TWO ALGORITHMS OF DETERMINING THE MIDDLE POINT OF THE SHOOT APEX BY SURROUNDING ORGAN PRIMORDIA POSITIONS AND THEIR USAGE FOR COMPUTER MEASUREMENTS OF DIVERGENCE ANGLES

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ABSTRACT

The measurements of the divergence angle between organ primordia in magnolia floral apices and vegetative apices (embryonic shoots) of coniferous trees were performed, using computer application Phyl for IRIX. It appears that the values of the angle are strongly affected by the position of the apex centre, which was calculated by the program on a base of input positions of surrounding primordia. Two algorithms were used to determine the centre position: in program version Phyl 1 it was calculated as the gravity centre whereas in Phyl 2 version as a geometrical midpoint. The both methods differ in resulting centre position. This is dependent on such apex features as: proportions between its size and the size of primordia (expression of phyllotaxis), the angular distances between succesive primordia (quality of phyllotaxis), radial distances between primordia of different age (profile of the apical dome), the number of recorded primordia. The accuracy and reliability of both algorithms for determination of the centre position and, consequently, the reliability of divergence measurements were verified by applying them to ideal, computer simulated spiral phyllotactic systems with divergence given arbitrarily by the user. The conclusions from the results of simulations are that there is a possibility of selecting more suitable algorithm for particular apex with regard to specific parameters of its phyllotactic system.

KEY WORDS: phyllotaxis, apex, geometrical centre, gravity centre, divergence angle, computer simulation.

INTRODUCTION

Studying regularity of phyllotactic patterns gives an important insight into the apical meristem structure and development. Apart from dealing with phyllotaxis itself (Zagórska-Marek 1987, 1994), also the function of some genes (Carpenter et al. 1995) as well as evolutionary aspects of plant development (Battjes et al. 1994, Battjes and Bachmann 1996) can be supported by detailed analysis of primordia arrangement on growing meristem. The very important parameters of the phyllotactic system generated by the apex are the angular distances between primordia. These are defined as the divergence angles with reference to two ontogenetically consecutive primordia. The divergence angle is commonly regarded as specific for each phyllotactic pattern, and especially important in spiral phyllotaxis. It is still not clear if the angle between consecutive primordia has the real meaning for the formation of new organs. It may also be only a secondary result of another regular phenomena in organogenesis as: defined numbers of contact parastichies or preserving an equal distance of newly arisen primordia from the older ones, as presumed by the PTU theory (Zagórska-Marek 1987, 1994, Meicenheimer and Zagórska-Marek 1993). However, the phyllotaxis can be determined by contact parastichies only if the sufficient number of primordia (or mature organs) is available at the time of observation. The measuring of angles between primordia, either the divergence angles or angles between organs neighbouring on contact parastichies, is important for comparison of different patterns and especially in the analysis of ontogenetic phyllotactic transitions (Zagórska-Marek 1985, 1987, Kwiatkowska 1995, Gola 1996,). The results of such measurements are also important for comparison to theoretical data from different mathematical models of phyllotaxis, which are often constructed with the computers (Hellendoorn and Lindenmayer 1974, Fowler et al. 1992, Douady and Couder 1996a, b, c, Couder 1998). Measuring the angles require a point to which all the primordia should correspond as to the theoretical midpoint (centre) of the apical dome. In order to make the measurements and determining the midpoint positions easy-to-use for any plant scientist who not necessarily must be a computer specialist, we have developed the set of applications for Silicon Graphics workstations operating with IRIX system. The middle point, necessary for measuring the angles can be defined in many different ways. We have selected two algorithms for calculating its position and compared their feasibility in measurements of real plants. We wanted to know which of those two algorithms is more reliable and, furthermore if the computer calculated midpoint can be used for detecting the centre shifts during meristem development. In stochastic meristems these are supposed to be one of the reasons for ontogenetic transformations in spiral patterns (Zagórska-Marek 1987, 1994, Nakielski and Zagórska-Marek 1995). On the other hand, the reliable detection of the midpoint could also enable measurements performed routinely in order to investigate the specific and intraspecific variation of the angles and localise any irregularities or asymmetry in a form of the apex possibly associated with the onset of phyllotactic transition.

Before applying both algorithms to real apices we have tested them on model phyllotaxis objects having constant divergence angle given by the user as predicted for each phyllotactic pattern, and having *a priori* defined position of the centre. We hoped to find out how the position of the centre calculated by algorithm is affected by the accuracy of the primordia input, by the number of primordia being measured, by the order and the type of phyllotaxis and by the type of applied algorithm.

MATERIAL AND METHODS

The Phyllotaxis program

There have been two versions of the Phyllotaxis (Phyl) program created for measuring angles between primordia, designed for X-Windows system for an SGI (Silicon Graphics) computer using GL graphics library.

