CAN PHYLLOTAXIS BE CONTROLLED BY A CELLULAR PROGRAM?

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I. Introduction

Phyllotaxis or the manner in which leaves are initiated and arranged on the shoot apex of plants has given rise to a great number of theories. Most of them are global approaches based on the question how the specific distribution of leaves evolves. The occupation of free areas, chemical interactions between primordia with inhibitory effects, etc. are the most commonly invoked processes. The most recent model to be proposed within this framework is a physical one [5] whereby a phyllotactic-like distribution anses when magnetic drops fall onto oil. Cellular theories are few. Cellulose reinforcement on the epidermal surface in meristems is more related to fields than to a cellular program [6]. An automata theoretical model based on 8-sided cells and the diffusion of an inhibitor [7] has shown how leaves can be disposed on a cylindrical surface.

For some years we have expressed the possibility that a cellular program is responsible for the way a cellular plate develops. It is based on differentiation of the peripheral cytoplasm, immediately below the plasmalemma, as a determinant of the position of each new division wall introduced by cytokinesis. Accordingly, the formulation of differential distributions of mother wall segments and the new-formed segments derived from cell division, can simulate most of the morphologies associated with plant life forms [11, 14]. One of the most interesting models is that which leads to a 2/5 phyllotactic pattern, in which the characteristic spatio-temporal formation of leave-like organs derives from a meristematic plate of autoreproductive cells [8, 12, 13].

This modelling is based on the development of topological wall nets described by parallel rewriting map systems. They are related to L-systems based on formal languages [17]. Several kinds of such map-systems have been proposed, differing particularly in the way wall labels are used (e.g. [3]). In our approach we use double-labelling of walls respecting its similarity to real cell walls which are built up of contributions from both cells that share a wall.

The main difference of the cellular tissue generated by a map system and a real tissue resides in the fact that (1) all divisions are, for the moment, considered as synchronous, and (2) that often four walls meet at their corners. In nature, these two conditions are scarcely realized. In the present paper we shall show that, in a cell layer, if only three walls meet at corners, the underlying model is not invalidated and a plant-like morphology of the cell plate can still be generated.

II. Map system generating a 2/5 phyllotaxis

A map is a finite set of bounded and non-intersecting regions lying on a plane. The walls separating the regions are labelled inside each region. In a region representing a cell, this labelling is always clockwise. Consequently, the entire circumference of a cell is described by a sequence of wall labels. A given wall separating two cells can thus be considered as a double-chain of two antiparallel sequences of wall segments (Fig.1). Binary subdivisions of regions are described by wall

label productions. Between two slashes introduced by these productions, a new wall is created, simulating a cell division. After each time step in a developmental sequence, the wall grid is rewritten and redrawn in the most suitable way as no physical additional drawing instructions are here involved (Fig.2). In any case, they would add nothing to the morphology implied by the generated maps, except to provide more realistic representations (as realized by [16].

A map system $G = (\Sigma, P, "/", M_o)$ consists of an alphabet Σ of wall labels, a set P of wall productions such as $P = \{\omega \rightarrow \alpha \mid \omega \in \Sigma$ and $\alpha \in \Sigma^* \cup \{/_x\}\}$, $x \in \Sigma$. There are metasymbols like slashes and an initial map M_o. The following system is at the base of the simplest constructable 2/5 phyllotaxis:

$$\Sigma = \{1,2,3,4,5,6,7,8,9,0\},$$

M_o is a cells a with the wall sequence (1.2.3.4.5) (Fig.1, step 1),

$$P = \left\{ \begin{array}{llll} 1 \rightarrow 3 & & 6 \rightarrow 9 \\ 2 \rightarrow 4 & & 7 \rightarrow 0/_1 2 \\ 3 \rightarrow 5/_6 7.8 & & 8 \rightarrow 3 \\ 4 \rightarrow 9 & & 9 \rightarrow 4.5/_6 7 \\ 5 \rightarrow 0/_1 2 & & 0 \rightarrow 8 \end{array} \right\} .$$

The set P of productions means (1) that each cell divides into a daughter cell a and a daughter cell b, (2) that in a cells the division wall will span between mother segments 3 and 5, and in b cells, the division wall spans mother segments 7 and 9, and (3) that the labels of the division wall are specified by the subscript of the slashes.

The derived maps are constructed by 3-, 4-, or 5-sided cells distinguished by variable distributions of wall segments over the walls

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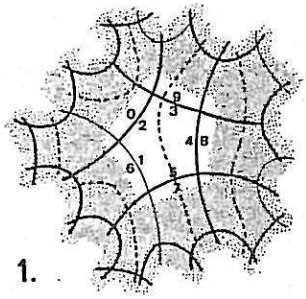
Fig. 1: Simulation of 2/5 phyllotaxis. - *Five map derivations obtained with the map system described in the text (section II). In each cell, walls are labelled clockwise. The position of the division wall, inserted at the next developmental step, is indicated by a broken line. (1): An intial cell a_5 with the wall sequence (1.2.3.4.5), entirely embedded in the tissue. (2): Map representing the division of the previous cell into the daughter cells a_5 and b_4. It is obtained by application of the wall substitution rules of the system and insertion of a new wall separating the two cells. The daughter cell a_5 is identical to the mother cell, i.e. autoreproduction. (3): A map of four cells resulting from the division of the two cells at step 2. A 3-sided autoreproductive cell appears on a protuberance constituted of four such cells, the three others coming from other cell filiations, in addition to that presently generated. The protuberance represents a leaf-like emergence. (4): A second leaf-like primordium protrudes on the left of the tissue. Primordia 1 continues its development by doubling the number of cells. ...(7): Map representing the generated tissue at step 7. Differently colored, 6 cell families successively derived by the division of the intial cell a_5. The serial numbering indicates the sequence of 'leaf' formation, situated on 2 parastichies. Family one (in grey), with leaf 1, is composed of 32 cells. Family two (in white), with leaf 2, is composed of 16 cells, etc.. Family 6, with one cell, which will produce leaf 6, is on the orthostichy of leaf 1. In the axil of leaf 1 (dotted) a new initial cell initiating an axillary meristem.*



