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STRUCTURAL CONTROL IN TISSUE DEVELOPMENT

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Occurrence of defects begins a process of destruction of a crystal, its existence is, however, necessary for the crystal growth. In an analogous manner as in propagation of defects during crystallization, the growing of a tissue stress leads to buckling and undulation down to order of the cell diameter. It is shown that the structural control in a tissue development is accomplished by wave-like rearrangement of 5-7 dislocations. The oriented cell divisions as 5-7 climbing can be explained analogously.

Key words: 2D crystallization, phyllotaxis, dislocations, plasticity, gliding and climbing dislocations, control

1. Introduction

It is supposed from the time of Alexander Braun (1831), Carl Schimper (1831), brothers Louis and Auguste Bravais (1837), by works of Schwendener (1878, 1883), Georgii Wulff (1908) and Frederic T. Lewis (1931, 1949) that the crystallization and growing of living tissue are similar. We propose that the dislocations gliding and climbing is basis for such similarity. In 2-dimensional packing it is realized by pentagons and heptagons (5-7) motion among crystalline hexagons (6).

Biological systems are the best prototypes of genuine smart structures. The unique opportunity is provided by considering the important and mysterious phenomenon of the spiral phyllotaxis – leaf primordia packing with Fibonacci differences between nearest neighbours (Fig. 1). As they grow, older primordia are displaced radially away from the center of the circular meristem. The newest primordium initiates in the least crowded space at the edge of the meristem. The growth process is accomplished in an exceptional order. Phyllotaxis compromises local interactions giving rise to a long range order and assures the best way of the optimal close packing.

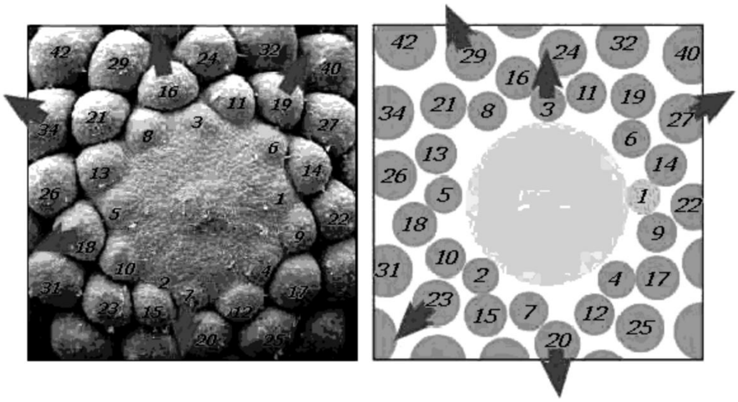

Fig. 1. Norway Spruce (Picea abies): spiral phyllotaxis of needle primordia emerging from central SAM. The primordial numbers are in the reverse order of their appearance. The newest primordium initiates at the periphery of the meristem where there is the largest free space. As they grow, older primordia are displaced radially away from the center of the circular meristem. Then the older the primordium is, the farther it is from the center. After http://www.math.smith.edu/ phyllo/About/math.html

D'Arcy W. Thompson (1917) emphasized the deep correlation between mathematical statements, physical laws and fundamental phenomena of organic growth of biological structures. At the end of 'On Growth and Form' we read:

> *...something of the use and beauty of mathematics I think I am able to understand. I know that in the study of material things number, order, and position are the threefold clue to exact knowledge.*

Remarkable symmetry characterizes crystals and organic forms because both are subdued primarily to topological laws of close-packing by the Descartes-Euler theorem. In a manner analogous to propagation of defects during crystallization, the growing of tissue stress leads to buckling and undulation down to the order of the cell diameter.

In 1868, from his microscopic study of plant meristems, botanist Wilhelm Hofmeister proposed that a new primordium always forms in the least crowded spot along the meristem ring, at the periphery of the shoot apical meristem (SAM). The emerging primordia areas are represented in our model by Voronoi polygons: penta-, hexa- and heptagons. Neighbouring pentagons and heptagons create edge dislocation (5-7) among the hexagons. Motion of such an edge dislocation (exchange of contacts) is called the 5-7 flip. The dislocation is, of course, the place of strong stress (strain) concentration.

Our goal is to interprete the Hofmeister idea as the local rule.