Both versions of Phyllotaxis (Phyl 1 and Phyl 2) are designed for measuring angles between primordia. The centres of primordia are input using a pointing device (a mouse or a digitizer). The measuring is performed using the numerically – calculated centre. The centre can be obtained using one of two algorithms:

1 *Gravity centre* in Phyl 1 program is computed as if the input points were material points of equal mass on a plane and the centre is the gravity centre of the set of points. This method does not limit the number of the points or the way they are positioned on the plane

2 *Geometrical centre* is computed as the geometrical centre of a polygon created by connecting input points with straight lines. The algorithm used in this method requires certain limitations about the input points: the polygon created from input points should be convex. When entering points – centres of primordia – this condition is usually satisfied. In some situations if the polygon is not convex the centre can be miscalculated. Here follows the full description of used algorithm:

a) Calculate the *gravity centre* for input points (see algorithm 1)
b) Create set of triangles. The corners are: the calculated gravity centre and consequent input points.
c) Calculate geometrical centres for the triangles.

The geometrical centre is calculated as a gravity centre of the geometrical centres of triangles using weight proportional to triangles area.

As can be seen from the algorithm, the calculated geometrical centre is correct as long as the input points create a convex polygon and this is the cause of the limitation on using the algorithm. The result could be correct for some non-convex polygons but whether it is or not, depends on the particular example. In general it is important that the gravity centre calculated in the first step belongs to the interior of the polygon. Then triangles created in step 2 belong to the polygon, have no common parts and the sum of the triangles area is equal to the area of the polygon. In practice (e.g. in examples found in nature) the mentioned condition is always satisfied, or at least we have not found an opposite example.

After entering points and calculating the centre the program lets the user to measure the angles. Angles can be measured between any two points. In addition the program lets also to measure the angle between any three input points. The results are stored in an output text file, which can be exported into a spreadsheet or another program for further analysis.

The Phyllotaxis program is designed to be used with a bitmap file. When starting the program user selects a file to be used when entering the input points. Having the picture displayed in the programs window the user enters points simply clicking with mouse.

The program in present issue allows input of up to 150 primordia points and the largest spruce apex had not more than 118 primordia visible.

In order to compare the measurements on real plant material to a model system, the add-in program Phyl-anim was written using GL library for an SGI computer. It creates a simple animation of a set of primordia with the angle being changed continuously. The middle points of such a set with number of primordia and the relative diameter of the meristem defined by the user were next calculated with both methods and shown on the display along with the ideal centre used for creating the system. The calculated coordinates to-

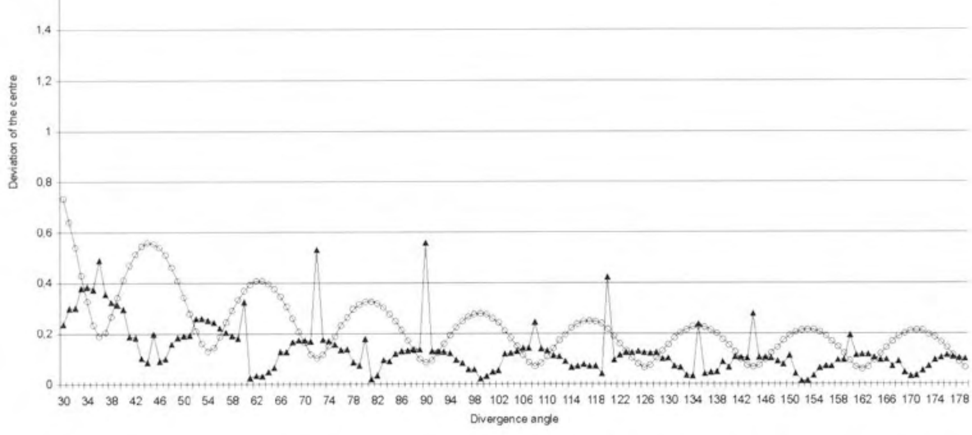

Fig. 1. Deviation of the centre position calculated for the ideal system with use of Phyl 1 and Phyl 2 programs as a function of the divergence angle. Deviation size is given as a fraction of a radius of the youngest (uppermost) primordium.

gether with corresponding divergence angles were shown as an output text file. This application has been regarded as a control for the reliability of measurements done with both methods.

The plant material

Floral apices of *Magnolia acuminata* and *M. denudata* in stage when carpel primordia are already formed but not elongated (Fig. 2A), and vegetative apices of coniferous trees: *Picea abies, Abies concolor* and *Torreya nucifera* (Fig. 2B) were isolated from the buds. In all cases at least several young primordia surrounded the apical dome.

