On the relationship between phyllotaxy and vasculature: a synthesis

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Abstract:

There is a definite relationship between the phyllotactic fraction and the sympodia uniting median leaf traces in a stem. The denominator of the phyllotactic fraction is the number of sympodia in the -stem, and the numerator is the -number of sympodia counted in passing from the sympodium of one leaf to that of an adjacent leaf on the genetic helix. This relationship holds for species with closed as well as open vascular systems. Of the 100 shoots (93 species) whose vasculature has been reviewed from the literature only one shows no apparent relationship between the phyllotactic fraction and the vasculature. Shoots for 87 species show the relationship described above while shoots of five species have both irregular phyllotaxis and vasculature. The mathematical constraints on this relationship are shown to depend on the divergence angle and the fact that sympodia do not cross one another. That there are biological controls on this relationship in addition to the purely mathematical ones is shown by the fact that sympodial connections are almost universally made along orthostichies. These controls most likely operate on factors that influence the formation of orthostichies such as the relationship between leaf-shape and use of the apical dome. KEY WORDS:—Leaf trace – orthostichy – parastichy – phyllotaxy vasculature.

Article:

INTRODUCTION

The developmental and structural relationships between leaf and stem (Esau, 1965; Fahn, 1982) are obviously close yet there has been no comprehensive explanation of leaf arrangement in context with the vascular system of the shoot. Most authors have concentrated on either phyllotaxy (Church, 1904; Maksymowych & Erickson, 1977; Mitchison, 1977; Richards, 1948, 1951; Rutishauser, 1981; among many others) or vasculature (see Beck, Schmid & Rothwell, 1982 for a review) and not on the relationship between the two.

Nowhere is the difference between the work on phyllotaxy and vasculature more apparent then in the interpretation of orthostichies. Workers on vasculature have traditionally considered this term to refer to leaves arranged in a straight line while workers on phyllotaxy have denied the existence of any straight line relationships in leaf arrangement and have focused on steep helices of leaves visible in the apical region (Fig. l) (Church, 1904; Loiseau, 1959; Richards, 1951; Snow, 1955). These two views of leaf arrangement can be harmonized by considering the vascular connections between leaves.

The primary vascular system of seed plants can be interpreted in terms of leaf traces and sympodial bundles (Beck et al., 1982; Philipson & Balfour, 1963; Esau, 1965), which generally connect leaves arranged along orthostichies (Crafts, 1943; Esau, 1943; Girolami, 1953; Skipworth, 1962; Sterling, 1954), However, when the sympodial bundles are followed upwards to the apical region it is found that they connect leaves along steep helices. Thus, a sequence of leaves vascularized by a sympodium (a sympodial bundle plus its associated leaf traces) may be considered an orthostichy. Slight torsions in the growing stem cause a straightening of the helical orthostichies of the apical region and give rise to the more or less directly superimposed leaves of the mature stem (Schwendener, 1878; Teitz, 1888; see Snow & Snow, 1934 for a summary). Lack of attention to this fact has caused some authors to insist that orthostichies must connect directly superimposed leaves (Beck et al., 1982; Girolami, 1953) while others accept that they may be helical (Esau, 1943; Troll, 1937: 99). In this paper the term orthostichy will be used to refer to the steep helix found at the apex, which may be followed down the stem.

DETERMINATION OF THE PHYLLOTACTIC FRACTION FROM VASCULATURE

The phyllotactic fraction is a fraction which expresses the arrangement of leaves on the stem. The denominator of the fraction is the number of internodes between two leaves on the same orthostichy. The numerator is the number of complete revolutions around the stem completed in moving between these leaves along the genetic spiral. From this definition it is clear that the concept of orthostichy is crucial to the understanding of the phyllotactic fraction. If we recognize that orthostichies are continuous sequences of leaves, which may be followed from the apical to the mature regions of the stem, this fraction becomes a useful tool in describing leaf and, as will be shown here, vascular arrangement.

The relationship between phyllotactic fraction and the vasculature is most apparent in species with helical phyllotaxy, open vascular systems and sympodia of median leaf traces (Beck et al., 1982). In these cases the denominator of the phyllotactic fraction is the number of sympodia in the stem (the number of orthostichies) and the numerator is the number of sympodia counted in passing from the sympodium of one leaf to the sympodium of the adjacent leaf on the genetic helix. To make this procedure clear consider Fig. 2. The primary vascular system presented in this figure consists of eight sympodia, and

