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Phyllotaxis triangular unit; phyllotactic transitions as the consequences of the apical wedge disclinations in a crystal-like pattern of the units

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Abstract

The complexity of helical phyllotaxis expressed in diverse phyllotactic patterns and the phenomenon of phyllotactic transformations were investigated theoretically. Two categories of transformations were distinguished: continuous and discontinuous, the latter being interpreted as the consequences of wedge disclinations present at the shoot apex when the number of initials changes. Phyllotaxis triangular unit was described as the common element of all patterns of helical phyllotaxis. It is proposed that the unit plays the same role in a process of the formation of phyllotactic pattern as the crystal basic unit does in a process of crystal growth.

Key words: helical phyllotaxis, phyllotactic transitions, crystal, initial, apical meristem

INTRODUCTION

Until recently, the relative simplicity of the phenomenon of ordered leaf distribution, expressed in one Fibonacci pattern being the most commonly occurring in plants with helical phyllotaxis, has been appreciated in botanical science. However, as many as twelve different phyllotactic patterns have been discovered lately in vegetative shoots of *Abies balsamea*, including rare multijugate patterns such as tetrajugy and secondary bijugy (Zagórska-Marek 1985). Similar diversity, albeit with different frequencies of the particular patterns, occurs in *Abies concolor* and in generative shoots (gynoecia)

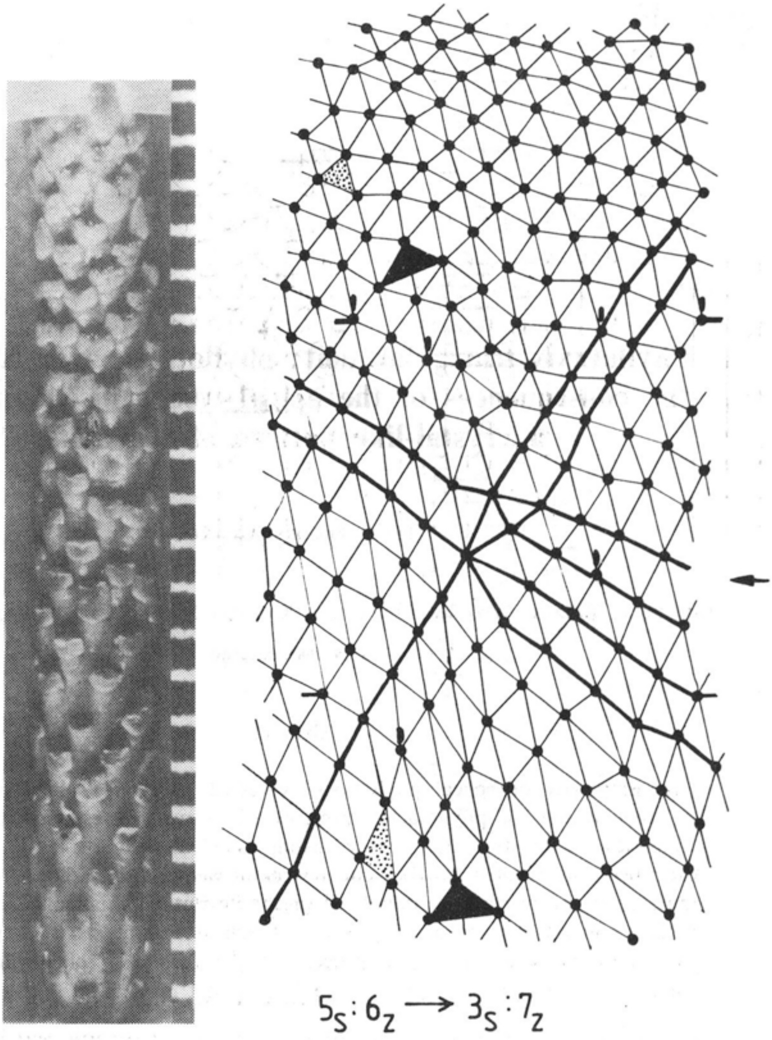

Fig. 1. *Abies balsamea* — phyllotactic transition between 3rd and 5th accessory patterns in the terminal main shoot of a 9-year old tree. The distance between horizontal bars on the scale is 1 mm. On the basis of photographs, such as the one presented on the picture, the whole shoot bark surface has been mapped and a diagram of leaf distribution has been drawn (dots). The diagram shows the shoot surface as seen from the side when unrolled. The horizontal arrow indicates the level of the shoot surface, where change in the number of parastichies takes place. Dots accompanied by a transverse dash represent the same leaf on both sides of the unrolled bark cylinder. Dots with a vertical dash show lateral buds used as markers on the surface (also shown on the photograph). The letters S and Z accompanying parastichy numbers below the diagram indicate orientation of helices in each set of opposed parastichies. Marked triangles (dotted and black) show the relationship between leaves located on the conspicuous contact parastichies, before and after the transition occurred (lower and upper part of the shoot respectively)

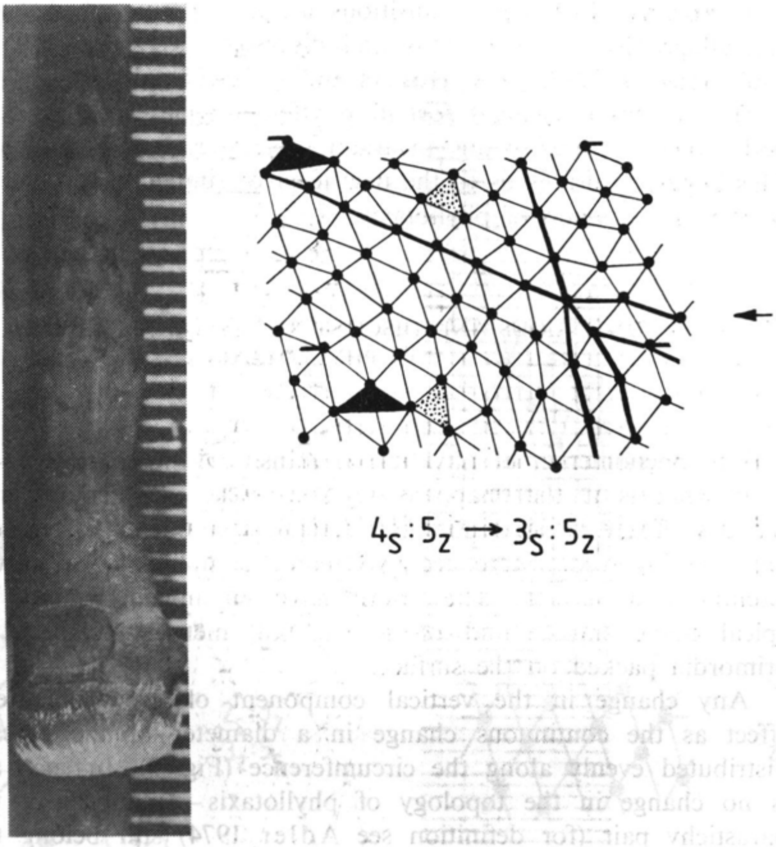

Fig. 2. *Magnolia soulangeana* — phyllotactic transition between 2nd accessory and Fibonacci patterns in carpels arrangement in generative shoot. Further description — as in Fig. 1

of three *Magnolia* species: *M. soulangeana*, *M. acuminata* and *M. kobus* (Zagórska-Marek — unpublished data). It is therefore becoming obvious that not only the potential for formation of different patterns exists in the apical meristem, but that it operates more often than it has been initially thought. A new level of phyllotaxis complexity suddenly appeared and new challenging questions had to be brought up. What is the meaning of phyllotactic diversity? What are conditions within the meristem, required for formation of the particular pattern? Finally, what is the nature of phyllotaxis in general?

Both in *Abies* and in *Magnolia*, relatively frequent pattern transformations have been found (Figs. 1, 2). The way the phyllotactic transitions occur shed some light on the nature of phyllotaxis itself and made it possible to respond to the challenges by conceiving and developing the model of phyllotaxis presented in this study. The model compares the process of ordered initiation of leaf primordia with the process of crystal growth and explains phyllotactic transitions as an example of defects known in crystallography as dislocations and disclinations (Frank 1951, Nabarro 1967, Harris 1977, 1978, Harris and Erickson 1980).

The common element for all phyllotactic patterns has been described with some features being invariant, regardless of the type of pattern. This hopefully brings us to the new level of simplicity in our understanding of the phenomenon of phyllotaxis.

CONTINUOUS AND DISCONTINUOUS TRANSFORMATIONS IN PHYLLOTAXIS

The phenomenon of phyllotactic transitions posses the following question: what is it that happens in the apical meristem when phyllotaxis changes? There is no doubt that changing parameters of meristem growth must be involved. There are two major components of growth: circumferential and vertical. They both have an impact on the size of the apical dome surface and on the spatial, metrical relations among leaf primordia packed on the surface.