The apices after removing the outer scales of the buds were positioned vertically, contrasted with water soluble nigrosine and observed from above, using SCALAR Videomicroscope connected to the Silicon Graphics INDY Workstation by composite video input. The effective magnification on the display was 400x. The images were grabbed with use of IRIX Capture utility and saved on the hard disk for further investigations.

The phyllotactic pattern and its expression, both defined by contact parastichy pair, were established for each apex and primordia were numbered according to their increasing ontogenetic age i.e. the youngest was numbered as 1, the next one on the ontogenetic helix as 2 and so on. The IRIX Showcase program was used for numbering. The images prepared this way were ready to be analysed by the program versions Phyl 1 and Phyl 2.

RESULTS AND DISCUSSION

The accuracy of centre positioning is good, what was confirmed by repeated calculations for the same apex in several sessions. The hand input of the primordia was also performed several times on the model systems of Phyl-anim and the results were also satisfying.

The calculations performed on simulated phyllotactic systems revealed that the resulting positions of the centre differ from the given centre used for creating the system. The deviation from the ideal centre depended on the algorithm used for calculations but also quite strongly on the size of divergence used for creating the system (Fig. 1). The latter should be considered in measurements of real apices, in which the mean divergence often differs from the ideal angle due for instance to the continuous transition of phyllotaxis. The angles between consecutive primordia were systematically altered by the shift of the midpoint. This became immediately apparent in measurement results, done automatically upon user request, in which the deviations from the original divergence occurred (Fig. 5A and 5B). As variability of the angles corresponds therefore to the deviation of the calculated centre it can be regarded as a substitutional parameter for estimation of reliability of the centre positioning in real apices, where the direct data on the deviation from the ideal centre do not exist.

The conclusion from the simulation analysis is such, that for each single apex there is a possibility to optimize the input parameters and the applied algorithm in order to have a most reliable information about the variability range of the measured angles or centre positions.

The features of the Phyl 1 and Phyl 2 algorithms important for application in various apices, differing in spatial arrangement of organ primordia, can be summarised as follows:

Phyl 1: The centre position depends on local differences in packing density on the surface. The precision of the data of circumferential position of each primordium and circumferential distance to other primordia input in the computer becomes then more important. Because of that, in case of regular apices, during the most distant primordia input (the sequence of input was according to the increasing age of primordia) the centre changed its position relatively slightly.

Phyl 2: Centre position does not depend on the density of the primordia arrangement around the meristem but is influenced by the radial distances of the primordia from the centre. It means that the primordia more distant, which are usually older, have greater significance in determining its position than the uppermost, initiated later. Thus, the direction of the input sequence: whether it follows either increasing or diminishing primordia age, is very important for observation of the centre shifts in the process of adding the positions of consecutive primordia.

For both versions of Phyl

The total amount of input primordia was of great importance in case of smaller apices or strongly asymmetric ones. The changes in centre position were then larger regardless of the version of the application. In many cases it was necessary to optimise for each apex the total amount of input primordia, until the best results were often obtained when the contact parastichies were represented by the equal number of primordia. It can be understood as avoiding the additional and unnecessary asymmetry in the system.

The divergence angles as well as the parastichy angles are determined by centre position that is calculated from all the primordia entered during one session. As a consequence, there is a need of entering separately the groups of primordia if we want to measure the angles for any age group of primordia according to the corresponding centre position (for instance before and after the transformation of phyllotaxis). Nevertheless, if we are interested in comparison of the angles for the whole apex or in investigating variability in the angles in different specimens, the measurements based on the common centre calculated for all primordia is more reliable.

The morphological irregularity of the apices can be described, even if quite indistinct, by observing the centre position as well as analyzing the spatial distribution of differences in the parastichy angles. As the reliability and accuracy of calculating the centre is crucial for this analysis, the possibility of applying both versions could not be underrated. With help of the Phyl-anim simulations (some of them shown on the illustrations) with variable meristematic dome diameter and total number of surrounding primordia-points we have noticed that each of the two versions has advantages in particular, different cases. The measurements on corresponding natural objects (Tab. 1.) confirmed the following conclusions from simulations:

Phyl 1 is suitable for apices with fewer primordia, regularly arranged on most of the surface of the apex. The meristematic dome remains smaller when compared to the size of primordia-occupied part of the apex. Primordia, in turn, have larger both radial and circumferential size and large differences in radial distances between them. Such apices have usually lower pattern expressions (Fig. 3B, Fig. 5C).

The apices with greater diameter, relatively large meristem dome and small primordia (higher expression) (Fig. 3A, Fig.