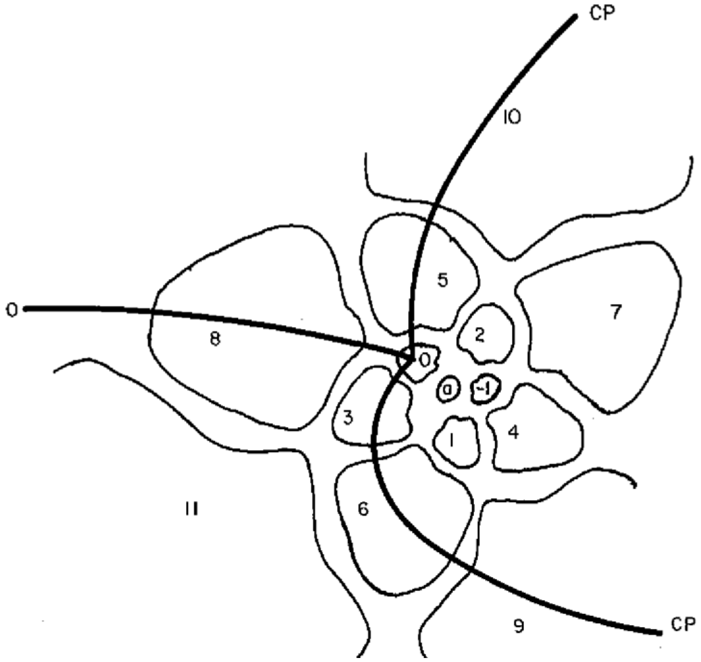


Figure 1. Diagramatic representation of leaf arrangement on a shoot apex. Leaves are numbered along the genetic spiral beginning with leaf — 1. The two contact parastichies (CP) and one orthostichy (0) passing through leaf 6 are shown. a= apical dome.

sequentially departing leaves are vascularized by median traces which arise from every third sympodium. The phyllotactic fraction is, therefore, s. This can be confirmed by counting the number of turns of the genetic spiral between two leaves along one orthostichy (3 turns) and dividing this number by the number of internodes counted in passing between these leaves (8).

The key to understanding why it is possible to determine the phyllotactic fraction by this method is the correspondence between orthostichies and sympodia. Leaves along an orthostichy are always separated by a fixed number of internodes so that, if the leaves are numbered along the genetic spiral from youngest to oldest (Fig. 1), leaves Ø, Ø-n, Ø+ n+n, etc. will lie on one orthostichy. Since every nth leaf is a member of the same orthostichy there must be n orthostichies to account for all the leaves on the stem and the denominator of the phyllotactic fraction is n. In Figs 1 and 2 every 8th leaf lies along the same orthostichy, there are 8 orthostichies on the stem, and the phyllotaxy, is 3/8.

Given the fact that there are *n* sympodia in a stem it is easy to show that the numerator of the phyllotactic fraction is the number of sympodia counted in passing from the sympodium of one leaf to that of the adjacent leaf on the genetic helix. If the phyllotactic fraction is denoted as *pin, p* turns of the genetic spiral are necessary to return to the same sympodium, and the sympodia of successive leaves along the genetic spiral must be separated by *pin* of a circle *(p* turns of the genetic spiral/n sympodia passed in *p* turns = *pin* of a circle for each sympodium). Since there are *n* sympodia in the stem every *(pion* = sympodium must connect to the subsequent leaf of the genetic spiral. Thus, the

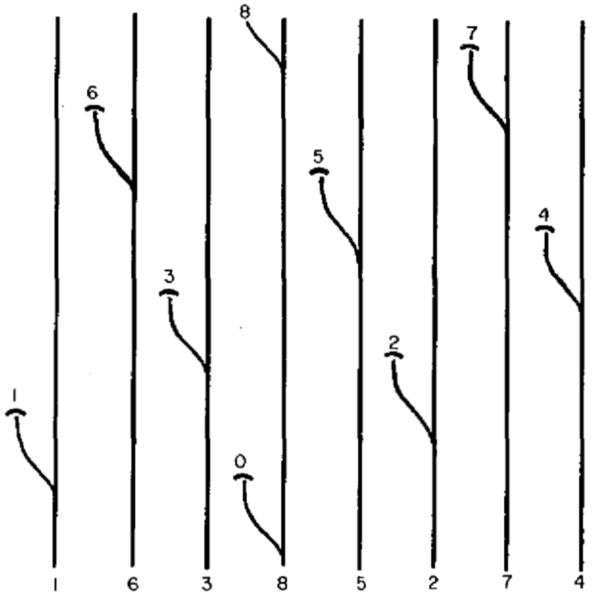


Figure 2. Idealized representation of the vascular system of a shoot. Leaves and sympodia are numbered in phyllotactic sequence from older to younger leaves.

numerator of the phyllotactic fraction is the number of sympodia counted in passing from the sympodium of one leaf to that of the adjacent leaf on the genetic helix.