Any change in the vertical component of growth causes the same effect as the continuous change in a diameter of the apical meristem, distributed evenly along the circumference (Fig. 3). In such a case there is no change in the topology of phyllotaxis — numbers of the opposed parastichy pair (for definition see Adler 1974) still belong to the same series, although the conspicuous contact parastichies change from lower to higher numbers or vice versa. This kind of phyllotactic change is of importance in connection with the structure of the primary vascular system, mainly with the inclination or, in the case of a more dramatic change, even with the number of vascular sympodia. When the diameter of the apical meristem changes, inclination of sympodia or their number change accordingly, albeit the number of sympodia still belongs to the same phyllotactic series (Larson 1977). This type of phyllotactic transition is homologous to the continuous contraction (transformation) in tubular arrays of spheres such as microtubuli, bacterial flagella or viral capsids (Harris and Erickson 1980). It does not alter the chirality of phyllotaxis as it is expressed in the direction of the ontogenetic helix and in the orientation of parastichies in consecutive sets. It does however affect the inclination of parastichies (Fig. 3).

There must be another, substantially different change in the apex growth, enabling transition between variant types of phyllotactic patterns, when parastichy and sympodia numbers change from one phyllotactic series to another. According to the concept presented in this paper, this type of phyllotactic transformation is possible by means of local, thus not evently distributed, change in the circumference of the apex. As a result, there is either local surplus or local deficit of the meristem surface, which creates suitable conditions for some parastichies being lost or introduced into the existing sets (Figs. 1, 2). A similar situation can be found in the atomic or molecular networks of crystals, where in the lattice, a new line of atoms (or molecules) can be inserted between the existing two, or two

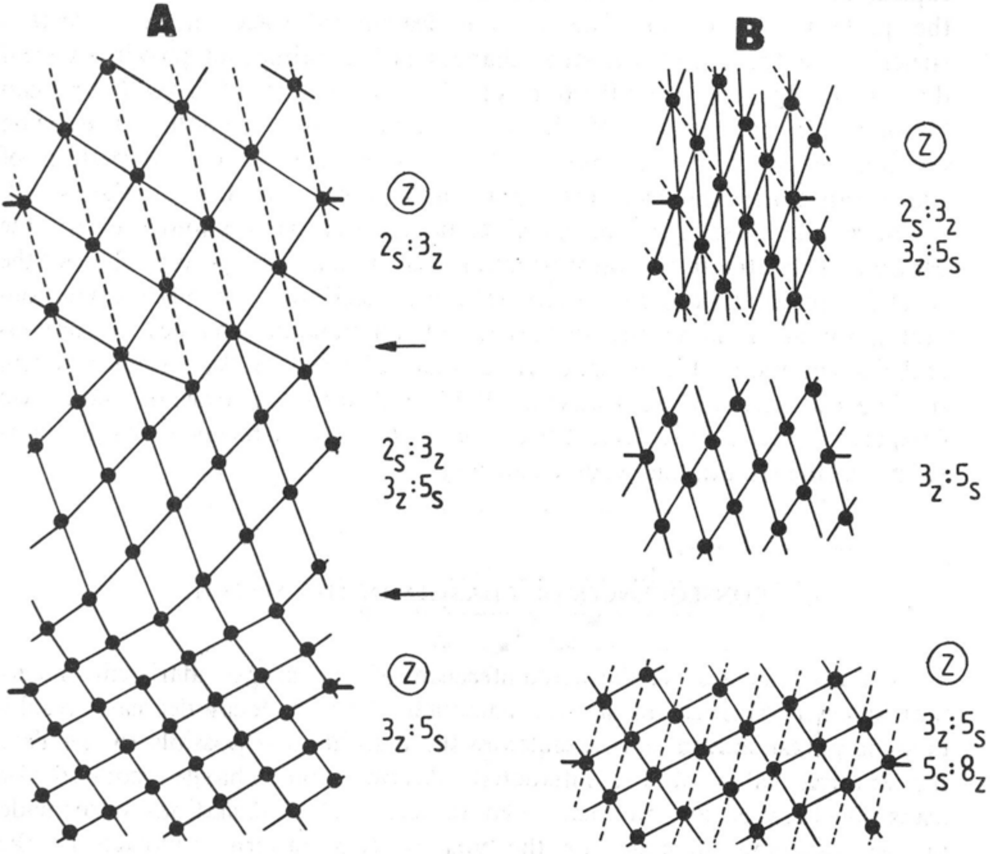

Fig. 3. The conspicuous parastichy pattern, as it changes in the shoot as the result of: A — increases in the vertical distance between successive leaves (from the levels indicated by arrows); B — continuous decreases in shoot circumference with horizontal distances between leaves changing proportionally. The type of phyllotactic pattern and the direction of ontogenetic helix, indicated by circled letter Z, in both cases remain unchanged. The opposed parastichy pair numbers on the side of each diagram belong to the same phyllotactic series, although they change within the series, as do the conspicuous parastichies on the different levels of shoot surface. Parastichies that become not obviously conspicuous are marked with a broken line. Dots accompanied by a transverse dash represent the same leaf position on both sides of the unrolled shoot bark surface. The letters S and Z accompanying parastichy numbers indicate the orientation of helices in each set of opposed parastichies

lines may join together forming one line instead of two. This kind of defect in crystals is called the edge dislocation (Frank 1951, Nabarro 1967). Dislocations in a parastichy pattern on the surface of the embryonic shoot mean transformation of one phyllotactic pattern into another. The change is homologous to discontinuous contraction in tubular arrays of spheres (Harris and Erickson 1980). The difference between tubules and the apical meristem is that in contracting tubular structure such as a viral capsid, one pattern of sphere packing is converted into another entirely — the pattern changes in time without leaving a trace of the previous structure. In the apical meristem changes in the primordia packing system due to ontogenetic modification of the parameters of growth, remain "printed" on the surface of the apex, because the leaf site, once being initiated, is fixed. As the result, there are differences in the pattern of leaf arrangement between the upper and lower surfaces of the shoot.

Since the first type of phyllotactic change is homological to the continuous contraction (transformation) in tubular arrays of spheres, the second to discontinuous contraction (Harris and Erickson 1980), correspondingly we shall name the two types of phyllotactic changes continuous and discontinuous. Phyllotactic transitions described in the vascular system of *Populus deltoides* by Larson (1977) fall into the first of these two categories, phyllotactic transitions found in *Abies balsamea* (Zagórska-Marek 1985) into the second category.

CONSEQUENCES OF CHANGES IN THE APEX SIZE

A local increase in the circumference of the apical maristem means that space is created for a new parastichy line. A local decrease results in some parastichies disappearing from the pattern. It is possible to calculate the limiting value of circumferential, discontinuous change required for transition between any two particular patterns. The calculations were made in the following manner: for the first of two patterns involved in the transition, the size of the arc occupied by one parastichy in each set was determined. The degrees were selected as the units of measure being assigned to the angle, by which a given arc (a part of the meristem circumference) is intercepted. Calculations of the limiting value itself were made by multiplying the number of parastichies being lost or acquired in the course of transition in consecutive sets, by the size of the arc typical for one parastichy in those sets, before the transition occurred. As an example let us consider the case of Fibonacci to 1st accessory transition. In the first pattern, for each of 2-parastichies, the size of the arc is 180, for 3-parastichy it is 120, for 5-parastichy — 72, etc. The pattern may be converted into the 1st accessory pattern in many ways (Fig. 4). The most probable transformations are: $3_s{:}5_z$ to $3_s{:}4_z$, $3_s{:}5_z$ to $1_s{:}3_z$, and $2_z{:}3_s$ to $3_z{:}4_s$. Any other possibility, involving higher numbers of parastichies having to be changed, like in $2_z{:}3_s$ to $4_z{:}7_s$ transformation, should be a'priori rejected by virtue of circumferential change being too great. Among the listed transitions only one, S chiral configu-