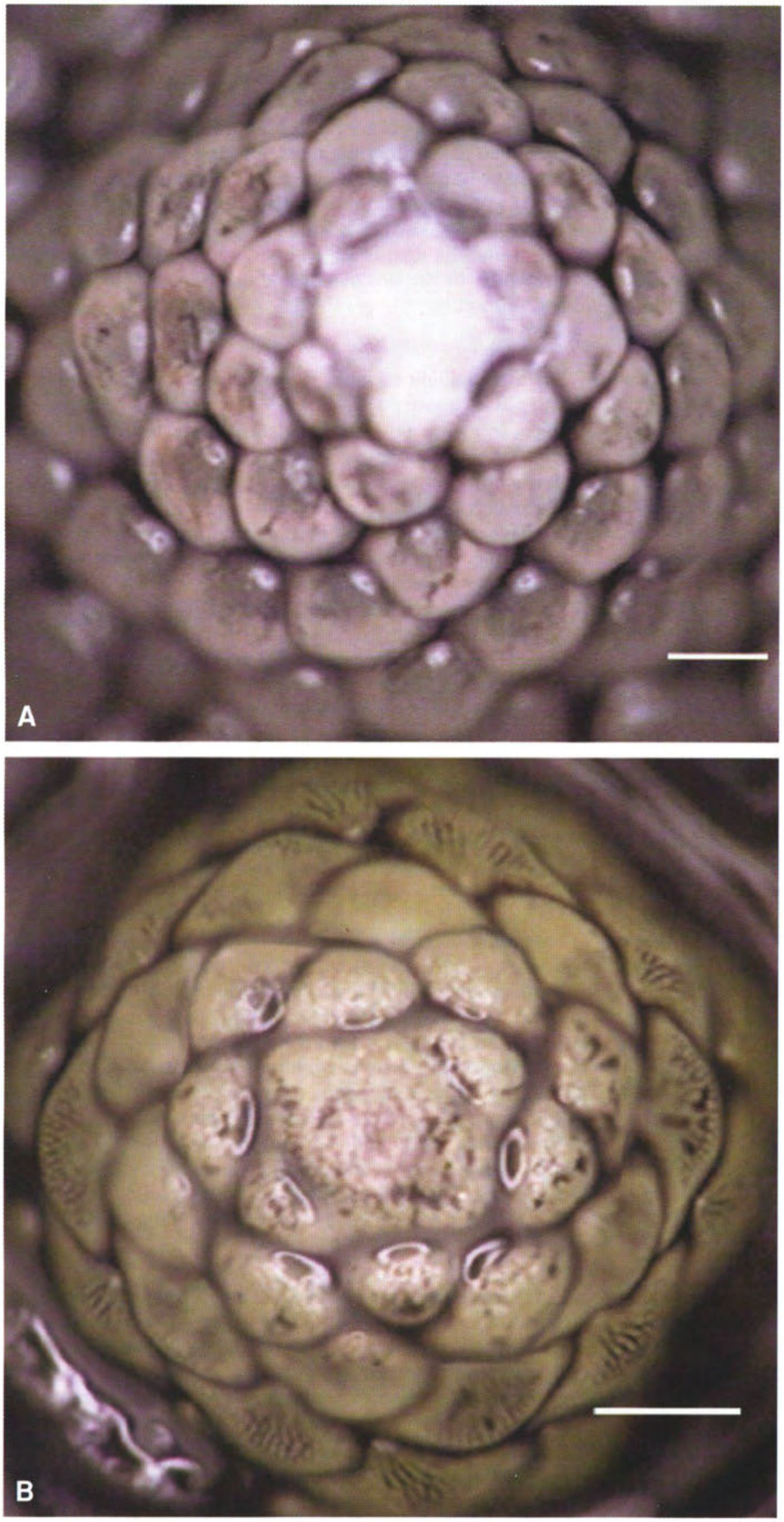

Fig. 2. Similarity in overall appearance of live apical meristems of different species, phyllotaxis and phase of development.

A. Floral apex of *Magnolia acuminata* forming carpel primordia with Lucas phyllotaxis expressed by **4s:7z** contact parastichy pair (**s** and **z** indexes refer to orientation of parastichies)