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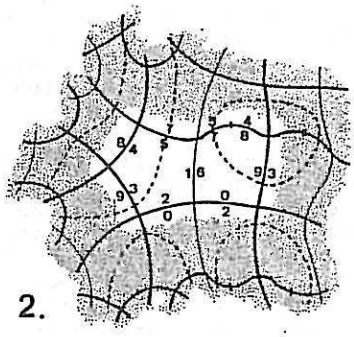

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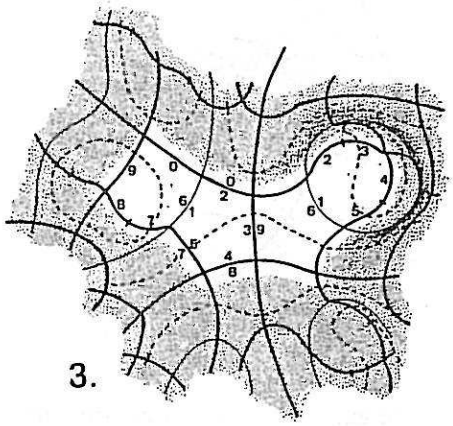

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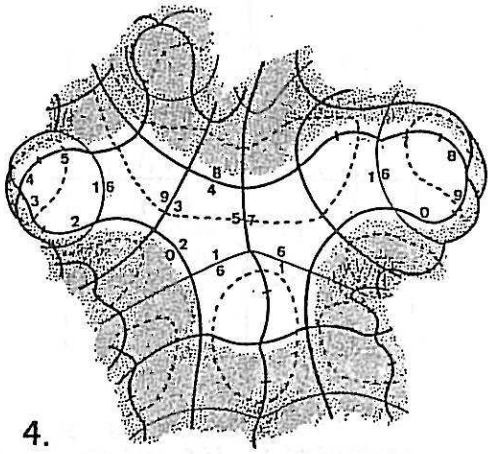

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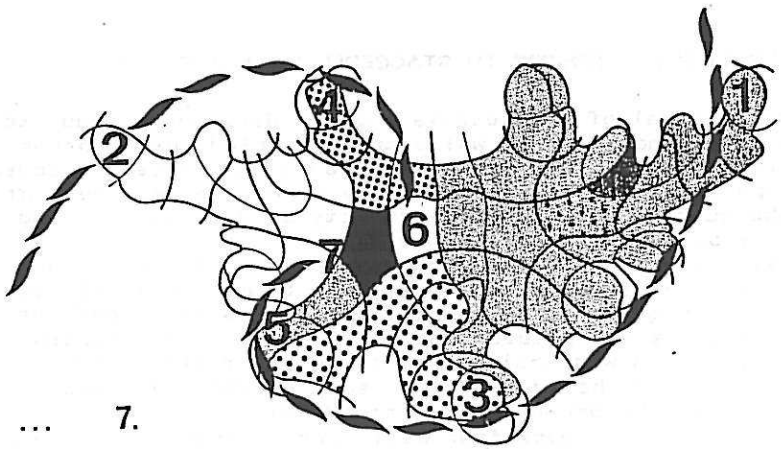


... 7.

shared with neighbour cells. If a daughter cell has exactly the same wall sequence of labels as its mother cell, we speak about 'autoreproductive' cells. After 9 map derivation steps, the cellular plate has obtained its full organization with an 11-celled plate of 5-sided autoreproductive cells in the centre which we consider as an analogue of the main shoot meristem (Fig.3). Numbers on the cellular protuberances highlight their successive inception at sites and states corresponding to a real phyllotaxic pattern. Each leaf-like primordium bears at its summit a plate of 4 autoreproductive cells, the analogue of a 'foliar tip meristem'. If such meristems mostly do not occur in leaves, they may exist in the early emerging primordia. It is interesting to see that the same program initiates autoreproductive shoot and leaf meristems with different kinds of cellular behaviour. No precise divergence angle is considered as the intended interpretation of the topological maps is arbitrary, i.e. only output-dependent. At each division step, the cellular meristematic plate of cells is split into two, with the re-establishment of a complete autoreproductive main shoot plate and another, new shoot plate, also autoreproductive, located in the axils of the 'leaf primordia', and thus symbolizing an axillary bud (Fig.3) [8, 9, 13].

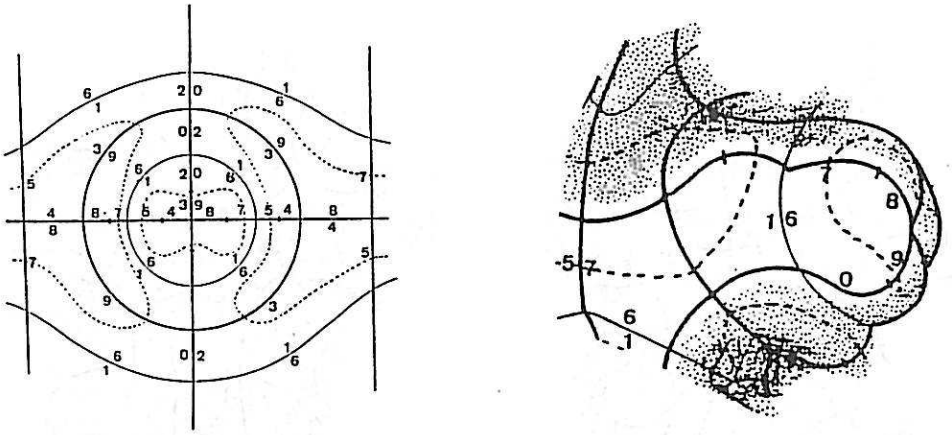


Fig. 2: Topological and topographical maps. - *The topological map generated by the map system is rendered more realistic by drawing all segments approximately of the same lengths and bending, if necessary, the layer towards one side of the plane. This is illustrated by the map representation of the top of a leaf-like protuberance.*