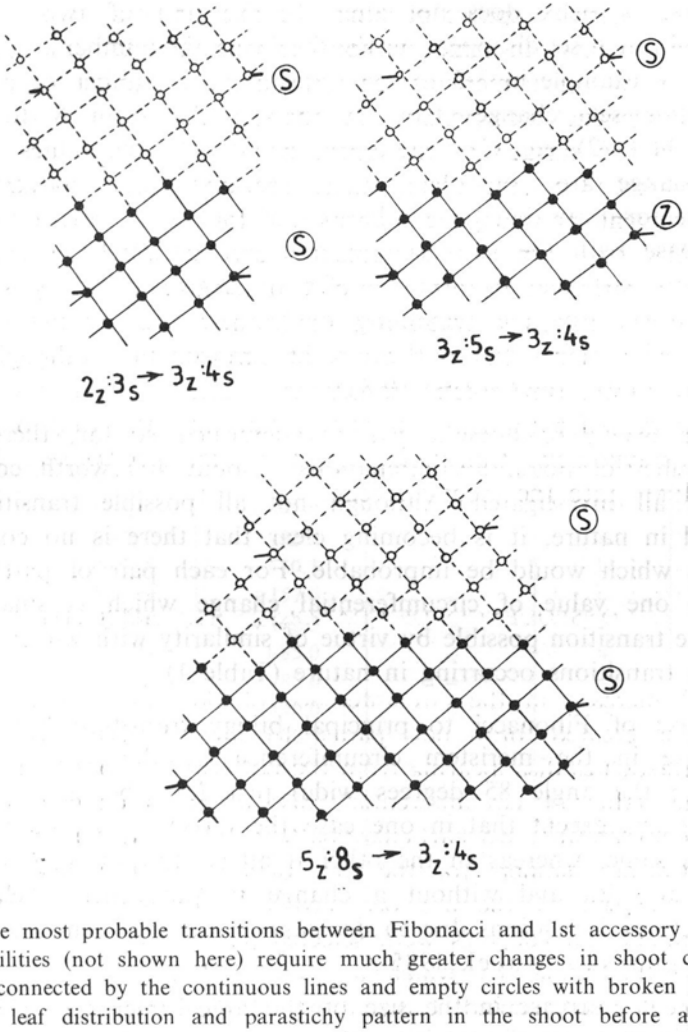

Fig. 4. Three most probable transitions between Fibonacci and 1st accessory patterns. All other possibilities (not shown here) require much greater changes in shoot circumference. Full circles connected by the continuous lines and empty circles with broken lines between them, show leaf distribution and parastichy pattern in the shoot before and after the transition occurred, respectively. A cricle with a transverse dash represents the same leaf on both sides of the unrolled bark surface of the shoot. The opposed parastichy pair numbers below each diagram indicate a change in a parastichy pattern associated with the transition. The letters S and Z accompanying parastichy numbers refer to orientation of helices in two opposed sets of parastichies. The direction of ontogenetic helix, indicated by circled letters S and Z, either alters or it remains unchanged, depending upon the type of transition

ration of the Fibonacci pattern is shown for the sake of simplicity. Obviously the number of possibilities doubles when mirror-like images of the patterns are included (with the Fibonacci pattern being of the Z-type). Since the numerical values of circumferential change are the same for both chiral configurations — it is enough to consider only one of them. In the first of the listed cases, the transition occurs with the change in the direction of the ontogenetic helix, in the other two, the direction of helix does not alter. In the first of two cases some parastichies in each set disappear, in the third case the number of parastichies increases. For example in 3:5 to 3:4 transition the number of parastichies in consecutive sets changes from 5 to 4 (−1), from 8 to 7 (−1), from 13 to 11 (−2), etc. Calculated correspondingly, the values of circumferential change are −1×(360:5), −1×(360:8), −2×(360:13) and so on. They demonstrate that the oscillations of the value around the limiting point decrease with the increasing number of parastichies. The limiting value for this particular transition is 52.5 (in degrees), making it the most probable of all. For the remaining two cases, the limiting values are 170.0 and 137.5 which makes them rather improbable, although not impossible (see Zagórska-Marek 1985).

For the twelve phyllotactic patterns described so far, there is quite a high number of possible combinations — about 400 worth considering. They were all investigated. Although not all possible transitions have been found in nature, it is becoming clear that there is no combination of patterns which would be improbable. For each pair of patterns there is at least one value of circumferential change which is small enough to make the transition possible by virtue of similarity with values calculated for pattern transitions occurring in nature (Table 1).

In a case of Fibonacci to principal bijugy transition both decrease and increase in the meristem circumference by the same arc length (assigned to the angle 85 degrees wide) produces the same effect, i.e. principal bijugy, except that in one case the direction of the ontogenetic helix is the same, whereas in the other it alters. Interestingly, both types of transition (with and without a change in ontogenetic helix course) occur in nature. Transitions due to decrease in the meristem size are more frequent (Zagórska-Marek 1985).

Generally a decrease in the size of the apical meristem produces an entirely different type of transition than an increase by the same value. In a shoot with principal bijugy pattern, discontinuous increase of the meristem circumference by the arc length assigned to the angle 111.2 results in transformation to a Fibonacci pattern. The decrease by the same arc causes the replacement of principal bijugy by 1st accessory pattern.

For all patterns investigated, the change in the direction of the on-

Table 1

Phyllotactic transitions and the limiting values of circumferential change attributed to them, according to theoretical expectations

Phyllotactic transition	Parastichy pattern *	Limiting value of circumfer. change	Ont. helix change **	Transition found	where ***
1	2	3	4	5	6
Fibonacci:					
— 1st acc.	3:5—3:4	−52.5	+	+	A,M
	2:3—3:4	+137.5	−	+?	A
	3:5—1:3	−170.0	−	+?	A
— 2nd acc.	3:5—4:5	+32.5	+	+	A
	2:3—4:5	+275.0	−	−	
	5:8—4:5	−117.4	−	−	
— 3rd acc.	5:8—5:6	−64.9	−	+	A
	5:8—6:11	+117.4	+	−	
	5:8—1:5	−177.6	+	−	
— 4th acc.	5:8—5:7	−32.5	+	+	A
	3:5—5:7	+170.0	−	−	
	5:8—2:5	−157.6	−	−	
— 5th acc.	5:8—3:7	−72.6	−	−	
	3:5—3:7	+105.0	+	−	
	8:13—3:7	−182.3	+	−	
— 6th acc.	3:5—2:7	+72.6	+	−	
	2:3—2:7	+340.0	−	−	
	5:8—2:7	−92.6	−	−	
— 7th acc.	5:8—3:8	−40.1	+	+	A
	3:5—3:8	+157.6	−	−	
	8:13—3:8	−162.3	−	−	
— bijugy P	2:3—2:4	+85.0	+	+	A
	3:5—2:4	−85.0	−	+	A
	5:8−2:4	−190.0	+	−	
— trijugy	3:5—3:6	+52.5	−	−	
	3:5–6:9	+307.5	+	−	
	5:8—3:6	−105.0	+	−	
— tetrajugy	5:8—4:8	−20.0	+	+	A
	3:5—4:8	+190.0	−	−	
	8:13—4:8	−149.9	−	−	
— bijugy S	5:8—6:8	+20.0	−	+	A
	3:5—6:8	+255.0	+	−	
	5:8—2:6	−125.1	+	−	
— Fibonacci	3:5—5:8	+222.5	+	+?	A
	3:5—2:3	−137.5	+	+?	A
1st accessory:					
— Fibonacci	3:4—3:5	+61.5	+	+	A
	3:4—2:3	−99.5	−	−	
— 2nd acc.	4:7—4:5	−76.0	+	−	
	3:4—4:5	+99.5	−	−	
— 3rd acc.	4:7—5:6	−14.5	+	−	

1	2	3	4	5	6
— 4th acc.	3:4—2:5	+23.5	−	−	
	4:7—2:5	−123.0	+	−	
— 5th acc.	4:7—3:7	−23.5	+	−	
— 6th acc.	4:7—2:7	−47.0	+	−	
— 7th acc.	4:7—3:8	+14.5	−	+	A
	3:4—3:8	−128.5	+	−	
— bijugy P	4:7—4:6	−38.0	+	+	A
— trijugy	4:7—3:6	−61.5	−	−	
	3:4—3:6	+123.0	+	−	
— tetrajugy	4:7—4:8	+38.0	−	−	
	7:11—4:8	−114.0	+	−	
— bijugy S	3:4—2:6	+85.0	+	−	
	4:7—2:6	−85.0	−	−	
— 1st acc.	3:4—4:7	+222.5	+	−	
	3:4—1:3	−137.5	+	−	
2nd accessory:					
— Fibonacci	4:5—3:5	−30.0	+	+	M
— 1st acc.	4:5—3:4	−77.9	−	−	
	1:4—3:4	+96.3	+	−	
— 3rd acc.	4:5—5:6	+77.9	−	−	
	5:9—5:6	−89.3	+	−	
— 4th acc.	5:9—5:7	−59.5	−	−	
	4:5—5:7	+126.1	+	−	
— 5th acc.	4:5—3:7	+66.6	−	−	
	5:9—3:7	−96.4	+	−	
— 6th acc.	4:5—2:7	+36.8	−	−	
	5:9—2:7	−114.8	+	−	
— 7th acc.	5:9—3:8	−66.6	−	−	
	4:5—3:8	+114.8	+	−	
— bijugy P	4:5—4:6	+48.2	−	−	
	4:5—2:4	−107.7	+	−	
— trijugy	4:5—3:6	+18.4	+	−	
	5:9—3:6	−126.1	−	−	
— tetrajugy	5:9—4:8	−48.2	−	−	
— bijugy S	4:5—2:6	−11.4	+	−	
— 2nd acc.	4:5—5:9	+222.5	+	−	
	5:9—4:5	−137.5	+	−	
3rd accessory:					
— Fibonacci	5:6—5:8	+79.2	−	−	
	5:6—3:5	−88.5	+	−	
— 1st acc.	5:6—4:7	+15.1	+	+	M
	5:6—3:4	−128.1	−	−	
—2nd acc.	5:6—4:5	−64.1	−	−	
	5:6—5:9	+118.8	+	−	
—4th acc.	5:6—5:7	+39.6	+	−	
	6:11—5:7	−113.0	−	−	
— 5th acc.	5:6—3:7	−9.3	−	+	A
— 6th acc.	5:6—2:7	−33.8	−	−	