B. Vegetative apex of *Torreya nucifera* with needle primordia arranged according to the bijugate system **4z:6s**

Bar length 0.25 mm

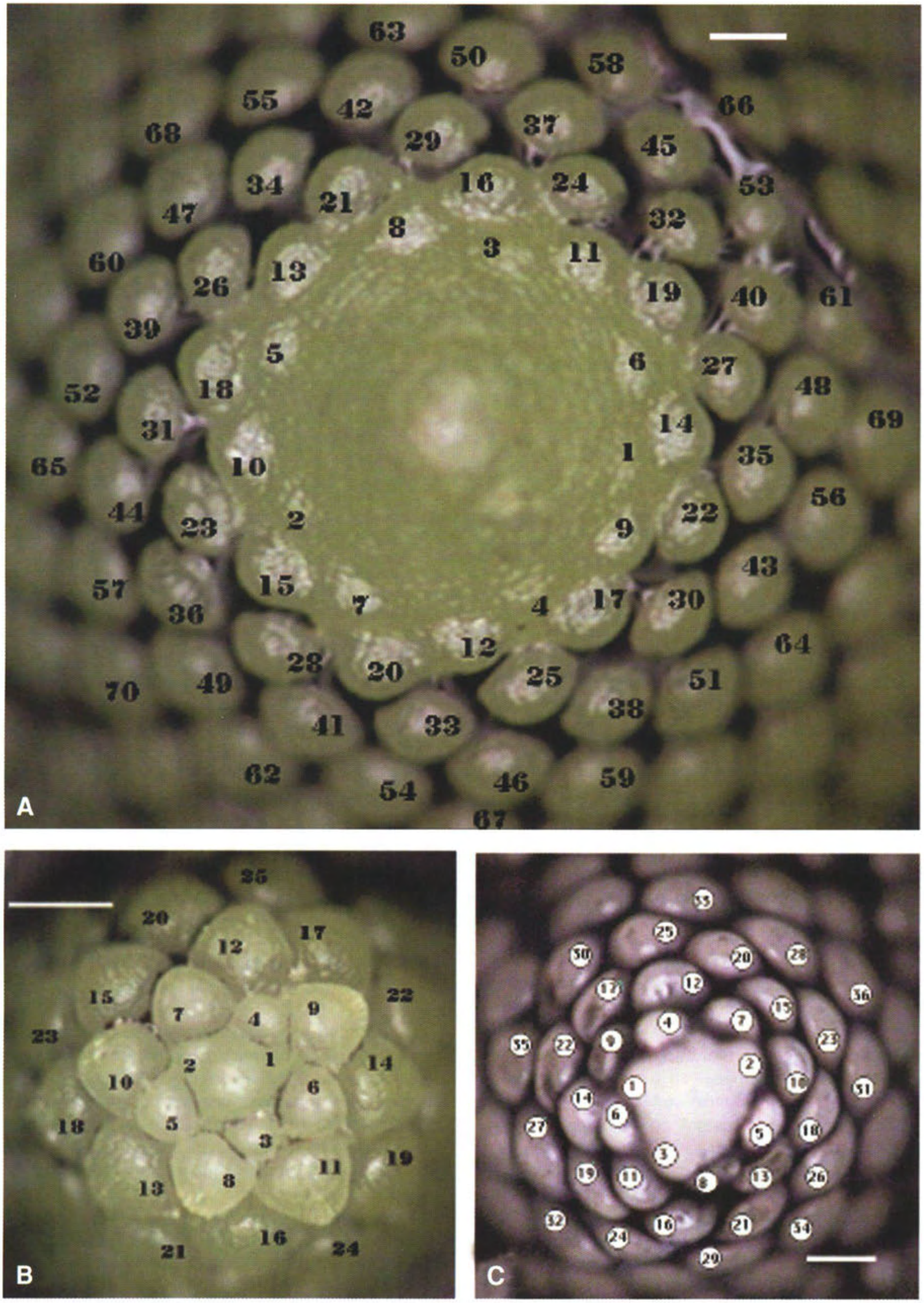

Fig. 3. Differences in a size and organographic order of various apices generating the same main Fibonacci pattern.
A. Large vegetative apex of *Picea abies* with contact parastichy pair **8z:13s**
B. Small vegetative apex of the same species with **3s:5z** expression of phyllotaxis.
C. Floral apex of *Magnolia acuminata* with carpel primordia positioned on contact parastichies **5s:8z.**
The primordia are numbered increasingly according to their plastochron age: the older primordium the higher its number.
Bar length 0.25 mm

TABLE 1. The example of summarised results of divergence angles measurements in three apices of different expression of a Fibonacci pattern; div. = divergence angle, Stand. dev. = standard deviation. The measured apices are the same as shown on Fig. 3.

	Picea abies 3:5		*Magnolia acuminata* 5:8		*Picea abies* 8:13	
	Phyl 1	Phyl 2	Phyl 1	Phyl 2	Phyl 1	Phyl 2
Mean div.°	138.000	138.053	137.246	137.352	137.223	137.522
Minimum	132.253	129.140	125.058	126.965	118.470	130.950
Maximum	148.369	146.058	150.761	147.117	142.946	143.389
Stand. dev.	3.599	4.731	5.642	5.081	3.353	2.380

TABLE 2. Results of simulations of phyllotactic patterns of defined divergence and meristem size. The centre = distance in pixels of the calculated centre from the ideal centre used by the simulation for creating the system