III. From wall crosses to staggered wall insertion

In the model of phyllotaxis, cell divisions lead to 3-, 4-, or 5-sided cells and all cell walls are connected by crosses. However, in real monocellular layers like the epidermis, the cells appear under the microscope mostly as 6-sided and only three walls meet at nodes. This opens the question of the realizability of a model leading to the same morphology by means of 6-sided cells.

Previous investigations have shown that there are systems with axiomatically 6-sided cells which generate more sophisticated patterns of phyllotaxis, e.g. a 2/5 phyllotaxis of bifid leaf structures [14]. Nevertheless, as the simplest map systems for phyllotaxis are based on 5-sided cells, is was challenging to check if six-sided cells in nature could not simply be due to a superimposed process reflecting wall instability in the presence of 5-sided cells.

A wall cross between four cells can be transformed into a staggered cross by replacing the nodes of degree 4 by two nodes of degree 3 connected by a segment:

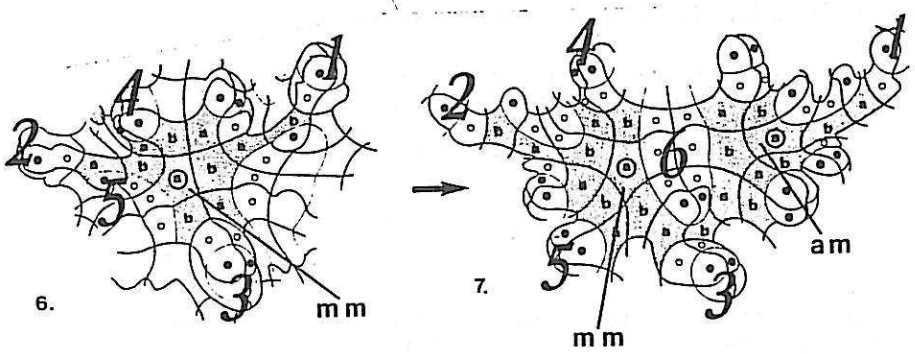
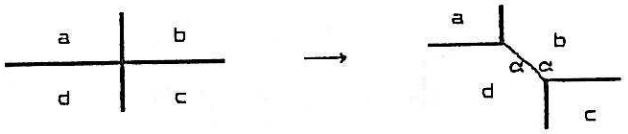


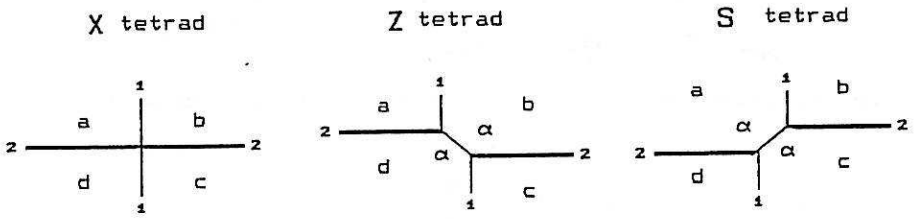
Fig. 3: Maps at step 6 and 7 of derivation in Fig.1. - *(step 6): In grey: a group of eleven autoreproductive cells, a_5 and b_5, in the position of the main meristem mm in a shoot apex. a: apical initial cell; • : autoreproductive a_3 and b_3 cells on the top of 'leaves'; ◦ : inter-meristematic cells. (step 7): one division step later, the previous 11-celled apical plate is split, producing a new 11-celled plate (mm) on the main apex and a second group of 11 autoreproductive cells (am) surrounding the axillary bud initial cell of 'leaf' 1.*

cells a,b,c, and d



By this transformation, the cells *b* and *d* each earn one side. It is a small additional segment, labelled α in both of two contiguous cells, and without any further development, i.e. α → α. It furnishes the supplementary wall for our 5-sided cells.

As in a wall cross of the X-type, the two intersecting walls are not of the same age, say that wall 22 is younger than the wall 11, the introduction of α-segments leads either to a *Z* or to an *S* configuration in the junction of younger to older walls [10]:



In the first case, Z, the cells *b* and *d* become adjacent, in the second case, S, the contact is established between the cells *a* and *c*. The segment α can be introduced into the given system by means of the following transitions:

3 → 5.α/$_6$7.8 and 5 → 0.α/$_1$2, generating a S wall junction,

or 3 → 5/$_6$α.7.8 and 5 → 0/$_1$α.2, generating a Z wall junction.

What determines the type of staggering? Is it related to the system, i.e. determinated by the cell division pattern or is it a random process, i.e. independant of the division pattern? Or is it subject to another, physical control?