1	2		4	5	6
— 7th acc.	5:6—3:8	+30.2	+	−	
	6:11—3:8	−118.8	−	−	
— bijugy P	5:6—4:6	−24.5	−	−	
— trijugy	5:6—3:6	−48.9	+	−	
— tetrajugy	5:6—4:8	+54.7	+	−	
	6:11—4:8	−103.7	−	−	
— bijugy S	5:6—2:6	−73.4	+	−	
	5:6—6:8	+103.7	−	−	
— 3rd acc.	5:6—6:11	+222.5	+	−	
	5:6—1:5	−137.5	+	−	
4th accessory:					
— Fibonacci	5:7—5:8	+35.7	+	+	A
	2:5—2:3	−115.4	−	−	
— 1st acc.	5:7—4:7	−22.0	−	+	A
— 2nd acc.	5:7—5:9	+71.4	−	−	
	5:7—4:5	−93.4	+	−	
— 3rd acc.	5:7—5:6	−35.7	+	−	
— 5th acc.	5:7—3:7	−44.1	+	−	
— 6th acc.	5:7—2:7	−66.1	+	−	
	2:5—2:7	+115.5	−	−	
— 7th acc.	5:7—3:8	−8.4	−	−	
— bijugy P	2:5—2:4	−57.7	+	+	M
	2:5—4:6	+129.1	−	−	
— trijugy	5:7—3:6	−79.8	−	−	
	2:5—3:6	+93.4	+	−	
— tetrajugy	5:7—4:8	+13.6	−	−	
	7:12—4:8	−129.1	+	−	
— bijugy S	2:5—2:6	+57.7	+	−	
	5:7—2:6	−101.8	−	−	
— 4th acc.	2:5—5:7	+222.5	+	−	
	5:7—2:5	−137.5	+	−	
5th accessory:					
— Fibonacci	3:7—3:5	−81.3	+	−	
	3:7—5:8	+91.0	−	−	
— 1st acc.	3:7—4:7	+25.1	+	−	
	3:7—3:4	−122.0	−	−	
— 2nd acc.	3:7—4:5	−56.2	−	−	
	3:7—5:9	+131.6	+	−	
— 3rd acc.	3:7—5:6	+9.6	−	−	
	3:7—1:5	−131.6	+	−	
— 4th acc.	3:7—5:7	+50.3	+	−	
	3:7—2:5	−106.4	−	−	
— 6th acc.	3:7—2:7	−25.1	−	−	
— 7th acc.	3:7—3:8	+40.7	+	−	
	7:10—3:8	−112.4	−	−	
— bijugy P	3:7—4:6	−15.5	−	−	
— trijugy	3:7—3:6	−40.7	+	−	
— tetrajugy	3:7—4:8	+65.8	+	−	
	7:10—4:8	−96.8	−	−	

1	2	3	4	5	6
— bijugy S	3:7—2:6	−65.8	+	−	
	3:7—6:8	+116.0	−	−	
— 5th acc.	3:7—7:10	+222.5	+	−	
	7:10—3:7	−137.5	+	−	
6th accessory:					
— Fibonacci	2:7—3:5	−60.4	+	−	
	2:7—5:8	+124.7	−	−	
— 1st acc.	2:7—4:7	+54.0	+	−	
	2:7—3:4	−104.0	−	−	
— 2nd acc.	2:7—4:5	−33.4	−	−	
— 3rd acc.	2:7—5:6	+37.3	−	−	
	7:9—5:6	−114.4	+	−	
— 4th acc.	2:7—5:7	+81.0	+	−	
	2:7—2:5	−87.4	−	−	
— 5th acc.	2:7—3:7	+27.0	−	−	
	7:9—3:7	−120.8	+	−	
— 7th acc.	2:7—3:8	+70.7	+	−	
	7:9—3:8	−93.8	−	−	
— bijugy P	2:7—4:6	+10.3	−	−	
	2:7—2:4	−131.1	+	−	
— trijugy	2:7—3:6	−16.7	+	−	
— tetrajugy	7:9—4:8	−77.1	−	−	
	2:7—4:8	+97.7	+	−	
— bijugy S	2:7—2:6	−43.7	+	−	
— 6th acc.	2:7—7:9	+222.5	+	−	
	7:9—2:7	−137.5	+	−	
7th accessory:					
— Fibonacci	3:8—5:8	+45.2	+	−	
	3:8—3:5	−109.6	−	−	
— 1st acc.	3:8—4:7	−14.0	−	+	A
— 2nd acc.	3:8—5:9	+81.7	−	−	
	3:8—4:5	−87.0	+	−	
— 3rd acc.	3:8—5:6	−27.9	+	−	
— 4th acc.	3:8—5:7	+8.6	−	+	A
	3:8—2:5	−132.2	+	−	
— 5th acc.	3:8—3:7	−36.5	+	−	
— 6th acc.	3:8—2:7	−59.1	+	−	
	3:8—7:9	+126.8	−	−	
— bijugy P	3:8—4:6	−50.5	+	−	
— trijugy	3:8—3:6	−73.1	−	−	
	3:8—6:9	+104.3	+	−	
— tetrajugy	3:8—4:8	+22.6	−	+	A
	8:11—4:8	−123.5	+	−	
— bijugy S	3:8—6:8	+67.7	+	−	
	3:8—2:6	−95.6	−	−	
— 7th acc.	3:8—8:11	+222.5	+	−	
	8:11—3:8	−137.5	+	−	

1	2	3	4	5	6
bijugy P:					
— Fibonacci	4:6—3:5	−68.7	+	+	A
	2:4—3:5	+111.2	−	+?	A
	4:6—2:3	−180.0	−	+?	A
— 1st acc.	2:4—3:4	+42.5	+	+	A
	2:4—1:3	−111.2	−	−	
— 2nd acc.	4:6—4:5	−42.5	−	−	
— 3rd acc.	4:6—5:6	+26.3	−	−	
	4:6—1:5	−121.2	+	−	
— 4th acc.	2:4—2:5	+68.7	+	+	A
	4:6—2:5	−95.0	−	−	
— 5th acc.	4:6—3:7	+16.2	−	+	A
	6:10—3:7	−127.5	+	−	
— 6th acc.	4:6—2:7	−10.0	−	+	A
— 7th acc.	4:6—3:8	+58.7	+	−	
	6:10—3:8	−101.2	−	−	
— trijugy	4:6—3:6	−26.2	+	+	M
— tetrajugy	6:10—4:8	−85.0	−	−	
	4:6—4:8	+85.0	+	−	
— bijugy S	4:6—2:6	−52.5	−	−	
	2:4—2:6	+137.5	+	−	
— bijugy P	2:4—4:6	+222.5	+	−	
	4:6—2:4	−137.5	+	−	
trijugy:					
— Fibonacci:	3:6—3:5	−45.8	−	+	A
— 1st acc.	3:6—4:7	+74.2	−	+	M
	3:6—3:4	−92.0	+	−	
— 2nd acc.	3:6—4:5	−17.5	+	−	
— 3rd acc.	3:6—5:6	+56.7	+	−	
	6:9—5:6	−102.5	−	−	
— 4th acc.	3:6—2:5	−74.2	+	−	
	3:6—5:7	+102.5	−	−	
— 5th acc.	3:6—3:7	+45.8	+	−	
	6:9—3:7	−109.2	−	−	
— 6th acc.	3:6—2:7	+17.5	+	−	
	6:9—2:7	−126.7	−	−	
— 7th acc.	6:9—3:8	−80.8	+	−	
	3:6—3:8	+91.7	−	−	
— bijugy P	3:6—4:6	+28.3	+	+	A
	3:6—2:4	−120.0	−	−	
— tetrajugy	6:9—4:8	−63.3	+	−	
	3:6—4:8	+120.0	−	−	
— bijugy S	3:6—2:6	−28.3	−	+	A
— trijugy	3:6—6:9	+222.5	+	−	
	6:9—3:6	−137.5	+	−	
tetrajugy:					
— Fibonacci	4:8—5:8	+21.2	+	+	A
	4:8—3:5	−124.4	−	−	
— 1st acc.	4:8—4:7	−34.4	−	+	A

1	2	3	4	5	6
— 2nd acc.	4:8—5:9	+55.6	–	–	
	4:8—4:5	–103.1	+	–	
— 3rd acc.	4:8—5:6	–47.5	+	–	
— 4th acc.	4:8—5:7	–13.1	–	+	A
— 5th acc.	4:8—3:7	–55.6	+	–	
— 6th acc.	4:8—2:7	–76.9	+	–	
	4:8—7:9	+98.1	–	–	
— 7th acc.	4:8—3:8	–21.2	–	–	
— bijugy P	4:8—4:6	–68.7	+	+	M
	4:8—6:10	+111.2	–	–	
— trijugy	4:8—6:9	+76.8	+	–	
	4:8—3:6	–90.0	–	–	
— bijugy S	4:8—6:8	+42.5	+	–	
	4:8—2:6	–111.2	–	–	
— tetrajugy	4:8—8:12	+222.5	+	–	
	4:8—4:4	–137.5	+	–	
bijugy S:					
— Fibonacci	6:8—5:8	–19.0	–	+	A
— 1st acc.	6:8—4:7	–68.7	+	–	
	2:6—4:7	+111.2	–	–	
— 2nd acc.	2:6—4:5	+11.7	+	+	A
	6:8—4:5	–130.2	–	–	
— 3rd acc.	6:8—5:6	–80.5	–	–	
	2:6—5:6	+92.2	+	–	
— 4th acc.	2:6—2:5	–49.7	+	–	
— 5th acc.	2:6—3:7	+80.5	+	–	
	6:8—3:7	–87.8	–	–	
— 6th acc.	2:6—2:7	+49.7	+	–	
	6:8—2:7	–106.8	–	–	
— 7th acc.	6:8—3:8	–57.0	+	–	
	2:6—3:8	+130.2	–	–	
— bijugy P	2:6—4:6	+61.5	+	–	
	2:6—2:4	–99.5	–	–	
— trijugy	2:6—3:6	+30.7	–	+	A
	6:8—3:6	–118.5	+	–	
— tetrajugy	6:8—4:8	–38.0	+	–	
— bijugy S	2:6—6:8	+222.5	+	–	
	6:8—2:6	–137.5	+	–	

* In the a:b → c:d pattern of transition, the orientation of a- and c-parastichies is the same (either S or Z) and opposite to the orientation of b- and d-parastichies.