	Simulation-small apex (Fig. 4A)		**Simulation-big apex (Fig. 4B)**	
	Phyl 1	Phyl 2	Phyl 1	Phyl 2
Mean div.°	137.545	137.422	137.473	137.492
Minimum	132.559	128.803	134.880	136.237
Maximum	142.932	149.885	140.337	138.833
Stand. dev.	2.4516	5.0090	1.5930	0.7055
The centre	3.6553	6.9400	5.3165	2.2368

5E), as well as the apices of average size, (Fig. 3C, Fig. 5D) should be measured with Phyl 2. The first case is frequent in torreyas and smallest spruce and magnolia apices, the second one in most of the spruce, fir and magnolia apices. For the asymmetric or irregular apices applying the Phyl 2 was always advantageous.

The simulation with larger diameter of the meristem surrounded by numerous primordia reflects the situation when contact parastichies can be drawn in pairs of higher order. In such cases the gravity centre was usually more distant from the ideal than the geometrical centre (Fig. 4B).

The gravity centre in turn was closer to the ideal centre than the geometrical centre only when the simulation resembled the apices with lowest pattern expression (Fig. 4A). The divergence angles were also less variable when the corresponding centre was closer to the ideal (Tab. 2, Fig. 5A, 5B).

It comes out from survey of literature that for measuring the divergence the method analogous to the Phyl 1 has been usually applied (Nakielski and Zagórska-Marek 1995, Battjes et al. 1993, Meicenheimer – personal communication). The way, Hellendoorn and Lindenmayer (1974) had estimated the apical centre, simply by drawing middle-lines the crossing point of which is the centre, is only suitable for their particular case and not for complex spiral patterns. In Fujitas work (1939) nothing is said about the method of measuring the divergence angles with regard to any reference point used as an angle vertex. Compared to the results of the present study, the formerly published data showing the centre shift in a course of phyllotactic transitions (Nakielski and Zagórska-Marek 1995) are probably also strongly affected by the method dependent error and consequently they should not be regarded as convincing explanation for those transitions. The second algorithm, however, does not improve the accuracy of the centre positioning enough to replace the first one. In some cases the reliability of the gravity centre was even greater as this of geometrical centre, especially in small apices of *Torreya nucifera*.

In a further detailed study on the transformations of phyllotaxis conducted in our laboratory we investigate if the subtle disclinations of the meristem longitudinal axis resulting in the centre shifts postulated to be as a reason for phyllotactic transitions could or could not be discovered by calculating the centre position from positions of surrounding primordia. The hypothesis itself would hereby not have to be rejected, but suitability of the previously used methods should be evaluated. The main question related to this problem is how large are the shifts of the centre in magnoliacean apices with transformations in comparison to those with uniform phyllotaxis. The results will be published separately.

The method of calculating the gravity centre, used by Battjes et al. (1993) for measuring the divergence angles resulted in satisfactory data. Nevertheless, using quite complicated and sophisticated programs for graphic analysis as Object Image (Vischer et al. 1994) is not necessary for the simple measurements as we have performed. Including an alternative method of calculating the centre in programs designed for other purposes is also not convenient. The programs described here can also be further developed and new functions can and will be added. It makes also the right base for creating a specialised set of applications for detailed analysis of plant morphology with use of computers which graphical and visual performance increase from year to year getting more affordable also for the non-computer oriented plant researchers.