If the determination of the phyllotactic fraction from the vasculature were always as clear cut as is presented above, this relationship would have been established long ago. Unfortunately there are several conditions which obscure this pattern. These can be grouped into the following five cases:

Case 1: Species with helical phyllotaxy and open vascular systems (Table 1, part I)

This is the most common condition and the one which best shows the relationship between phyllotaxy and vasculature depicted in Fig. 2. Only one variation must be mentioned. Benzing (1967a, b) reconstructed the vascular systems of several species of the Ranales which lack sympodia. The median leaf traces enter and continue down the stem in close proximity to the traces of other leaves on the same orthostichy but without forming any connections with these traces. In these cases the denominator of the phyllotactic fraction is the number of closely associated groups of median traces in the stem and the numerator is the number of groups skipped between adjacent leaves plus one. With this modification the proposed method provides an exact determination of the phyllotactic fraction from the vasculature.

Case 2: Species with helical phyllotaxy and closed vascular systems (Table 1, part II)

In species with closed vascular systems there are no distinct sympodia in the mature stern. However, there are several ways in which the proposed method can be used to determine the phyllotaxy of these species. Esau (1943) for *Linum perenne* L. and Skipworth (1962) for *Hectorella caespitosa* Hooker Fil. both note that the closed vascular systems of these species originate as open systems through vascular connections along one of the orthostichies (parastichies of Skipworth, 1962). In L. perenne leaves n, n+ 8, n+ 16, etc. are connected along the orthostichy. In *H. caespitosa* leaves n, n+ 5, n+ 10, etc. are connected. If the vascular connections of these orthostichies are taken as the sympodia, the phyllotaxies are 3/8 and 2/5respectively, and the method proposed here can be used to determine phyllotaxy. I agree with Esau (194.3) that the phyllotaxy of these species should be evaluated with reference to the earliest vascular connections. Unfortunately, Girolami (1953) and Skipworth (1962) do not agree and determine the phyllotaxy of *Linum usitatissimum L.* and *H. caespitosa* from the external superposition of leaves on the stem. This gives a phyllotactic fraction of for both species (other phyllotaxies also occur in *L. usitatissimum* (Williams, 1974); Table l, part II). It is important to note that there are no direct connections between leaves separated by 13 nodes and that these determinations of phyllotaxy cannot be considered to have the same importance as do those determined from the first-formed vascular connections. Nevertheless, these fractions may be determined directly from the vasculature by considering the total number of median leaf traces at any level in the stem (13) and the number of median traces counted in passing from the median trace of one leaf to that of the adjacent leaf on the genetic helix (5). Thus, closed vascular systems do not present a problem for the determination of the phyllotactic fraction from the vasculature.

Case 3: Species with distichous phyllotaxy (Table 2)

In these cases the lateral leaf traces as well as the median traces unite to form sympodia. In the species with symmetrical shoots (Table 2, part I) the total number of sympodia in the stem is increased by some factor. Where two would be predicted, based on the sympodia of median traces, there may be 6 (12-fold system of Dormer, 1946) or 4 (8-fold system of Dormer, 1946). The situation is similar in species with dorsiventral shoots (Table 2, part II), but here the number of sympodia in the stem is not an even number. In the simplest case there are three sympodia in the stem, two are composed of median traces and one is composed solely of laterals. Since the median traces of sequentially formed leaves connect to alternating sympodia of medians, it is clear that first one and then zero (or vice versa) sympodia of laterals will be skipped between adjacent leaves. In both of these cases the proposed method will work if only those sympodia uniting median traces are counted. This is a reasonable suggestion since these are the only sympodia in non-distichous species.

Case 4: Species with helical sympodia (Table 3)

It has long been realized that in certain species the sympodia pursue a helical course in the stem (Beck et al., 1982; de Bary, 1877; Dormer, 1945; Johnson & Truscott, 1956). In these cases leaves which are directly superimposed are not vascularized from the same sympodium. Thus, there is no correspondence between the phyllotactic fraction determined from the external appearance of the stem and that determined from the vasculature by the method proposed