** (+), (–) — Transition occurring with or without a change in a direction of ontogenetic helix.

*** A, M — Transition found in *Abies* (vegetative shoots) or in *Magnolia* (generative shoots).

togenetic helix without a change of the pattern itself requires the meristem circumference either to increase by 222.5 or to decrease by 137.5. Both values appear to be quite high, therefore these types of phyllotactic transformations should be unlikely and infrequent in nature. However, they are not impossible as is indicated by the data presented in the previous paper (Zagórska-Marek 1985). In such cases the analysis of the vascular system would be helpful in determining whether the transformation was due to an increase or to a decrease in the meristem size. Intuition says that cases found in nature were most likely due to diminishing size of the apex. This would set the upper limit of circumferential changes on 137.5. But now, however, the other possibility can not be excluded.

That the discontinuous changes of the apex circumference can be high, is suggested by the case of dichotomic shoots. Frequent phyllotactic transitions in such shoots (Zagórska-Marek 1985) in the best way support the idea of discontinuous circumferential changes being a cause of transitions. Moreover, the split of the apex into two has grave consequences on the apical meristem surface decreasing dramatically on one side of each of two newly formed meristems. It would be interesting to check whether there is any correlation between dichotomy of the shoot and the type of phyllotactic transition. It should be expected that the transitions due to decreasing size of the meristem are mostly present there.

In nature both decreases and increases of the meristem size occur. This conclusion must be drawn when the results of theoretical calculations are used to interpret phyllotactic transitions that have been found in *Abies* and in *Magnolia*. It seems that transitions resulting from the diminishing size of the apical meristem slightly prevail (Table 1, Fig. 5). In trees such as *Abies*, many axes, particularly lateral, may lose their vigor in time, due to their position in a crown. The main axis, sometimes supressed by unfavorable environmental conditions, may regain its vigorous growth, thus phyllotactic transitions connected with an increasing size of the apex can be expected. There is a possibility of designing an adequate experiment followed by thorough anatomical investigation, which could demonstrate possible correlation between the vigor of the shoot and the type of phyllotactic transitions occurring in it.

A diagram has been designed which makes possible the construction of many different phyllotactic patterns (Fig. 6). It also summarizes the results shown in Table 1, by simple demonstration that only certain transitions are probable, namely those which require relatively small changes in the size of the apex circumference (horizontal coordinate of the system) and in inclination of the meristem axis (vertical coordinate). On the diagram, the phyllotactic patterns that have not been found in nature and are probably the least likely to occur, are located at its peripheries. It seems that 6:7 and 4:9 pattern by virtue of their position in the diagram show a certain degree of probability. Indeed, just recently the 6:7 pattern has been found in the gynoecium of *Magnolia acuminata* flowers (Zagórska-Marek — unpublished data).

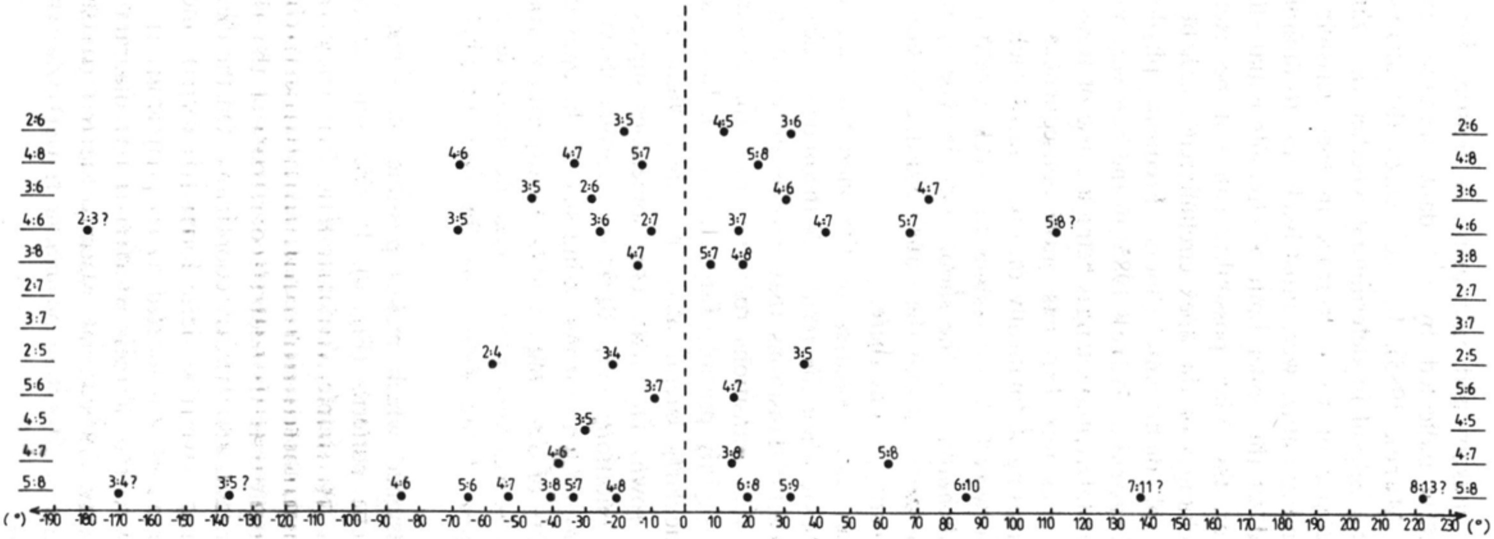

Fig. 5. Phyllotactic transitions found in *Abies* and in *Magnolia* as they are related to the magnitude and to the direction of circumferential change in the apex. Horizontal coordinate indicates the extent of circumferential change in degrees. Twelve phyllotactic patterns are listed in two vertical columns on both sides of the diagram. Each is featured by the opposed parastichy pair numbers. Transformation of the pattern into another pattern is associated with the specific value of circumferential change. The value is indicated by the position of a black dot located at the same level (horizontally) as the particular pattern in the vertical column. The pair of numbers accompanying the dot is the opposed parastichy pair of the pattern developing in the shoot after transition. A question mark is placed beside those dots where it was impossible to determine whether the transition was due to the increase or to the decrease in shoot circumference. Noticeable grouping of dots in the center of the diagram means that the circumferential changes occurring in nature are rather small and that there is an upper and lower limit of changes which is of about 70 and 10 degrees respectively