III.1. Determined direction of wall staggering

In a first attempt to treat the problem, it is supposed that the staggering is controlled by cellular behavioural rules, the productions leading to, and operating during, the cell divisions. Then, everywhere in the generated tissue, Z staggering can be introduced by means of the following productions:

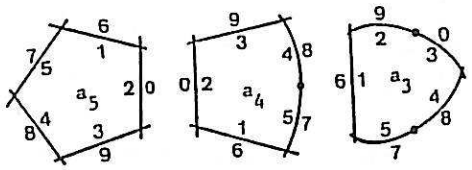
$$3 \rightarrow 5/_{\sigma}\alpha.7.8 \quad \text{and} \quad 5 \rightarrow 0/_{1}\alpha.2 \ ,$$
$$7 \rightarrow 0/_{1}\alpha.2 \quad \text{and} \quad 9 \rightarrow 4.5/_{\sigma}\alpha.7 \ .$$

The double-walls with their antiparallel label sequences (slash subscripts are omitted) show the Z configuration:

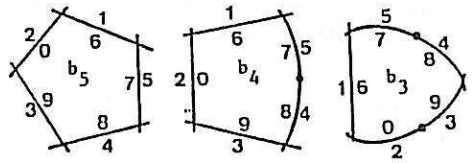
$$\rightleftarrows : \frac{8.7.\alpha/5}{4.5/\alpha.7} \quad \text{and} \quad \frac{2.\alpha/0}{0/\alpha.2} \ .$$

As slashes are wall separators, each wall cross generates a double wall $\frac{\alpha}{\alpha}$ in addition to the double-walls $\frac{8.7}{4.5}$, $\frac{5}{7}$, and $\frac{2}{0}$ (or $\frac{0}{2}$).

In the basic system, the apical pattern is a very simple construction realized by only six types of cells, a and b sisters which are 3-, 4- or 5-sided as indicated by the subscript. These cells are [13]:

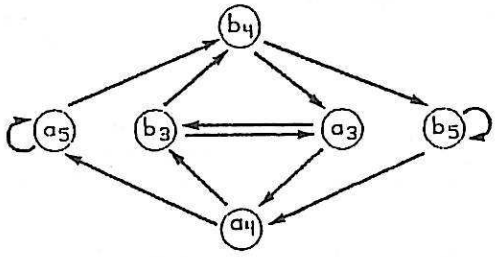


$a_5 \rightarrow a_5\ b_4$
$a_4 \rightarrow a_5\ b_3$
$a_3 \rightarrow a_4\ b_3$



$b_5 \rightarrow a_4.b_5$
$b_4 \rightarrow a_3.b_5$
$b_3 \rightarrow a_3\ b_4$

The cell type filiation graph relates them in the following way:

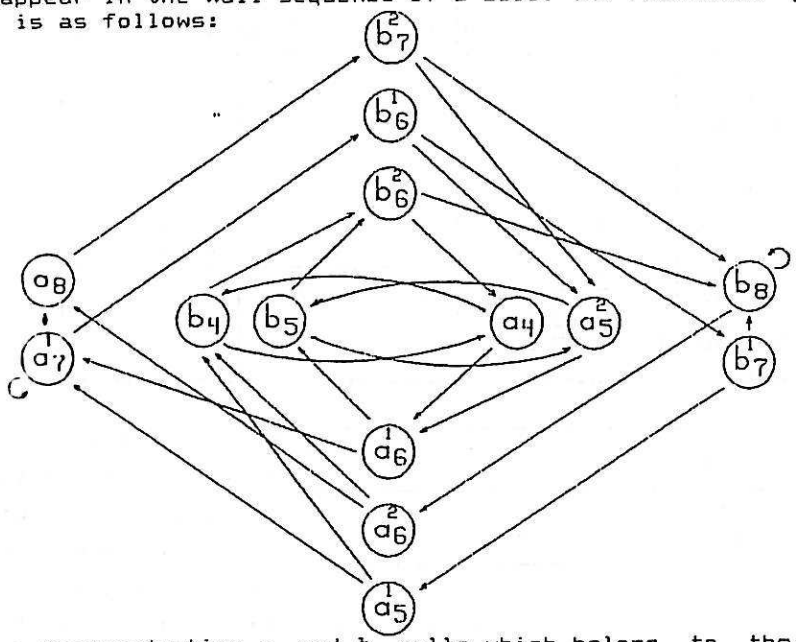


5-sided a and b cells are autoreproductive in the shoot meristem and 3-sided ones are autoreproductive in the foliar appendages, even if the a cells switch to b cells and vice versa. The remaining 4-sided a and b cells form the inter-meristematic tissue. Attaching Z wall junctions to

these originally 3-, 4- or 5-sided cells, each cross is replaced by two nodes joined by an α-segment. The cell derivation in the new system procures seven different α cells and seven different ὁ cells with specific wall sequences, i.e. 14 types of cells instead of 6 types. Nevertheless, the alphabet remains finite. Each cell is still symbolized by α or ὁ specifying the daughter type, and by an index indicating the polygonal degree. Cell types with different wall sequences, but of the same polygonal degree, are differentiated by an superscript. In the following explicit wall sequences of cell types, two wall segments combined to a single wall are underlined and separated by a virtual node. On the left, in parentheses, is given the cell types of the basic system which are replaced:

(a_3)	a_4 (1. α. 2.3. 4.5)	(b_3)	b_4 (6. α. 7.8. 9.0)
	a_5^2 (1. α. 2.3. α. 4.5)		b_5 (6. α. 7.8. α. 9.0)
(a_4)	a_5^1 (1. α. 2. 3. 4.5)	(b_4)	b_6^1 (6. α. 7.8. α. 9. 0)
	a_6^1 (1. α. 2. 3. α. 4.5)		b_6^2 (6. α. 7.8. 9. α. 0)
	a_6^2 (1. α. 2. α. 3. 4.5)		b_7^2 (6. α. 7.8. α. 9. α. 0)
(a_5)	a_7 (1. α. 2. 3. α. 4. 5)	(b_5)	b_7^1 (6. α. 7. 8. 9. α. 0)
	a_8 (1. α. 2. 3. α. 4. α. 5)		b_8 (6. α. 7. α. 8. 9. α. 0)