Table 1. Data on the determination of phyllotaxy from the primary vasculature

Species	Family	Phyllotactic fraction	Number of sympodia or groups	Number of sympodia separating adjacent leaves*	Source
I. Species with helical phyllotaxy and open vascular systems					
Champhorosma sp.	Chenopodiaceae	$\frac{2}{5}$	5	2	Bisalputra, 1962
Kochia astrotricha L. A. S. Johnson	Chenopodiaceae	$\frac{2}{5}$	5	2	Bisalputra, 1962
Bassia brachyptera R. Anderson	Chenopodiaceae	$\frac{2}{5}$	5	2	Bisalputra, 1962
Salsola kali L.	Chenopodiaceae	$\frac{2}{5}$	5	2	Bisalputra, 1962
Chenopodium glaucum L.	Chenopodiaceae	$\frac{2}{5}$	5	2	Wilson, 1924
Physocarpus opulifolius (L.) Maxim.	Leguminosae	$\frac{2}{5}$	5	2	Devadas & Beck, 1972
Cassia didymobotrya Fresen.	Leguminosae	$\frac{2}{5}$	5	2	Devadas & Beck, 1971
Acacia baileyana F. Muell.	Leguminosae	$\frac{2}{5}$	5	2	Dormer, 1945
Sophora tetraptera J. Mill.	Leguminosae	$\frac{2}{5}$	5	2	Dormer, 1945
Adromischus jasminiflorus (Salm.) Lem.	Crassulaceae	$\frac{2}{5}$	5	2	Jensen, 1968
Sedum ebracteatum Moq. & Sessé ex DC.	Crassulaceae	$\frac{2}{5}$	5	2	Jensen, 1968
Lyginopteris oldhamia (Binney) Potonié	Lyginopteridaceae	$\frac{2}{5}$	5	2	Beck, 1970
Rubus occidentalis L.	Rosaceae	$\frac{2}{5}$	5	2	Devadas & Beck, 1972
Prunus avium L.	Rosaceae	$\frac{2}{5}$	5	2	Devadas & Beck, 1972
Potentilla fruticosa L.	Rosaceae	$\frac{2}{5}$	5	2	Devadas & Beck, 1971
Pereskia grandifolia Haw.	Cactaceae	$\frac{2}{5}$	5	2	Gibson, 1976
P. hamboldtii Britton & Rose	Cactaceae	$\frac{2}{5}$	5	2	Gibson, 1976
P. aculeata (Eichlam) Rose	Cactaceae	$\frac{2}{5}$	5	2	Gibson, 1976
Bubbia sp.	Winteraceae	$\frac{2}{5}$	5	2	Benzing, 1967b
Drimys winteri Forster	Winteraceae	$\frac{2}{5}$	5	2	Benzing, 1967b
D. colorata Raoul	Winteraceae	$\frac{2}{5}$	5	2	Benzing, 1967b
Canella alba Murr	Canellaceae	$\frac{2}{5}$	5	2	Benzing, 1967b
Warburgia ugandensis Sprague	Canellaceae	$\frac{2}{5}$	5	2	Benzing, 1967b
Persea americana Mill.	Lauraceae	$\frac{2}{5}$	5	2	Benzing, 1967a