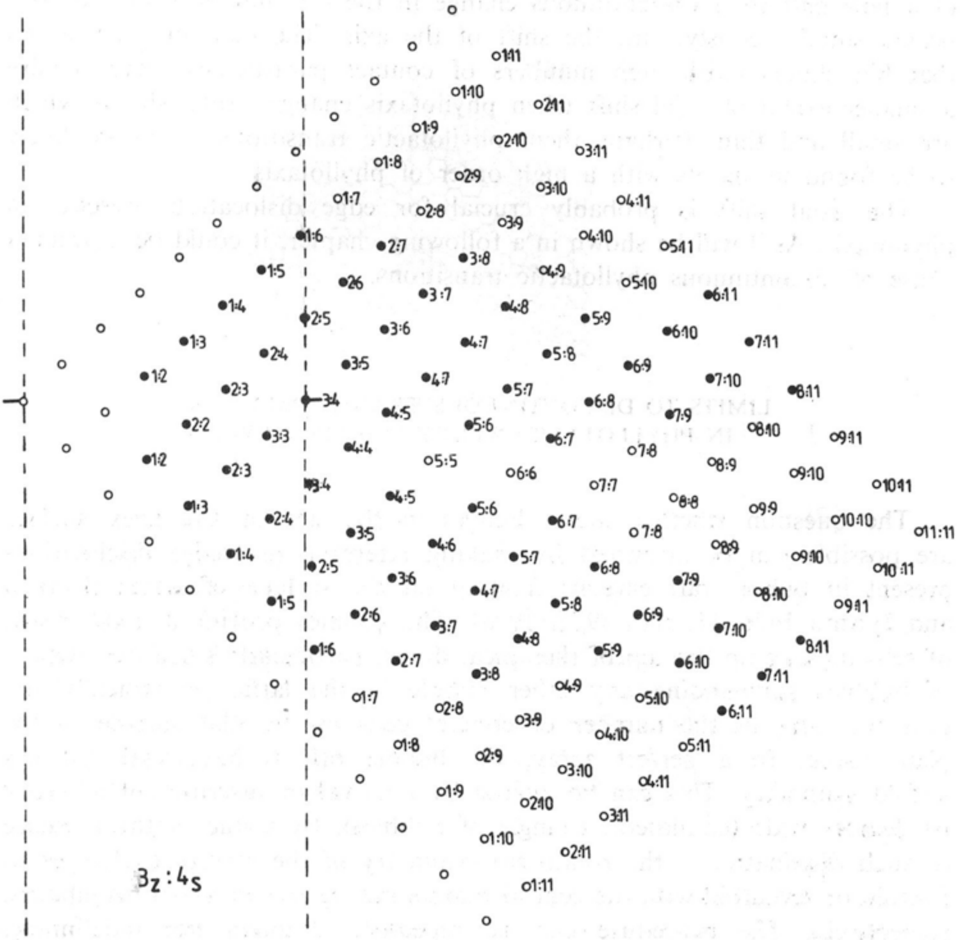

Fig. 6. Common basic structure of leaf distribution in different phyllotactic patterns. Each circle represents a point of leaf insertion on the shoot surface. When an empty circle with a transverse dash is identified with any other circle in the diagram, so as to represent the same leaf on both sides of the unrolled shoot surface, the pair of numbers accompanying the other circle becomes the opposed parastichy pair. It indicates the type and the order of phyllotactic pattern present in the shoot. By the selection of the circle, the magnitude of shoot circumference and inclination of contact parastichies in respect to the shoot axis is set up. Both features vary in different patterns. A circle selected on the picture (full circle with transverse dash) indicates 1st accessory pattern in the shoot. Broken vertical lines show split edges on both sides of the unrolled shoot cylinder. Full and empty circles refer to those patterns that have or have not been found in nature, respectively

It is noticeable that any new phyllotactic pattern can develop without major metrical transformations of certain basic elements of the preexisting pattern. These elements are indicated by the opposite sets of contact parastichies intersecting each other at a right angle (see in the last chapter — the idea of phyllotactic unit). It is enough for the development of a new pattern if discontinuous change in the circumference of the apex occurs simultaneously with the shift of the axis. The diagram also shows that big shoots (with high numbers of contact parastichies) may require a smaller extent of axial shift when phyllotaxis changes, than shoots which are small and thin. Perhaps then, phyllotactic transitions are more likely to be found in shoots with a high order of phyllotaxis.

The axial shift is probably crucial for edge dislocation presence in phyllotaxis. As it will be shown in a following chapter, it could be a primary cause of discontinuous phyllotactic transitions.

LIMITS TO DISCONTINUOUS TRANSFORMATIONS IN PHYLLOTAXIS; WEDGE DISCLINATIONS

The question whether local changes in the size of the apex surface are possible can be answered by making reference to wedge disclinations present in bubble raft crystals floating on the surface of water (Ishida and Iyama 1976, Harris 1977, 1978). The bubbles provide a good model of cells making up the top of the apical dome, particularly since the number of bubbles surrounding any other bubble in the lattice is typically six, thus the same as the number of contact cells on the flat surface of the plant tissue. In a perfect array, the bubble raft is hexagonal — it has sixfold symmetry. This can be altered by removal or insertion of a wedge 60 degrees wide (equilateral triangle of bubbles). By virtue of the presence of such disclination — the rotational symmetry of the structure changes to fivefold or sevenfold with the central bubble having five or seven neighbours, respectively. The procedure can be repeated, although not indefinitely, bacause of growing circumferential tensions (Fig. 7).

It is possible for a botanist to accept that similar wedge disclinations can be present on the surface of the apical meristem: by either loss or addition of the cell to the group of initials located at the top of the apex, the wedge sector of cells produced by the initial can be lost or added to the surface of the apical dome. Any slight shift in a position of the initial group located at the top of the apex, toward its lateral flank, introduces a change in the inclination of the meristem axis. Since there are some cells in contact with five or seven other cells, the axial shift is likely to cause a change in a number of contacts within a newly established group of initials. The other possibility is that some cells may stop dividing radially, or they may produce twin cells, increasing the number of initials. The effect is the same: discontinuous change of the apex circumference causing in turn phyllotactic transition. The size of the change depends upon two factors. The first is the number of initials being added

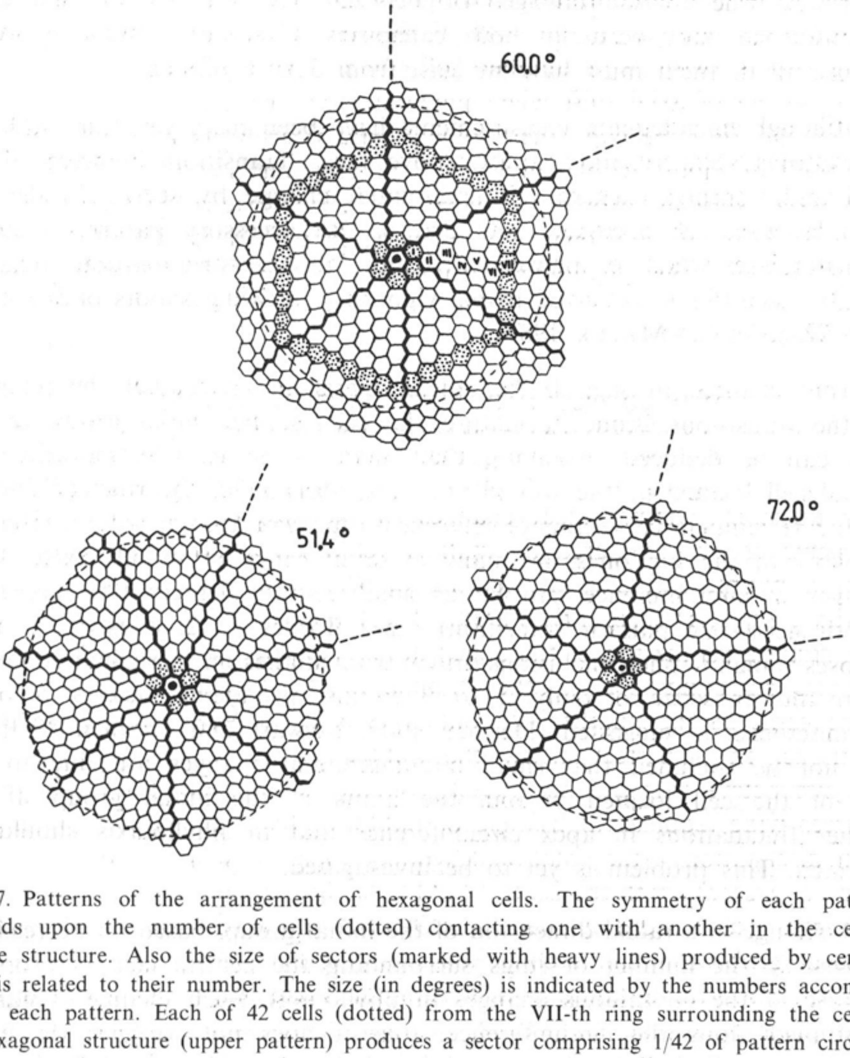

Fig. 7. Patterns of the arrangement of hexagonal cells. The symmetry of each pattern depends upon the number of cells (dotted) contacting one with another in the center of the structure. Also the size of sectors (marked with heavy lines) produced by central cells is related to their number. The size (in degrees) is indicated by the numbers accompanying each pattern. Each of 42 cells (dotted) from the VII-th ring surrounding the center of hexagonal structure (upper pattern) produces a sector comprising 1/42 of pattern circumference. Angular extent of such sector is 8.6 degrees. Structures do not necessarily imply the existence of one apical cell. In nature sectors of cells produced by the group of apical initials do not have to be as equal and symmetrical as in this idealized situation. The possible presence of 5- or 7-contact cells in other locations within each structure is not shown. However, the problem is considered in Table 2. Drawings have been based on photographs of bubble raft crystals published in the paper by Harris (1977)

or lost from the group, the second — location of the event, namely the radial (meridional) distance of the change site from the top of the apex (Fig. 7, Table 2).

It is suggested that: 1) transitions which require small changes in shoot circumference are possible only in big shoots, where the number of initials is big, thus the sectors produced by each initial are narrow, 2) transitions which are due to the changes of between 1/3 and 1/6 of the apex circumference, may occur in both categories of shoots — big and small, because all of them must have at least from 3 to 6 initials.

Although no adequate measurements have been made yet, this author's observations seem to support the above idea. Transitions between Fibonacci and tetrajugy pattern (circumferential change by sector 20 degrees wide), between 1st accessory and 3rd or 7th accessory patterns (change by sector 14.5 wide), or between 3rd and 5th accessory patterns (change by 9.3) — see Fig. 1, occurred in big vigorously growing shoots of the main stems (Zagórska-Marek 1985).