At the most, three, instead of the five, theoretically possible α-segments appear in the wall sequence of a cell. The filiation graph of these cells is as follows:



Basic autoreproductive a_5 and $ὁ_5$ cells which belong to the central apical meristematic cellplate are now replaced by a_7^1, a_8, and $ὁ_7^1$, $ὁ_8$, respectively. Their filiation becomes:

$$a_8 \rightarrow a_7^1 \rightarrow a_7^1 \qquad \text{and} \qquad ὁ_7^1 \rightarrow ὁ_8 \rightarrow ὁ_8.$$

They remain autoreproductive under the abstraction of the α-segments which

do not play any active role. Basic cells a_3 and b_3, which were found in the meristems of lateral 'foliar' appendices, are replaced by a_4, a_5^2, and b_4, b_5, respectively. Their filiation forms two cycles:

$$a_4 \rightleftarrows b_4 \quad \text{and} \quad a_5^2 \rightleftarrows b_5.$$

The other basic cell types, a_4 and b_4, appearing in the intercalary tissue between the two types of meristems, give rise to a_5^1, a_6^1, a_6^2, and b_6^1, b_6^2, b_7^2, respectively. Their daughter cells initiate simultaneously a new foliar meristem and a new axillary meristem.

As two b_5 cells and two a_4 cells are associated in the 4-celled 'foliar' meristem, four axillary buds are initiated by the model. In real plants, mostly, only one develops.

The frequency distribution A (Table 1) of cells with different numbers of neighbours in a descent incepted by a a_7^1 cell, and with Z-staggered walls everywhere, shows that there is no maximum for six-sided cells, as is found in a real epidermal cell plate.

TABLE 1: FREQUENCY DISTRIBUTION OF CELLS OF DIFFERENT POLYGONAL DEGREE

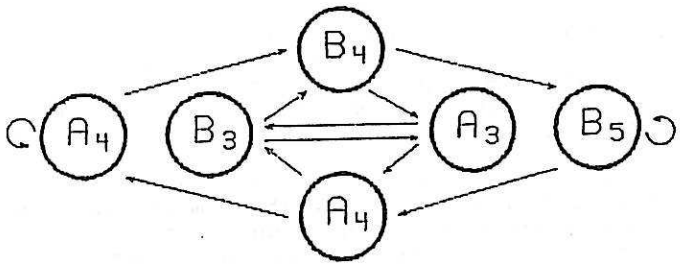
Distribution		A					B					C				D					
Polygonal degree		4	5	6	7	8	4	5	6	7	8	5	6	7	8	4	5	6	7	8	9
# of cells in a map derivation																					
step 1	1			1					1				1					1			
2	2		1	1					2				2					2			
3	4		1	1	2				4				4				1	2	1		
4	8		3	2	2	1		2	4	2		2	4	2			2	4	2		
5	16		5	3	5	3	1	2	10	2	1	2	11	2	1	1	4	7	3	.	1
6	32	2	7	7	9	7	2	5	17	7	1										
7	64	7	12	13	18	13															
8	128	17	24	27	34	25															

Distribution		E							
Polygonal degree		3	4	5	6	7	8	9	10
# of cells									
	57	2	5	19	7	14	8	1	1
	47	2	4	17	6	11	6	1	

A: all wall junctions of Z type,
B and C: S and Z junctions with least difference of polygonal degree between sister cells; cycle of 2 apical cells.
D: ditto, cycle of 3 apical cells.
E: random distribution of S and Z junctions.

III.2. Random distribution of the direction of wall staggering.

A second, random, possibility to change a wall cross into either a Z or a S configuration has, as a consequence, that each basic cell in the model of 2/5 phyllotaxis can be replaced by a very large but finite number of cell varieties. The basic wall sequence itself belongs to each set of varieties, but all combinations with α-segments may occur. The complete sets of wall varieties are related in the same way as does the filiation graph of basic cells:



In each set corresponding to a basic cell type c_x,

$c \in \{\alpha, b\}$ and $x \in \{3, 4, 5\}$,

there are 2^x varieties of wall sequences. For example, in the set A_3 containing varieties which can replace the cell α_3 chacterized by the wall sequence (1. 2.3. 4.5), there are $2^3 = 8$ varieties; 1 cell is 3-sided (the basic sequence), 3 cells are 4-sided, 3 other cells are 5-sided and 1 cell is 6-sided with α-segments on each node. The frequencies are binomial coefficients. The set is:

$$A_3 = \left\{ \begin{array}{ll} (1.\ \underline{2.3}.\ \underline{4.5}) & (1.\ \alpha.\ \underline{2.3}.\ \alpha.\ \underline{4.5}) \\ (1.\ \alpha.\ \underline{2.3}.\ \underline{4.5}) & (1.\ \alpha.\ \underline{2.3}.\ \underline{4.5}\ \alpha) \\ (1.\ \underline{2.3}.\ \alpha.\ \underline{4.5}) & (1.\ \underline{2.3}.\ \alpha.\ \underline{4.5}\ \alpha) \\ (1.\ \underline{2.3}.\ \underline{4.5}\ \alpha) & (1.\ \alpha.\ \underline{2.3}.\ \alpha.\ \underline{4.5}\ \alpha) \end{array} \right\}$$

For $x = 4$, $2^4 = 16$ varieties are dispatched in 1 4-sided sequence,
4 5-sided sequences,
6 6-sided sequences,
4 7-sided sequences,
1 8-sided sequence.

For $x = 5$, $2^5 = 32$ varieties are dispatched in 1 5-sided sequence,
5 6-side sequence,
10 7-side sequence,
10 8-side sequence,
5 9-side sequence,
1 10-sided sequence.