Lindera benzoin Meissner	Lauraceae	$\frac{2}{5}$	5 groups	2 groups	Benzing, 1967a
Illicium parviflorum Michaux	Illiciaceae	$\frac{2}{5}$	5 groups	2 groups	Benzing, 1967a
Schisandra glabra Brickell	Schisandraceae	$\frac{2}{5}$	5 groups	2 groups	Benzing, 1967a
Euptelea polyandra Siebold & Zucc.	Eupteleaceae	$\frac{2}{5}$	5 groups	2 groups	Benzing, 1967a
Hernandia peltata Meissner	Hernandiaceae	$\frac{2}{5}$	5 groups	2 groups	Benzing, 1967a
Himantandra belgraveana F. Muell.	Himantandraceae	$\frac{2}{5}$	5 groups	2 groups	Benzing, 1967b
Serjania subdentata Juss. ex Poir.	Sapindaceae	$\frac{3}{8}$	8	3	Johnson & Truscott, 1956
Sequoia sempervirens Endl.	Taxodiaceae	$\frac{3}{8}$	8	3	Crafts, 1943
Cotyledon paniculata L.f.	Crassulaceae	$\frac{3}{8}$	8	3	Jensen, 1968
Populus deltoides Marshall	Salicaceae	$\frac{3}{8}$	8	3	Larson & Dickson, 1973
Sutherlandia frutescens R. Br.	Leguminosae	$\frac{3}{8}$	8	3	Dormer, 1945
Ginkgo biloba L.	Ginkgoaceae	$\frac{5}{13}$	13	5	Gunckel & Wetmore, 1946
Kalanchoë tubiflora (Harvey) Ham.	Crassulaceae	$\frac{5}{13}$	13	5	Jensen, 1968
Populus deltoides Marshall	Salicaceae	$\frac{5}{13}$	13	5	Larson, 1975
Sequoia sempervirens Endl.	Taxodiaceae	$\frac{5}{15}$	13	5	Sterling, 1945
Lupinus albus L.	Leguminosae	$\frac{5}{13}$	13	5	O'Neill, 1961
Sequoia sempervirens Endl.	Taxodiaceae	$\frac{3}{11}$	11	3	Sterling, 1945
S. sempervirens Endl.	Taxodiaceae	Bijugate $\frac{1}{5}$	5	1	Sterling, 1945
II. Species with helical phyllotaxy and closed vascular systems					
Sassafras albidum Nees	Lauraceae	$\frac{2}{5}$	5 groups	2 groups	Benzing, 1967a
Euryale ferox Salisb.	Nymphaeaceae	$\frac{2}{5}$	5	2	Weidlich, 1980
Victoria regia Lindley	Nymphaeaceae	$\frac{2}{5}$	5	2	Weidlich, 1980
V. regia Lindley	Nymphaeaceae	$\frac{3}{8}$	8	3	Weidlich, 1980
Nymphaea gigantea Hook.	Nymphaeaceae	$\frac{3}{8}$	8	3	Weidlich, 1976b
N. blanda Hook.	Nymphaeaceae	$\frac{3}{8}$	8	3	Weidlich, 1976a
N. odorata Sol.	Nymphaeaceae	$\frac{3}{8}$	8	3	Weidlich, 1976a
Linum perenne L.	Linaceae	$\frac{3}{8}$	8	3	Esau, 1943
L. perenne L.	Linaceae	$\frac{5}{15}$	13	5	Esau, 1943
L. usitatissimum L.	Linaceae	$\frac{5}{13}$	13	5	Girolami, 1953
Hectorella caespitosa Hook.	Hectorellaceae	$\frac{5}{13}$	13	5	Skipworth, 1962
Linum usitatissimum L.	Linaceae	$\frac{8}{21}$	21	8	Girolami, 1953
L. usitatissimum L.	Linaceae	$\frac{5}{18}$	18	5	Girolami, 1953

*More correctly: number of sympodia counted in passing from the sympodium of one leaf to that of an adjacent leaf on the genetic helix.

Table 2. Data on the determination of phyllotaxy from the primary vasculature in species with distichous phyllotaxy

Species	Family	Phyllotactic fraction	Number of sympodia	Number of sympodia separating adjacent leaves*	Number of sympodia supplying medial traces	Number of sympodia of median traces separating adjacent leaves†	Source
I. Species with radially symmetrical shoots							
Lotus tetragonolobus L.	Leguminosae	$\frac{1}{2}$	6	3	2	1	Dormer, 1946
L. corniculatus L.	Leguminosae	$\frac{1}{2}$	6	3	2	1	Dormer, 1946
Dorycnium suffruticosum Villars	Leguminosae	$\frac{1}{2}$	6	3	2	1	Dormer, 1946
D. rectum Ser.	Leguminosae	$\frac{1}{2}$	6	3	2	1	Dormer, 1946
Anthyllis vulneraria L.	Leguminosae	$\frac{1}{2}$	6	3	2	1	Dormer, 1946
Coronilla emerus L.	Leguminosae	$\frac{1}{2}$	6	3	2	1	Dormer, 1946
C. varia L.	Leguminosae	$\frac{1}{2}$	6	3	2	1	Dormer, 1946
C. cappadocica Willd.	Leguminosae	$\frac{1}{2}$	4	2	2	1	Dormer, 1946
C. glauca L.	Leguminosae	$\frac{1}{2}$	4	2	2	1	Dormer, 1946
C. valentina L.	Leguminosae	$\frac{1}{2}$	4	2	2	1	Dormer, 1946
C. scorpioides Koch	Leguminosae	$\frac{1}{2}$	4	2	2	1	Dormer, 1946