From changes in size of the apical meristem, calculated theoretically for the transitions found in nature the size of the initial group in the apex can be deduced. Assuming that there is, at least temporarily, the central cell located at the top of the axis, surrounded by rings of initials producing symmetrical sectors of cells, we must accept that in some meristems, probably in the big ones, as many as seven rings of initials exist, since changes in circumference can be as small as 8.6 degrees (7th accessory to 4th accessory pattern transition) — see Tables 1, 2, Figs. 5, 7. This opposes somehow the conclusions drawn from studies on mericlinal chimeras, where the presence of only 2 to 3 initials producing sectors of apex circumference, is suggested (Dermen 1945, Stewart and Dermen 1970). It can not be excluded that small circumferential changes are due to the loss of the cell located beyond the limits of the initial group. If so, further fluctuations in apex circumference and in phyllotaxis should be expected. This problem is yet to be investigated.

A change in a radial dimension of the initial group, based on decrease or increase in the number of rings surrounding the central cell, is probably a cause of the continuous changes in phyllotaxis. Such change is equally distributed along the circumference, thus it does not produce the effect of one type of phyllotaxis converting into another. It does influence the number of contact parastichies. A similar effect is caused by changes in a vertical component of the meristem growth. Taking into account all of these considerations, we assume that the size of the shoot is positively correlated with the size of the initial group. This is almost certainly true since the average size of the cell is the same in the big and in the small apices of the same species. However, another factor, possibly implementing the continuous phyllotactic transition, is a change in primordia size without simultaneous change in the apex circumference. The effect of this is the same as the effect of continuous circumferential change. An increase in the primordia size has the same meaning for phyllotaxis as does the continuous decrease of the apex circumference.

Table 2

The extent of cricumferential change in the apex as it is related to the number of cells changing in a group of initials and to the site of the event

Ring No.	No. of cells in a ring	Change in a cell number	Circumferential change*
	4		n × 90.0
	5		n × 72.0
I	6	1, 2, ..., n	n × 60.0
	7		n × 51.4
	8		n × 45.0
	9		n × 40.0
	10		n × 36.0
	11		n × 32.7
II	12	1, 2, ..., n	n × 30.0
	13		n × 27.7
	14		n × 25.7
	15		n × 24.0
	16		n × 22.5
	17		n × 21.2
III	18	1, 2, ..., n	n × 20.0
	19		n × 18.9
	20		n × 18.0
	21		n × 17.1
	22		n × 16.4
	23		n × 15.6
IV	24	1, 2, ..., n	n × 15.0
	25		n × 14.4
	26		n × 13.8
	27		n × 13.3
	28		n × 12.9
	29		n × 12.4
V	30	1, 2, ..., n	n × 12.0
	31		n × 11.6
	32		n × 11.2
	33		n × 10.9
	34		n × 10.6
	35		n × 10.3
VI	36	1, 2, ..., n	n × 10.0
	37		n × 9.7
	38		n × 9.5
	39		n × 9.2
	40		n × 9.0
	41		n × 8.8
VII	42	1, 2, ..., n	n × 8.6
	43		n × 8.4
	44		n × 8.2

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* Either increase or decrease (expressed in degrees).

THE CONCEPT OF PHYLLOTAXIS UNIT

In the developing shoot apex, phyllotactic pattern formation is based on situational similarity between primordia being initiated. As a result, leaves are arranged periodically. Sometimes dislocations of parastichies occur. Pattern development resembles therefore a process of crystal growth. The principles of physics that pertain to crystallization are the same, regardless whether nature deals with protein molecules in viral capsids, with atoms in a crystal lattice or with primordia in a phyllotactic pattern. The principle is that the physical environment for each element must be the same.

In crystallography there exists the idea of a crystal basic unit or building block. It is the smallest group of atoms or molecules within a crystal, which yields the crystal structure by repetition of the pattern. By virtue of similarity between crystallization and phyllotactic pattern formation, an analogous basic unit could be proposed for helical phyllotaxis. The search for such a unit brought the following results: some invariant features have been found in the groups of three neighbouring leaves located on contact parastichies bearing consecutive numbers of phyllotactic series typical for the pattern. These characters are common for all patterns investigated. It seems therefore that the triads of leaf primordia located on contact parastichies (as they are before elongation of the embryonic shoot takes place) at the point of intersection, might be accepted as the phyllotaxis basic units. The term to denote the unit in the present study will be: phyllotaxis triangular unit, or in short — the triangular unit.

The phyllotactic pattern is generated from the base of the meristem upward by simple repetition of the triangular unit module. The ruling principle is that the two upper leaves of two triangles being adjacent laterally make the base of the third triangle located above. The process is perpetuated on each side of the apical meristem quite independently. This is suggested by the fact that any local disruption of pattern formation in some inflorescences, such as the capitulum, does not affect the formation of the pattern on the opposite side of the same inflorescence (Hejnowicz — personal communication).

The type of pattern depends upon the relationship between the size of the triangular unit and the circumferential size of the apical meristem. Any discontinuous change in circumference creates spatial conditions for triangular unit(s) being added or lost from the pattern. Theoretically it should automatically change the relationship between the triangular units still of the same size and the newly established circumference of the apex. In this manner, the ratio of these two values becomes characteristic for a new pattern. For example, in a transition from Fibonacci to 1st accessory pattern, with parastichy numbers changing from 3:5 to 3:4, the arc size

Table 3

Phyllotaxis triangular units in different phyllotactic patterns — spatial relations between three leaves located on contact parastichies

Phyllotactic pattern	Contact parastichy pattern	Triangular unit characteristics*						
		x	y	x/y	a	b	b/a	incl.
Fibonacci	$1_S{:}2_Z$	85.0	137.5	0.6	157.3	174.9	1.1	S
	$2_Z{:}3_S$	85.0	52.5	1.6	97.2	101.0	1.0	Z
	$3_S{:}5_Z$	32.5	52.5	0.6	61.5	62.4	1.0	S
	$5_Z{:}8_S$	32.5	20.0	1.6	37.9	38.2	1.0	Z
	$8_S{:}13_Z$	12.5	20.0	0.6	23.5	23.7	1.0	S
1st acc.	$1_S{:}3_Z$	61.5	99.5	0.6	109.3	148.8	1.4	S
	$3_Z{:}4_S$	61.5	38.0	1.6	67.5	74.4	1.1	Z
	$4_S{:}7_Z$	23.5	38.0	0.6	44.2	46.0	1.0	S
	$7_Z{:}11_S$	23.5	14.5	1.6	27.3	27.7	1.0	Z
2nd acc.	$1_S{:}4_Z$	48.2	77.9	0.6	83.8	131.7	1.6	S
	$4_Z{:}5_S$	48.2	29.7	1.6	51.7	58.9	1.1	Z
	$5_S{:}9_Z$	18.4	29.7	0.6	34.5	36.4	1.1	S
	$9_Z{:}14_S$	18.4	11.3	1.6	21.3	21.8	1.0	Z
3rd acc.	$1_S{:}5_Z$	39.5	64.1	0.6	67.9	119.2	1.8	S
	$5_Z{:}6_S$	39.5	24.6	1.6	42.1	48.7	1.2	Z
	$6_S{:}11_Z$	14.9	24.6	0.6	28.4	29.9	1.0	S
4th acc.	$2_Z{:}5_S$	57.7	35.7	1.6	80.1	64.5	0.8	Z
	$5_S{:}7_Z$	22.0	35.7	0.6	42.8	39.8	0.9	S
	$7_Z{:}12_S$	22.0	13.7	1.6	26.5	25.7	1.0	Z
5th acc.	$3_Z{:}7_S$	40.6	25.1	1.6	54.9	45.7	0.8	Z
	$7_S{:}10_Z$	15.5	25.1	0.6	30.1	28.2	0.9	S
	$10_Z{:}17_S$	15.5	9.6	1.6	18.6	18.1	1.0	Z
6th acc.	$2_Z{:}7_S$	43.7	27.0	1.6	69.7	47.4	0.7	Z
	$7_S{:}9_Z$	16.7	27.0	0.6	32.8	29.3	0.9	S
	$9_Z{:}16_S$	16.7	10.2	1.6	20.2	19.4	1.0	Z
7th acc.	$3_S{:}8_Z$	22.6	36.5	0.6	40.5	52.0	1.3	S
	$8_Z{:}11_S$	22.6	14.0	1.6	25.1	27.2	1.1	Z
bijugy P	$2_S{:}4_Z$	42.5	68.7	0.6	78.7	87.5	1.1	S
	$4_Z{:}6_S$	42.5	26.2	1.6	48.6	50.5	1.0	Z
	$6_S{:}10_Z$	16.2	26.2	0.6	30.7	31.2	1.0	S
trijugy	$3_S{:}6_Z$	28.3	45.8	0.6	52.4	58.3	1.1	S
	$6_Z{:}9_S$	28.3	17.5	1.6	32.4	33.7	1.0	Z
	$9_S{:}15_Z$	10.8	17.5	0.6	20.5	20.8	1.0	S
tetrajugy	$4_Z{:}4_S$	55.6	34.4	1.6	55.6	70.7	1.3	Z
	$4_S{:}8_Z$	21.2	34.4	0.6	39.3	43.7	1.1	S
	$8_Z{:}12_S$	21.2	13.1	1.6	24.3	25.2	1.0	Z
bijugy S	$2_S{:}6_Z$	30.7	49.7	0.6	54.6	74.4	1.4	S
	$6_Z{:}8_S$	30.7	19.0	1.6	33.8	37.2	1.1	Z
	$8_S{:}14_Z$	11.7	19.0	0.6	22.1	23.0	1.0	S

* Length of the left (b, x) and right (a, y) side of traingular unit: 1) as it is when contact parastichies intersect each other at right angles — a, b; 2) projected onto the circumference — x, y.