In nature, mostly 6-sided sequences occur, and few 5- and 7-sided ones.

The basic filiation graph in the initial map system uses only one variety from each set, i.e. the shortest one. The previous system, with exclusively Z junctions, uses two varieties from the sets A_3, B_3, A_5, and

B_5, and three varieties from the sets A_4 and B_4.

For the case of a choice at random of S or Z wall junctions, two examples of map derivations lead to the distributions E (Table 1) of the number of cell neighbours. The absence of prevailing 6-sided cells and the widespread frequency distributions reflect the variability of the sets of varieties over wall sequences. It becomes obvious that too many cells have a too high a polygonal degree.

III.3. Introduction of context sensitive S and Z wall staggering

As a consequence of the direction of wall staggering being neither related to the division program of the meristem nor to a random process, it can be supposed that a special program controls the direction of staggering. It is well known that the tessellation or natural subdivision of 2D-areas leads to 6-sided regions (ceramics, sand, Bénard cells, soap bubbles, etc).

We now accept as the criterion for the choice of a division wall attached by either a Z or a S junction the aim of searching for a minimal difference between sister cells with respect to their number of cell neighbours. In this case, again, a certain number of wall sequence varieties are used, taken from the sets of varieties given before. For example, b_5 cells with the sequence (6.7.8.9.0) can be replaced by four sequential varieties (instead of 32) which appear during four cell generations:

b_5 (6.7.8.9.0)	appears like	b_6^a	(6.7.8.9.α.0)
		b_7	(6.7.8.α.9.α.0)
		b_7	(6.α.7.α.8.9.0)
		b_8	(6.α.7.8.9.α.0.α)
b_4 (6.7.8.9.0)	appears like	b_7	(6.α.7.8.α.9.0)
		b_7	(6.α.7.8.9.0.α)
		b_7	(6.7.8.α.9.α.0)

The frequency distribution of the polygonal degree of the cells (Table 1, B) shows that in this case the maximal frequency is obtained for 6-sided cells. Replacing X by Z or S configurations is done sequentially during a given division step. Another sequence adopted for the treatment of mother cells would lead to a slightly different result, as in distribution C (Table 1, C). The polygonal degree of each cell becomes context sensitive in space and time, as a consequence of the adopted criterion of choice.

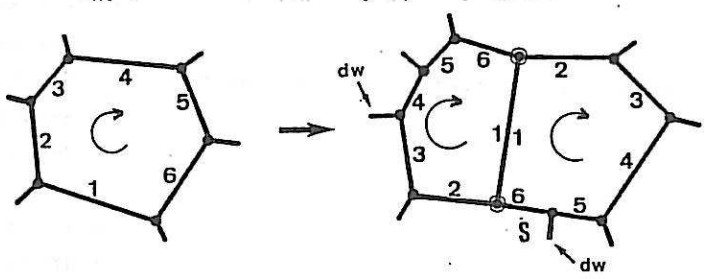


Fig. 4: General case of a cell division. - *Double nodes: attachment points of the division wall 1/1; dw: division wall in a neighbour cell; S: S wall junction.*

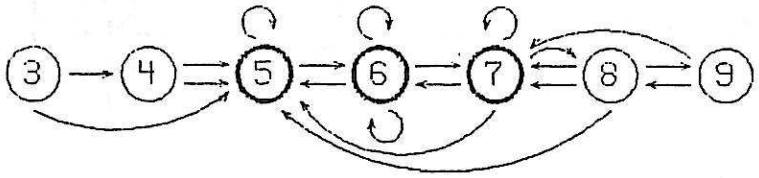
The number of varieties used in the construction of the tissue is not very high. Polygonal degrees outside the range of 5 to 7 are avoided, even though they are possible. This may be due to another constraint. Dormer [4] emphasized that in a cell layer, each dividing cell creates 2 walls represented by the two faces of the division wall (walls 1 and 1 in Fig.4). Two other additional walls result from the subdivision of older walls at the anchor points of the division wall (mother walls 1 and 4 divide both into 6 and 2, (Fig.4). And, on average, there are two division walls in two neighbour cells subdividing also two walls, e.g. walls 2 and 1 divide into 3 and 4, and 5 and 6, respectively Fig.4). So, at each division step, 6 new walls are added to a mother wall sequence with n walls. The resulting $n + 6$ walls are distributed over the boundaries of the two daughters. In the given example $n = 6$, each daughter has six walls (Fig.4). If $n = 5$, the daughters will share $5 + 6 = 11$ walls, i.e. they will be 5- and 6-sided, respectively, or, eventually, they may be 4- and 7-sided.

Table 2 and the corresponding graph highlight the most probable lengths of wall sequences of daughter cells. The table shows that 3- and 4-sided cells are unstable as they create 4- or 5-sided cells. The same can be said for wall lengths greater than 7 which, after one or more divisions, return to fewer-sided cells. Only 5-, 6- and 7-sided cells replicate in cells of similar degrees. But once a 5-sided cell exists, it gives rise to a filiation of 5-sided ones, just as do 7-sided cells. This is only true in the framework of a given system. As soon as a division wall is attached elsewhere or if some cells do not divide, the number of wall sides may be altered. In any case, this rule implies that cells have a polygonal degree in the range from 5 to 7.