Ornithopus sativus Brot.	Leguminosae	$\frac{1}{2}$	6	3	2	1	Dormer, 1946
Hippocrepis comosa L.	Leguminosae	$\frac{1}{2}$	4	2	2	1	Dormer, 1946
H. multisiliquosus L.	Leguminosae	$\frac{1}{2}$	6	3	2	1	Dormer, 1946
Annona muricata L.	Annonaceae	$\frac{1}{2}$	4	2	2	1	Benzing, 1967b
Asimina triloba Dunal	Annonaceae	$\frac{1}{2}$	4	2	2	1	Benzing, 1967b
Cananga odorata Hook. F. & Thoms.	Annonaceae	$\frac{1}{2}$	4	2	2	1	Benzing, 1967b
Geum canadense Jacq.	Rosaceae	$\frac{1}{2}$	6	3	2	1	Devadas & Beck, 1972
Himantandra belgraveana F. Muell.	Himantandraceae	$\frac{1}{2}$	2 groups	1 group	—	—	Benzing, 1967b
Michelia figo (Lour.) Sprengel	Magnoliaceae	$\frac{1}{2}$	2 groups	1 group	—	—	Benzing, 1967b
Eupomatia laurina R. Br.	Eupomatiaceae	$\frac{1}{2}$	2 groups	1 group	—	—	Benzing, 1967b
Degeneria vitensis I. Bailey & A. C. Smith	Degeneriaceae	$\frac{1}{2}$	2 groups	1 group	—	—	Benzing, 1967b
Hibbertia scandens (Willd.) Dryander	Dilleniaceae	Orthodistichous $\frac{1}{2}$	2 groups	1 group	—	—	Benzing, 1967b
II. Species with dorsiventral shoots							
Coronilla minima L.	Leguminosae	$\frac{1}{2}$	3	1 or 2	2	1	Dormer, 1946
C. vaginalis Lam.	Leguminosae	$\frac{1}{2}$	3	1 or 2	2	1	Dormer, 1946
Scorpiurus spp.	Leguminosae	$\frac{1}{2}$	5	2 or 3	2	1	Dormer, 1946
Trifolium repens L.	Leguminosae	$\frac{1}{2}$	4	1 or 3	2	1	Devadas & Beck, 1971

*More correctly: number of sympodia counted in passing from the sympodium of one leaf to that of an adjacent leaf on the genetic helix.

†As above, but only sympodia of median traces are counted.

Table 3. Data on the determination of phyllotaxy from the primary vasculature in species with helical sympodia or where there is no evaluation of phyllotaxy in the source

Species	Family	Source phyllotactic fraction*	Phyllotactic fraction from leaves along one sympodium	Number of sympodia	Number of sympodia separating adjacent leaves†	Source
Rhagodia spinescens R. Br.	Chenopodiaceae	$\frac{2}{5}$	$\frac{1}{3}$	3	1	Bisalputra, 1962
Atriplex spongiosa F. Muel.	Chenopodiaceae	$\frac{2}{5}$	$\frac{1}{3}$	3	1	Bisalputra, 1962
Salix babylonica L.	Salicaceae	—	$\frac{1}{3}$	3	1	Balfour & Philipson, 1962
Chenopodium album L.	Chenopodiaceae	—	$\frac{2}{5}$	5	2	Wilson, 1924
C. ambrosioides L. var. *anthelminticum* (L.) A. Gray	Chenopodiaceae	—	$\frac{2}{5}$	5	2	Wilson, 1924
Cocculus trilobus D. C.	Menispermaceae	—	$\frac{2}{5}$	5	2	Dormer, 1954
Suaeda maritima Dumort.	Chenopodiaceae	$\frac{5}{13}$	$\frac{2}{5}$	5	2	Balfour & Philipson, 1962
Godetia whitneyi (A. Gray) T. Moore	Onograceae	$\frac{5}{13}$	$\frac{2}{5}$	5	2	Balfour & Philipson, 1962
Iberis amara L.	Cruciferae	$\frac{5}{13}$	$\frac{2}{5}$	5	2	Balfour & Philipson, 1962
Menispermum canadense L.	Menispermaceae	—	$\frac{3}{8}$	8	3	Dormer, 1954
Abies concolor Lindley & Gordon	Pinaceae	$\frac{3}{8}$	$\frac{5}{13}$	13	5	Namboodiri & Beck, 1968
Serjania mexicana Willd.	Sapindaceae	$\frac{3}{8}$	$\frac{4}{11}$	11	4	Johnson & Truscott, 1956

*—, No determination of phyllotaxy in source.

†More correctly: number of sympodia counted in passing from the sympodium of one leaf to that of an adjacent leaf on the genetic helix.

here. The reliance on the external superposition of leaves to determine the phyllotactic fraction caused Beck et al. (1982) to conclude that there are a number of species in which the phyllotactic fraction and the number of sympodia are not related. However, if the phyllotactic fraction is determined by counting the number of turns of the genetic helix between leaves vascularized by the same sympodium and dividing this by the number of internodes between these leaves (Esau, 1943; Tucker, 1961) a fraction is obtained which is in complete agreement with the one obtained by the method described here (number of sympodia counted in passing between adjacent leaves on the genetic helix/number of sympodia in the stem). By determining the phyllotaxy from the leaves connected to the same sympodium the effect of the helical course of the sympodia is removed.

Besides data on species with helical sympodia, Table 3 presents data for species for which the original author did not provide a determination of phyllotaxy. In these cases the phyllotactic fraction was determined directly from the connection of leaves to a sympodium.

