·65	1·2468	2·8708	0·2
13·56	1·1324	2·6074	0·3
10·68	1·0285	2·3682	0·4
8·592	0·9341	2·1509	0·5
7·053	0·8484	1·9535	0·6
5·896	0·7706	1·7743	0·7
5·010	0·6999	1·6115	0·8
4·322	0·6356	1·4636	0·9
3·778	0·5773	1·3293	1·0
3·345	0·5243	1·2073	1·1
2·994	0·4762	1·0966	1·2
2·707	0·4325	0·9959	1·3
2·471	0·3928	0·9046	1·4
2·274	0·3568	0·8216	1·5
2·109	0·3241	0·7462	1·6
1·969	0·2943	0·6777	1·7
1·851	0·2673	0·6155	1·8
1·7490	0·2428	0·5591	1·9
1·6616	0·2205	0·5078	2·0
1·5859	0·2003	0·4612	2·1
1·5202	0·1819	0·4189	2·2
1·4629	0·1652	0·3804	2·3
1·4127	0·1501	0·3455	2·4
1·3686	0·1363	0·3138	2·5
1·3298	0·1238	0·2850	2·6
1·2955	0·1124	0·2589	2·7
1·2650	0·1021	0·2351	2·8
1·2380	0·09274	0·2135	2·9
1·2140	0·08423	0·1939	3·0
1·1926	0·07650	0·1762	3·1
1·1735	0·06948	0·1600	3·2
1·1564	0·06311	0·1453	3·3
1·1411	0·05732	0·1320	3·4
1·1273	0·05206	0·1199	3·5
1·1150	0·04728	0·1089	3·6
1·1039	0·04294	0·09888	3·7
1·09396	0·03900	0·08980	3·8
1·08498	0·03542	0·08156	3·9
1·07689	0·03217	0·07408	4·0
1·06960	0·02922	0·06728	
1·06960	0·02922	0·06728	4·1
1·06301	0·02654	0·06111	4·2
1·05707	0·02410	0·05550	4·3
1·05170	0·02189	0·05041	4·4
1·04685	0·01988	0·04578	4·5
1·04246	0·01806	0·04158	4·6
1·03849	0·01640	0·03777	4·7
1·03490	0·01490	0·03430	4·8
1·03164	0·01353	0·03116	4·9
1·02870	0·01229	0·02830	5·0
1·02603	0·01116	0·02570	5·1
1·02362	0·01014	0·02334	5·2
1·02143	0·009207	0·02120	5·3
1·01944	0·008362	0·01926	5·4
1·01764	0·007595	0·01749	5·5
1·01601	0·006898	0·01588	5·6
1·01453	0·006265	0·01443	5·7
1·01319	0·005690	0·01310	5·8
1·01197	0·005168	0·01190	5·9
1·01087	0·004694	0·01081	6·0
1·009865	0·004263	0·009816	6·1
1·008956	0·003872	0·008916	6·2
1·008131	0·003517	0·008098	6·3
1·007382	0·003194	0·007355	6·4
1·006702	0·002901	0·006680	6·5
1·006085	0·002635	0·006067	6·6
1·005525	0·002393	0·005510	6·7
1·005017	0·002174	0·005005	6·8
1·004556	0·001974	0·004545	6·9
1·004137	0·001793	0·004128	7·0
1·003757	0·001628	0·003750	7·1
1·003411	0·001479	0·003406	7·2
1·003098	0·001343	0·003093	7·3
1·002813	0·001220	0·002809	7·4
1·002555	0·001108	0·002551	7·5
1·002320	0·001006	0·002317	7·6
1·002107	0·0009141	0·002105	7·7
1·001913	0·0008302	0·001912	7·8
1·001738	0·0007540	0·001736	7·9
1·001578	0·0006848	0·001577	8·0
1·001433	0·0006220	0·001432	

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