Inclination of the triangular unit: either S or Z as indicated by the orientation of the triangle height in respect to the meristem axis.

All magnitudes are expressed in angular measure; leaf positions were calculated with use of the divergencies characteristic for particular patterns.

Only S chiral configuration of phyllotaxis is considered, since the triangular units in Z phyllotaxis are mirror-like images of these pressented in the table.

between the positions of two lower leaves (making a base of the triangular unit) projected onto the circumference is initially 85 (in degrees). This makes 23.6% of the apex circumference. After cicumference changes by 52.5 (the limiting value required for this particular transition), the same metrically arc length becomes 27.6% of the new circumference. This percentage is characteristic for the 1st accessory pattern (Fig. 8). The same is true for any other transition. Indeed in nature the triangular units from the upper and from the lower surface of the shoot, in which phyllotactic transition occurred, maintain the direction of their inclination and do not differ one from another topologically. They may differ as far as vertical distances are concerned due to continuous changes taking place in the shoot (Figs. 1, 2).

The characteristic properties of the triangular unit that are invariant when pattern changes and universal, i.e. independent of the pattern the unit belongs to, are: 1) the base of the triangle, thus the unit itself, is inclined in respect to the meristem axis; when lateral leaves are located at the same level, phyllotaxis is not helical but decussate or tetracussate; 2) the leaf positioned at the top of the triangle is always shifted toward that of its two lateral, not necessarily consecutive, neighbours, which is located below the other; 3) when the position of each leaf is projected onto the

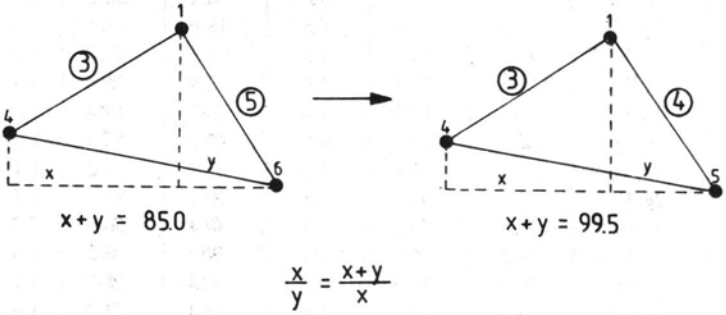

Fig. 8. Geometry of the triangular unit as it remains unchanged despite transformation in phyllotaxis of the shoot. The transition from Fibonacci (left) to 1st accessory pattern (right), caused by discontinuous decrease in the shoot circumference, introduces a new relationship between constant magnitudes of triangle sides and changed magnitude of shoot circumference. The equation below the picture shows the relationship between magnitudes of triangle sides while projected onto the circumference (horizontal broken line); X and Y are the projections of left and right side respectively. The angular extent of the base side projection (X+Y) is 85.0 in Fibonacci pattern. After decrease in shoot circumference, the projection, metrically the same, makes an arc length, the angular extent of which is 99.5, typical for the 1st accessory pattern. The positions of leaves making the triangular unit are marked with dots accompanied by numbers of leaf initiation. Leaves are numbered in reverse order of initiation, the oldest leaf having the highest number. Circled numbers indicate number of parastichies parallel to the triangle sides

horizontal line (circumference), the distance between two leaves making the base of triangle is sectioned by the position of the upper leaf according to divine proportion: the longer section to the shorter one is as the whole distance to the longer section, and their ratio is as 1.6 to 1; 4) the ratio of two lateral sides of the triangular unit is close to one if only contact parastichies intersect each other at a right angle (90 degrees). Detailed description of triangular units of different phyllotactic patterns is given in Table 3.

The triangular unit is established within the apical meristem, where primordia are packed and in physical contact one with another. An interesting property of the pattern generated by repetition of such units is that once the position of the upper leaf is initiated according to principle No. 3 (see above) it automatically sets the same proportion within other triad of leaves located on other parastichies bearing higher (or lower) numbers than contact parastichies, but still from the same phyllotactic series. Because of this, it must be remembered that if an elongated shoot is analysed, the conspicuous parastichies in it, thus also triangular units, are of a lower order than contact parastichies of the same shoot at its embryonic stage of development (Cannel and Bowler 1978).

The model based on the phyllotaxis unit concept explains a quite common and so far not fully understood situation, in which leaves with a higher number of initiation (supposedly older) are sometimes positioned above those having lower numbers, thus expected to be inserted closer to the apex. Since on each side of the meristem the build-up of triangular units is independent, it is not surprising that some disparities in the pattern growth may occur. These must affect the position of leaves, if followed along the ontogenetic helix.

The very character of phyllotactic transitions indicates that such formal attributes of phyllotaxis as ontogenetic helix, leaf initiation number or divergence, matter much less than contact parastichies made up of triangular units. It seems that these attributes are artificial, imaginary constructions rather than the natural features of phyllotaxis. They proved to be quite useful in determining the type of phyllotactic pattern or its chirality. However, the author of this work recomends that we use the opposed parastichy pair formula supplemented by indexes showing the orientation of parastichies rather than the old ways of pattern identification by the limiting value of divergence angle, by name, or by the number of ontogenetic helices in monojugate versus multijugate patterns.

The first consideration of the idea that the type of phyllotactic pattern depends upon the relationship among three neighbouring leaves can be found in one chapter of book by Hejnowicz (1973). The author still taking into account an importance of leaf initiation numbers, considered the position of a new leaf, initiated above and between two, necessarily consecutive (with numbers of initiation differing by one) leaves. According to his concept, the type of phyllotactic pattern depends upon how high the numbers of two consecutive leaves are and whether the newly initiated leaf is closer to the younger or to the older of its two lateral, sectorial neighbours. Of course such triads of leaves exist and can be considered for each pattern. Between patterns, however, they differ one from another topologically very much. It can be seen clearly when the comparison of these triads is made between Fibonacci and 7th or 6th accessory patterns: in the latter the consecutive leaves and the leaf sited above them are located on parastichies bearing numbers that do not belong to the phyllotactic series characteristic for the pattern.

Although being very close to it, Hejnowicz failed to recognize the triads of leaves defined by contact parastichies as phyllotactic units, having common and invariant features. His work, however, has greatly inspired this study and it was a starting point for the model presented in this paper.

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Trójkątna jednostka filotaksji; zmiany wzoru filotaksji jako następstwo apikalnych dysklinacji w kryształopodobnym układzie jednostek

Streszczenie

W niniejszej pracy podjęto próbę interpretacji zjawiska różnorodności wzorów filotaksji helikalnej oraz przechodzenia jednego wzoru w drugi. Wyróżniono dwie kategorie transformacji wzoru filotaksji helikalnej związanych ze zmianą obwodu merystemu apikalnego: transformację ciągłą oraz nieciągłą. W pierwszej z nich takie parametry wzoru filotaksji jak dywergencja, kierunek helisy ontogenetycznej oraz liczby parastych tworzące serię filotaktyczną nie ulegają zmianie. Zmienia się jedynie, choć wciąż w obrębie tej samej serii filotaktycznej, rząd wielkości liczb odnoszących się do parastych kontaktowych. W przypadku transformacji nieciągłej zmienia się typ wzoru a więc i dywergencja, i rodzaj ciągu liczb tworzących serię filotaktyczną, często również kierunek helisy ontogenetycznej. Liczby parastych kontaktowych zmieniają się nieznacznie, przy czym często powstają efekty łączenia się lub rozdzielania parastych analogicznie jak w przypadku dyslokacji krawędziowych w kryształach. Dyslokacje we wzorze parastych powstają w wyniku lokalnych zmian wielkości powierzchni bocznej merystemu apikalnego, te z kolei można interpretować jako następstwo dysklinacji na szczycie wierzchołka, tzn. utraty istniejącego sektora komórek lub powstania nowego sektora wskutek zmiany liczby komórek inicjalnych.

Skomplikowanie zjawiska filotaksji helikalnej wyrażające się w różnorodności wzorów da się uprościć przez wprowadzenie pojęcia trójkątnej jednostki filotaksji. Jest to rodzaj modułu — element o cechach niezmienniczych, wspólnych dla wszystkich wzorów dotąd poznanych. Każdy bez wyjątku wzór może być generowany za pomocą tego samego modułu. Analogię stanowi wzrost kryształu o określonym kształcie, który odbywa się poprzez powtarzanie się pewnej podstawowej jednostki strukturalnej.