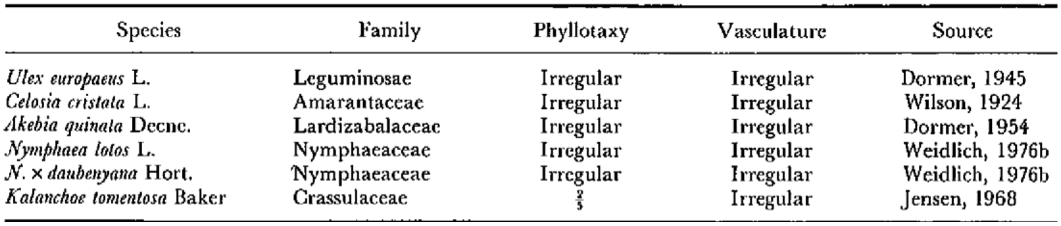
Case 5: Species with irregular phyllotaxy or irregular sympodia (Table 4)

Although most species in this group have irreglar phyllotaxy a correspondence can still be found between phyllotaxy and vasculature. Those species which have irregular phyllotaxy also have an irregular vascular system. *Kalanchoe tomentosa* Baker (Jensen, 1968) is the only species found to have regular phyllotaxy (determined by external superposition of leaves) and an irregular vasculature. No sympodia can be recognized in this species because the branching of the vascular bundles in the stem does not appear to follow a regular pattern. This is the only species known of which it can be said definitively that the determination of the phyllotactic fraction from the vasculature cannot be made.

THE PHYLLOTACTIC FRACTION AND THE FIBONACCI SERIES

It is a well-known fact that the Fibonacci series (the series of integers beginning with the numbers l, 1 and formed such that successive terms are the sum of the previous two, i.e. 1, 1, 2, 3, 5, 8, 13 . . .), plays an important role in describing the pattern of leaf arrangement on a stem (Esau, 1965; Dormer, 1972). In most plants the two sets of contact parastichies and the set of orthostichies visible at the apex are characteriZed by sequential numbers from this sequence (Fig. 1). These numbers express the constant difference between adjacent leaves along a helix and are also the number of helices in a set. In the notation of Church (1904) the phyllotaxy of the apex in Fig. 1 is referred to as a (3 + 5) system. These numbers refer to the two sets of parastichies visible in this apex. If the orthostichies are included in this analysis the three numbers that characterize this apex are 3, 5 and 8. Although numbers drawn from other

Table 4. Data on species with irregular phyllotaxy or with sympodia with an irregular course



Species	Family	Phyllotaxy	Vasculature	Source
Ulex europaeus L.	Leguminosae	Irregular	Irregular	Dormer, 1945
Celosia cristata L.	Amarantaceae	Irregular	Irregular	Wilson, 1924
Akebia quinata Decne.	Lardizabalaceae	Irregular	Irregular	Dormer, 1954
Nymphaea lotos L.	Nymphaeaceae	Irregular	Irregular	Weidlich, 1976b
N. × *daubenyana* Hort.	Nymphaeaceae	Irregular	Irregular	Weidlich, 1976b
Kalanchoe tomentosa Baker	Crassulaceae	$\frac{2}{5}$	Irregular	Jensen, 1968

Fibonacci-like series occur in the description of some apical systems, these systems are less common that those characterized by the Fibonacci numbers (Dormer, 1972). The following discussion will centre on apices with Fibonacci phyllotaxis, but analogous arguments can be made for other systems.

The fractional Fibonacci series converges to an irrational number which, when expressed in terms of a divergence angle, is 137,5° (Dormer, 1972). Each term of the series is a successive approximation to this number (Hardy & Wright, 1975: chapter X). Mitchison (1977) has shown that on an apex with this divergence angle, and with leaves numbered from youngest to oldest, the leaves which come circumferentially nearer to leaf Ø (an arbitrarily chosen leaf) than any preceding (lower number) leaf are the leaves numbered in the Fibonacci sequence. As this result is a consequence of elementary number theory (Khinchin, 1963; Hardy & Wright 1975: chapter XI) a similar result can be shown for the other less common divergence angles.

Since a vascular connection from leaf Ø will always be made to some higher number leaf (n) below it, and since leaf traces do not cross (Larson, 1975), this connection will be made with the sympodium which is closest circumferentially to leaf Ø and whose last connection is to leaf n. From this it is clear that given the divergence angle of 137.5° and the fact that leaf traces do not cross, connections between leaves must be made such that every nth leaf is connected to the same sympodium, there are n such sympodia in the stem, and n is a number drawn from the Fibonacci sequence. Since n is the denominator of the phyllotactic fraction, the method for determining this fraction from the vasculature must work given the above two conditions. In its most general form this proposition states:

> Given a shoot with any of the irrational divergence angles yet discovered and given the fact that leaf traces do not cross, the denominator of the phyllotactic function will be the number of sympodia in the stem, and the numerator will be the number of sympodia counted in passing from the sympodium of one leaf to the sympodium of the adjacent leaf on the genetic helix.