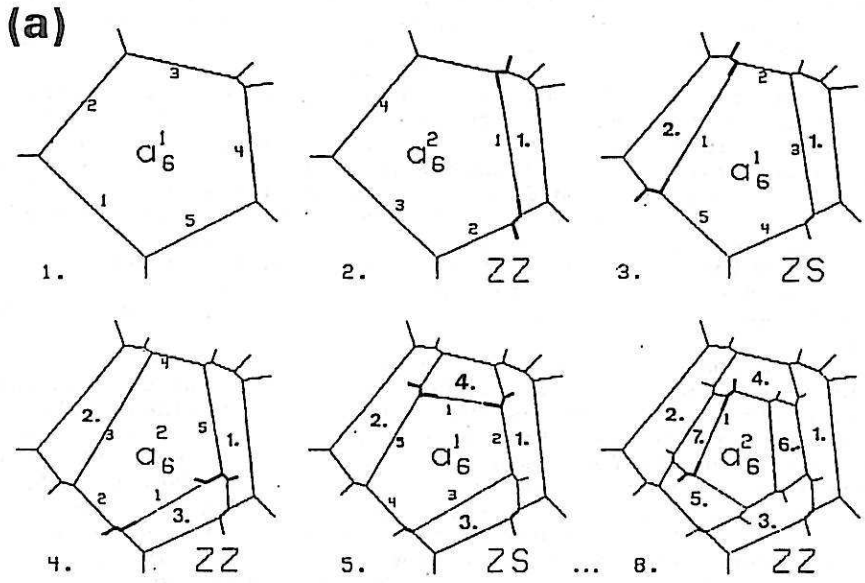
TABLE 2: VARIATIONS OF THE POLYGONAL DEGREE OF DAUGHTER CELLS COMPARED WITH THEIR MOTHER CELLS

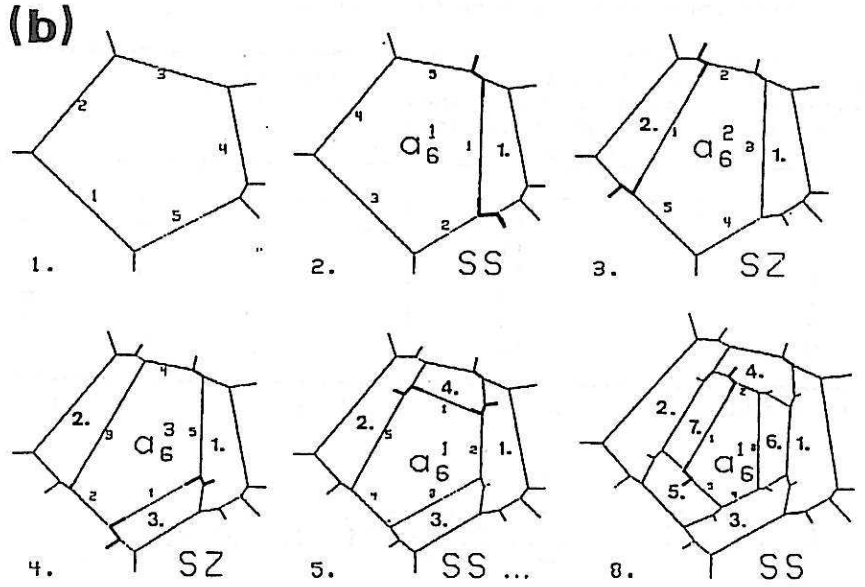
Polygonal degree of mother cells n	# of walls available for the 2 daughter cells n + 6	Polygonal degree of the two daughters
3	3 + 6 = 9	4 and 5 or 3 and 6
4	10	5 5 4 6
5	11	5 6 4 7
6	12	6 6 5 7
7	13	6 7 5 8
8	14	7 7 6 8
9	15	7 8 6 9

Cell filiation graph: sinks for 5, 6, and 7 sided cells



In the special case of our system, there are fewer than 6-sided cells in the meristem of 'foliar' appendages. They will continue to form 5-sided cells. There are also often two wall segments combined on a single wall, so reducing the number of neighbours. Under these constraints is it possible to develop a phyllotactic pattern in which both the basic wall


(a)
1.
2. ZZ
3. ZS
4. ZZ
5. ZS ... 8. ZZ


(b)
1.
2. SS
3. SZ
4. SZ
5. SS ...
8. SS

transitions are conserved like in the basic system and the number of cell sides are maintained as closely as possible to 6?

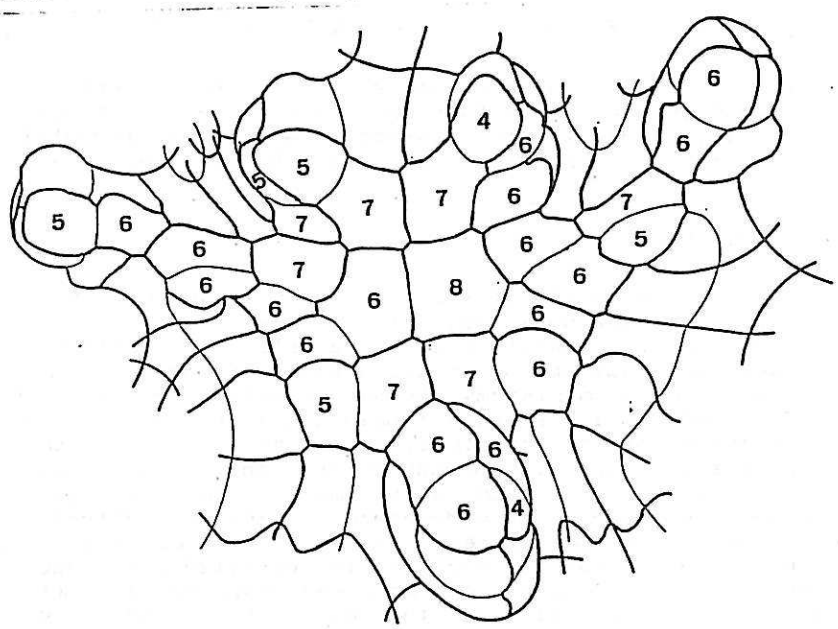


Fig. 6: Generated cell plate without cell crosses. *Topological apical cell plate based on the map of step 6 in Fig.3. Wall crosses have been replaced by S or Z junctions so that the difference of the polygonal degree between sister cells is minimal. Numbers: polygonal degree of the cell. Cells outside the 32 numbered ones do not belong to the same descent.*