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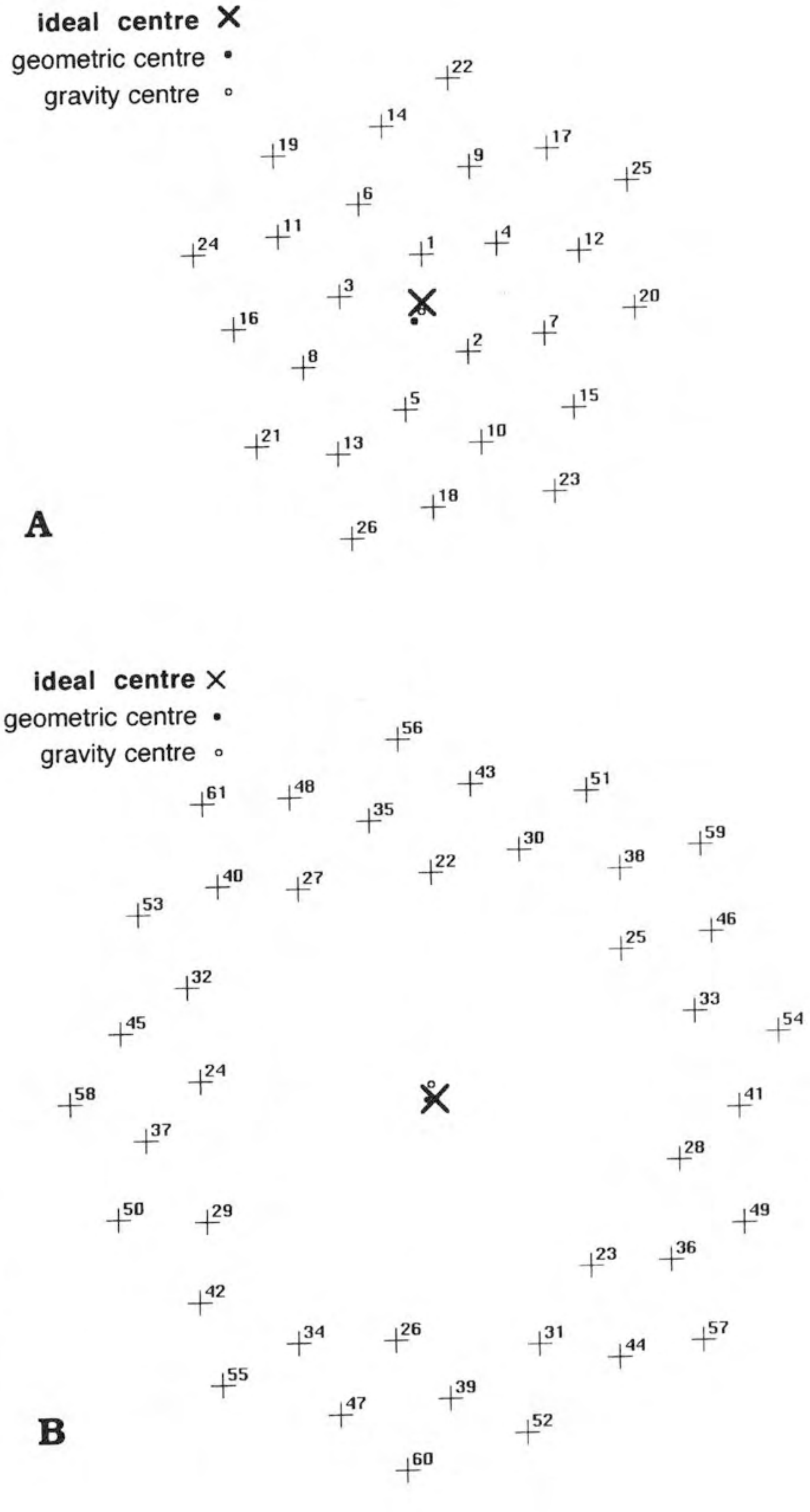

Fig. 4. The computer simulation of the Fibonacci phyllotactic system with the ideal and calculated centres;
Simulation mimicking small apex, expression of phyllotaxis low;
B. Large apex, expression of phyllotaxis high;
An area free of the numbered crossing points, which corresponds to the size of the apical dome is small (A) or large (B) when compared to the distances among neighbouring elements of the system (primordia). B situation has been obtained in simulation by ignoring the elements positioned closely to the centre. This is why the point closest to the centre bears the number 22 instead of 1. Therefore for both cases the divergence used for creating the system is the same: 137.5.