2. Geometry of phyllotaxis

One of the most striking aspects of symmetry in plants is in phyllotaxis – the arrangement of leaves on a stem or of flowers in inflorescenses. It is an interdisciplinary study the mathematics, botanics and crystallography among others. The phyllotaxis should be properly studied at the shoot apical meristem (SAM). It is at the meristemic apex that the organs of shoot originate, such as primordia of leaves, buds or flowers. From the position of the growing tip of a plant, one might visualize the SAM as being propelled by a jet of tissue behind it as it advances. The arrangement of leaf primordia at the SAM may be modelled as a centric array of points in the plane. The points are arrayed along a generative spiral or, equivalently, at the intersections of a set of secondary spirals of opposite chirality, parastichies. The position of each primordium is identified in polar coordinates by its radial distance r from the center and its angle ϕ along the generative spiral, see Hejnowicz (1980), Harris and Erickson (1980), Erickson (1998), Green *et al.* (1998) and Wojnar (2003). Thus, a clear and specific relationship is observed between the primordial phyllotactic pattern at the SAM and the phyllotaxis of the mature shoot: the relationship can be formulated as a transformation (mapping) of the primordial pattern, into the mature pattern and the phyllotactic symmetry of the plant is inherent in its growth processes.

3. Ring shaped grain boundary

The emerging primordia areas could be represented by Voronoi's polygons or dual to it Delone's triangulation. Such areas pass through the exchange of contacts (5-7 dislocation glide – 5-7 flip shown in Fig. 2) sequentially establishing Fibonacci differencess 1,2,3,5,8,... up to highest number reached by the plant. The ring of pentagons and heptagons with a strictly equilibrated Fibonacci structure is clearly seen at the periphery of Fig. 2. It exchanges a single contact (during the appearance of next primordium) to the next Fibonacci difference by the most gentle – Fibonacci structured – 5-7 flip. Near the center of the SAM surface, a complicated overlapping of such rings is seen, but the 5-7 flip similarly exchanges a single contact at each ring.

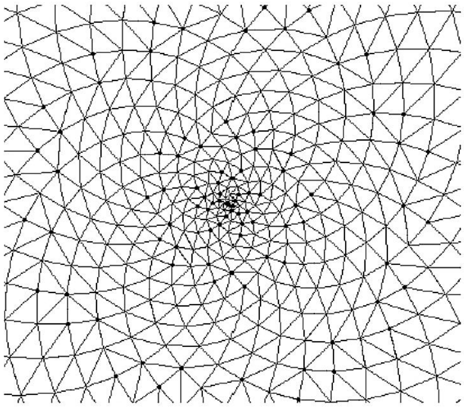

Fig. 2. Consecutive stages of SAM growth differing by 1 primordium in Delone's triangulation (compare Fig. 3 and Fig. 4 for other representations). Notice the last outer ring of 5-7 dislocations and the square-like distribution of primordial in the ring

In Figures 2-4 we can see a few rings of dislocations (overlapping in the center) in different representations. The dislocations appear in those rings either separately (1) or in pairs (2). The arrangement of the pairs in the interior ring is: 2 | 1 1 1 2 2 | 1 (the vertical bars end the full rotation). We observe only two combinations: combination (2 1) denoted further by 3 and combination (221) denoted by 4. So the structure of this ring is: (3 4).

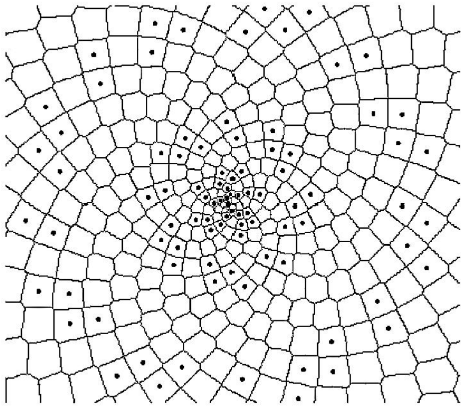

Fig. 3. Consecutive stages of SAM growth (the same as in Fig. 2) in Voronoi's representation