A filiation of autoreproductive 6-sided α cells can be established which conserves a wall sequence of length 6 if the division wall is inserted with Z and S staggering in order to attribute the two α segments to the sister cell *b* (Fig.5a, steps 3 and 5). However, at each second cell generation, the α-segment, already present in α, is now incorporated into the sister cell *b*. Consequently, the division wall has to be attached by two Z junctions so that the α cell recovers an α segment (Fig.5a, steps 2, 4 and 8):

$$ZZ \rightarrow ZS \rightarrow ZZ \rightarrow ZS \rightarrow \ldots$$

The site at which the α-segment is introduced, is also important. Previously, it was on the side of the slash 5/7 (cf. Fig.5a). If it appears on the opposite side, at the slash 0/7, the division wall should

Fig. 5: Derivation of an initial cell, a_5 *of Fig.1 with addition of wall staggerings. Step 1. to 8: successive division steps.*
Fig. 5a: Derivation of the initial cell $a_6^1 \rightarrow a_6^2 \rightarrow a_6^1$: *with wall labels clockwise from 1 to 5, and a supplementary small wall between walls 3 and 4, and 5 and 1, respectively. 1., 2., ..., 7.: merophytes or cell families deriving from sister cells of the initial autoreproductive a cell; for example, at step 2, merophyte 1 is composed of 1 cell, at step 8, of 64 cells; at step 3, merophyte 2 is composed of 1 cell, and in step 8 of 32 cells, etc. Highlighted S and Z division wall attachment points.*
Fig. 5b: A cell derivation with an apical cell going through 3 states, $a_6^1 \rightarrow a_6^2 \rightarrow a_6^3 \rightarrow a_6^1$. *Merophytes as in Fig.5a.*

be attached at each third division step only by two S staggerings, in order to recover in the α sister the lost α-segment (Fig.5b, steps 2,5 and 8).

S S → Z S → Z S → S S → Z S → Z S → ...

The frequency distributions (Table 1, C and D) of cell neighbours in a development corresponding to these devices are very close to the observed ones. To illustrate these processes, the 6th developmental step, based on a system with an apical cycle of length 2, is given in detail in Fig.6.

IV. Discussion

One of the most striking results from map systems is that a determined division wall positioning in each cell with, respect to the last-formed division wall, leads to a cellular organization which, after a given developmental depth, produces autoreproductive configurations. They mimic simple plant meristems. In more complicated real shoot meristems, with 2/5 phyllotaxis, special single apical cells are not recognizable. The present model, nevertheless, allows the prediction that such cells or cell plates are possible and may control the sites of leaf inception.

The control in such meristems is not realized by an overall morphogenetic field or by widespread inhibitory effects, but would be located in the peripheral region of cellular cytoplasm supposed to be non-uniform and whose organization is recreated after each cell division. Microtubule organizing centres or preprophase bands of microtubules could assume such a control. In the maize root, the presence of subtle differences between the cells of different tissues regarding the arrangement of cortical microtubules has been highlighted. This system, in continuity with the endoplasmic microtubules encircling the nucleus, could transmit information from the exterior of the cell to the nucleus [1].

The fact that wall staggering cannot be a deterministic device of the cell itself, nor a randomized dissociation of the cross walls, shows that the appearance of a cellular plate with mostly 6-sided cells results essentially from an unknown physical control with interaction between adjacent cells. This is independant of the process which controls the orientation of division walls within dividing cells and which is responsable for the appearance of patterns like that of spiral 2/5 phyllotaxis. As this program is based on a 5-sided differentiation of the cytoplasmic periphery or of the plasmalemma in a 2-dimensional view, it could be of the pentameric nature governing liquid crystals.

From this assumption it results that the plasmalemma structure is slightly rotated with respect to the cell wall structure based on an hexagonal device. As cells communicate by plasmodesmata, the program governed by a differentiation of the cortical region of a cell can nevertheless be conserved nothwithstanding the rigid wall net. Each time a new wall is according to the cell division rules inserted, the physical process interveins and cells become hexagonal. Perhaps the introduction of the topological cellular maps into a system of coordinates as considered in the tensor method [15] would automatically design the place α-segments have to occupy on the cellular border in order to create 6-sided, staggered cells.

The presence of 4 axillary buds at the base of each 'foliar' meristem signifies that if, in reality, the development is subject to a cellular program like the one proposed, there must be a choice between which axillary bud continues to grow. Indeed, in some cases, there exist serial and colateral axillary buds.

A superimposition of wall staggering through small segments does not invalidate, in our framework, the cellular division program leading to morphogenesis, but points to other processes which may play a role. Discussing the possibility of a deterministic behaviour in morphogenesis, Barlow [2] suggests that if stochastic elements are at work these must be integrated with the deterministic aspect of the morphogenetic program.

Obviously it is impossible to recognize in real cell layers an underlying construction plan like the described one. The only way would be the reverse, i.e. reducing the staggering to crosses by eliminating α segments. However, these segments are not always differentiable from real walls which will actively develop later on.

In any case, the present study shows that staggered walls in a layer do not invalidate the presence of a cellular pentameric program controlling morphogenesis through the control of the orientation of division planes.

ACKNOWLEDGMENT

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