Since there is no mention of orthostichies in this proposition, it should be possible to find both plants in which the sympodia do not follow orthostichies and plants in which the sympodia do follow orthostichies. That this is nOt the case indicates that there are biological constraints which exist beyond the mathematical ones. These most likely concern the relationship between leaf-shape and the size of the apical dome, which, as Richards (1951) has shown, is an important factor in determining the contact parastichies and, thus, the orthostichies. Once the orthostichies have been established, the linkage of leaf- traces along them is most likely caused by a basipetal movement of hormones from the leaf (Sachs, 1981) or an interaction between these hormones and an acropetally developing procambial strand (Larson, 1975).

One further point needs consideration. Orthostichies seem to play an important role in determining vascular connections, and thus, deviations in the divergence angle which do not change the orthostichies will leave the vascular system unaltered. The precise relationship between the divergence angle and contact parastichies (and therefore orthostichies) has been exhaustively explored by Richards (1951) and Adler (1974). For lower phyllotactic systems (such as (2 + 3) or 2/3) they found that a wide range of divergence angles will give the same set of contact parastichies. For these phyllotaxies the observed divergence angles (Fujita, 1939; Maksymowych & Erickson, 1977; Snow & Snow, 1934) are always well within these limits. In cases where the phyllotactic fraction is smaller (5/13 for example) the range of allowable divergence angles decreases, approaching the ideal angle as a limit.

SUMMARY AND CONCLUSIONS

It has been shown that there is a simple relationship between the phyllotaxy of a shoot and the arrangement of vascular sympodia in it. If the phyllotaxy is expressed as a fraction the denominator is the number of sympodia in the stem, and the numerator is the number of sympodia counted in moving from the sympodium of one leaf to the sympodium of the adjacent leaf on the genetic helix.

At least part of this relationship is noted by a number of authors (Beck et al., 1982). The most frequent statement of this relationship is that the number of sympodia is equal to the denominator of the phyllotactic fraction (Beck, 1970; Dormer, 1945, 1946; Gibson, 1976; Jensen, 1968; Larson, 1975), but even in this there is no general agreement. BenZing (1976b) states that there is no regular relationship between phyllotaxy and vasculature. Tucker (1961) finds that the sympodia in the receptacle of *Michelia fuscata* Blume are associated with the sequential development of carpels and are, therefore, intimately related to phyllotaxis. Namboodiri & Beck (1968) show that there is a specific relationship between number of sympodia in a stem and number of sympodia skipped between adjacent leaves in species with open vascular systems. When there are 13 sympodia present four are skipped between leaves (i.e. every fifth sympodium vascularizes an adjacent leaf), when 8, two are skipped (every third to an adjacent leaf) and when 5, one is skipped (every second to an adjacent leaf). However, they do not connect these facts with the phyllotactic fraction which they determine from the external superposition of leaves. Beck (1970) recognizes that "In *Lyginopteris* there is a 2/5 phyllotaxis. Since there are only 5 sympodia, sequentially formed leaf traces must arise along the ontogenetic spiral from every other sympodium in the system. In other words, one sympodium intervenes between those from which successive leaf traces develop". However, he does not elaborate and in a later article (Devadas & Beck, 1972) he is unable to find a general relationship between the denominator of the phyllotactic fraction and the number of sympodia in a stem.

As has been previously noted, Esau (1943) and Tucker (1961) use their knowledge of the vascular system to determine the phyllotactic fraction in *Linum perenne* and *Michelia fascata* respectively. In this method the numerator is determined by the number of turns of the genetic spiral separating two leaves connected to the same sympodium and the denominator by the number of internodes between these leaves. This method has consistently been found to give the same results as the method presented here, while the determination of the phyllotactic fraction from external superposition of leaves does not, in the case of helical sympodia.

The total number of species on which the method of determining phyllotaxy from the vasculature has been tested in this paper is 93. If species with more than one phyllotactic arrangement of leaves (*Sequoia sempervirens* (Lamb.) Endl., Table 1, Part I, for example) are counted more than once the total number of shoots is raised to 100. Of these the phyllotaxy of only one shoot (one species, *Kalanthoë tomentosa*) shows no apparent relationship to the vasculature.

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