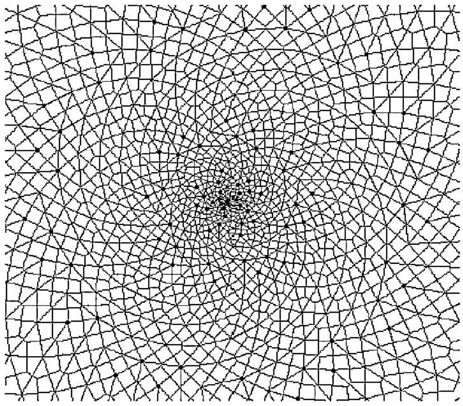

Fig. 4. Voronoi's and Delone's representations

The distribution of pairs in the middle ring is: 2 | 1 2 2 1 2 2 1 2 | 1 and in the exterior ring: 2 2 | 1, 2 1, 2 2 1, 2 2 1, 2 1, 2 2 | 1. We have here also two combinations only: 3 and 4. The distribution of those combinations in the middle ring is (3 4 4) and in the exterior ring: (3 4 4 3 4). In these two last distributions we find only two combinations: the first (4 3) denoted by 5 and the second (4 4 3) denoted by 6. Thus we see that the full period on the middle ring reads as 6 and of the exterior ring as 5 6. Let us consider for instance the reduction of groups in the exterior ring which counts 21 dislocations; after the first grouping we get 5 of "1" and 8 of "2"; notice $5 + 8 = 13$; after next grouping we have 2 of "3" and 3 of "4"; and after the last redistribution it is one "5" and one "6". We see that the reduction of a number of groups is realized by the hierarchical Fibonacci sequence, and the increase of groups is connected with the decrease of Fibonacci numbers.

4. Biological smart structure

We propose natural extension of the Hofmeister rule in phyllotaxis as edge dislocation motion: the close-packing of virtual areas of soon emerging primordia is approaching the final Fibonacci differences through 5-7 flips from previous lower Fibonacci differences. In sequel, those virtual areas will be shortly called the "primordia". The actual, already established primordia, are called "real primordia". For example, the contact on the parastichy spiral with difference 5 (between 8 and 13 spirals) changes after 5-7 flip to the contact on the spiral with difference 21, see Fig. 1. The ring of pentagonal and heptagonal promordia with the strictly equilibrated Fibonacci structure appears at the periphery of SAM. It exchanges a single contact (during the emerging of next primordium) to the next Fibonacci difference by the most gentle – fully Fibonacci structured – 5-7 flip. If a new primordium emerges from the meristem only, one flip is performed in every ring – so there are as many flips as rings. As the effect of flip, the ring rotates but the distribution of dislocations in it never changes. Thus the nature prompts the method, unknown in plasticity mechanics, of control of uniformity of particle distribution.

During the growth of SAM, most frequently as result of stretching, the wall of primordia moves proportionally to their age. Then the Fibonacci spirals develop. However, sometimes (4% of cases) a certain irregularity appears and a different stretching is developed; then we have the Lucas spirals.

5. Final remarks

Morphogenesis in plants is precisely controlled by plastic deformation of cells, tissues and organs brought about by growth processes. With the SAM development given as an example, we observe that:

- Hofmeister's rule follows from the addition of flips on consecutive dislocation rings
- the emerging of a new initial (central) virtual primordium area is associated with exactly one flip in each ring
- higher Fibonacci numbers are reached, which assures the best geometrical packing.

The above analysis is a starting point for development of a growth model of other biological tissues. Models of a compact bone as structure of osteons and of osteons structured by osteocytes could be treated in a similar way. In particular, the Wolff law of bone remodelling could be explained on the basis of the Hofmeister rule.

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Sterowanie rozwojem tkanki

Streszczenie

Pojawienie się defektów w krysztale zapoczątkowuje jego zniszczenie, jednak ich istnienie i ruch jest konieczne także podczas wzrostu. W podobny sposób, w jaki powstaje ruch defektów w czasie krystalizacji, napięcia wzrostu tkanki wywołują wyboczenie i falowanie struktury na różnych poziomach aż do poziomu komórki.

Pokazujemy, że sterowanie rozwojem tkanki biologicznej zachodzi poprzez falopodobną zmianę układu dyslokacji typu 5-7. Podobnie jako pojawianie się układów komórek typu 5- i 7-kątów można wyjaśnić podział zorientowanych komórek.

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