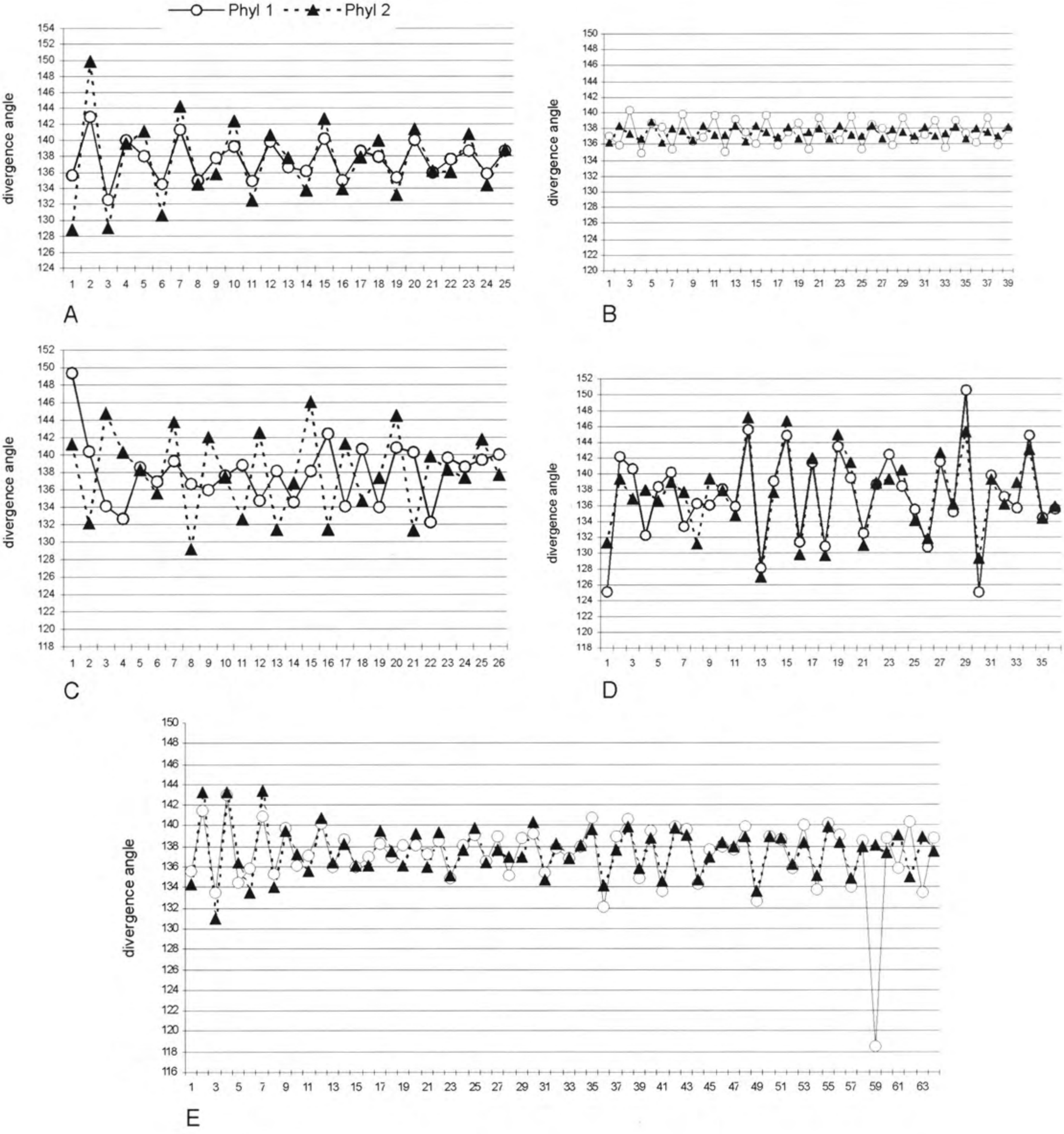

Fig. 5. Fluctuations of the divergence angles measured according to the gravity centre (Phyl 1) or the geometrical centre (Phyl 2) in simulated and real apices shown earlier in Figs 3 and 4.

A. Simulated apex from Fig. 4A
B. Simulated apex from Fig. 4B
C. *Picea abies* apex from Fig. 3B
D. *Magnolia acuminata* apex from Fig. 3C
E. *Picea abies* apex from Fig. 3A

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DWA ALGORYTMY WYZNACZANIA ŚRODKA WIERZCHOŁKA PĘDU PRZEZ POZYCJE ZAWIĄZKÓW ORGANÓW I ICH WYKORZYSTANIE DO KOMPUTEROWYCH POMIARÓW KĄTÓW DYWERGENCJI

STRESZCZENIE

Przy użyciu programu komputerowego Phyl dla systemu IRIX wykonano pomiary kątów dywergencji między zawiązkami organów w wierzchołkach kwiatowych magnolii oraz wegetatywnych wierzchołkach kilku gatunków drzew iglastych. Wykazano dużą zależność wartości zmierzonych od położenia środka wierzchołka, obliczanego przez program na podstawie wprowadzonych pozycji zawiązków. Użyto dwóch algorytmów wyznaczania pozycji środka: w wersji Phyl 1 był on obliczany jako środek ciężkości, podczas gdy w wersji Phyl 2 jako środek geometryczny. Obie metody różniły się otrzymanymi jako rezultat obliczeń położeniami środka, zależnie od następujących cech wierzchołka: proporcji między jego wielkością, a rozmiarami zawiązków (ekspresja wzoru filotaksji), kątowych odległości między kolejnymi zawiązkami (rodzaj wzoru filotaksji), promieniowymi odległościami między zawiązkami o różnym wieku ontogenetycznym (profil wierzchołka), ilość wprowadzonych zawiązków. Dokładność i rzetelność obu algorytmów, a równocześnie wiarygodność pomiarów dywergencji zostały przetestowane na idealnych, symulowanych komputerowo układach filotaksji skrętoległej o dywergencji zadanej przez użytkownika. Rezultatem tych badań była możliwość dobrania odpowiedniego algorytmu dla każdego mierzonego wierzchołka z uwzględnieniem indywidualnych parametrów układu filotaktycznego.

SŁOWA KLUCZOWE: filotaksja, wierzchołek, środek geometryczny, środek ciężkości, kąt dywergencji, symulacja komputerowa.