Method for practical assessment of cylindrically represented spiral phyllotaxis

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Abstract. The study analyses a method for practical assessment of cylindrically represented spiral phyllotaxis. In a phyllotaxis model represented by the conspicuous parastichy pair and the linear distances among the three closest situated primordia, the following traits can be determined: generative spiral direction, rise, angle of intersection of the opposite parastiches in the conspicuous parastichy pair, bud radius, linear and angular divergences. The results of application of the method for assessment of the existing in nature phyllotactic patterns correspond well to the results of theoretical investigations by other authors.

Key words: assessment, phyllotaxis

Introduction

According to Jean (1994), spiral phyllotaxis can be represented either centrically or cylindrically. Cylindrical representation has been adopted for the description of organs with nearly cylindrical form – the stems of plants, the cones of some species of pine and spruce and the buds of some trees. The phyllotactic patterns observed in nature should be evaluated by different parameters: a conspicuous parastichy pair determining the pattern, divergence angle, the angle of intersection of the opposed parastichies in the conspicuous parastichy pair, and plastochrone ratio (Jean 1987, 1994). The last parameter refers to the centrically represented phyllotaxis.

Jean (1987) developed a mathematical model and method for practical assessment of phyllotactic patterns. Some parameters of the model can be predicted on the basis of some already known parameters. The Pattern Determination Table illustrates the ratio between the plastochrone ratio (R) and the phyllotactic pattern (m, n) for different values of the angle (γ) of intersection of the opposed parastichies in the conspicuous parastichy pair. The Table is designed for centric phyllotaxis representation.

Jean (1994) has derived a model that shows a definite relationship between the rise (r), the angle of intersection of the parastichy pair (γ) and (m+n) for cylindrically represented spiral phyllotaxis. At known γ and (m+n), r could be determined.

Assuming that the generative spiral is logarithmic or equi-angular, Thomas & Cannell (1980) had postulated different relations between the separate characteristics of the phyllotactic system: the generative angle (φ), orthochrone ratio (r_0), divergence angle (γ), angle between two adjacent orthostichies (ψ), and plastochrone ratio (r). According to them, the spatial relations of primordia can be defined on the basis of linear measurements, which could be made on plants. Here, as in Jean (1987), the relationships are derived for centrically represented phyllotaxis.

The aim of the current study is to propose a method for practical assessment of cylindrically represented spiral phyllotaxis. A prerequisite for the proposed approach is the requirement that the input characteristics on the basis of which the assessment of the phyllotaxis will be performed should be: the conspicuous parastichy pair determining the pattern (*n, m*), and the linear distances among the three closest positioned primordia.

Objects and methods

The buds of *Pinus mugo* Turra have been used as experimental material to provide a basis for the development of the method. They are almost cylindrical in form, with spirally arranged scales and primordia of the leaves. The buds have been gathered from natural populations of the species in Rila Mts, at three different altitudes of 1900 m, 2200 m and 2500 m, 50 buds from each altitude. The buds were collected in November, when fully grown and developed, and were fixed in 70 % alcohol. Determination of the phyllotactic pattern of each bud was carried out with a reflected light microscope after removing the covering scales of the bud. The lengths of the legs of the triangle into which vertexes are situated, the three most closely positioned primordia determining the phyllotactic pattern have been defined. This triangle has been termed *phyllotactic triangle*. Thus, on the basis of the phyllotactic pattern and the phyllotactic triangle the following elements can be calculated: the rise (r), radius of the bud (R), linear divergence (a_x), angular divergence (d), and angle (γ) of the intersection of the opposed parastichies of the conspicuous parastichy pair. If data on the width of the primordium (l) in a direction perpendicular to the axis of the bud are obtained, it will be possible to calculate $\Gamma = l/R$, as well as the parameter $\rho = l^2/2\pi Rr$ determining the packing compactness of the primordia.

Direction of the generative spiral is determined by the direction of the two opposed parastichies of the conspicuous parastichy pair.

Results

Determination of direction of the generative spiral

Figure 1 represents an unrolled phyllotactic pattern (3, 5), with three parastichies going up to the right and five parastichies going up to the left. Since the numbers 3 and 5 are terms of the Fibonacci sequence, the terms of the sequence before those determining the phyllotactic pattern can be found by subtraction. Bearing in mind that number 3 stands to the right, while number 5 stands to the left of the vertical axis O, we have the following picture of the sequence:

$$\begin{array}{c|c} 5 & \\ & 3 \\ 2 & \\ & 1 \end{array}$$

Thus the first term of the sequence – number 1 – positioned to the right of the vertical axis O is determined. By definition, the generative spiral is a parastichy which connects all consecutively originating primordia. In this case parastichy 1 is simultaneously the generative spiral, which goes to the right. This approach is valid for all phyllotactic patterns in the cases of normal phyllotaxis (Jean 1990, 1994), expressed by the formulas:

$$J\,\langle 1,2,3,5,8,\ldots\rangle,\ J \geq 1$$

$$J\,\langle a,a+1,2a+1,3a+2,\ldots\rangle,\ J=1,2,\ a \geq 3$$

In the cases of anomalous phyllotaxis, expressed by the formula

$$\langle 2a+1,2a+3,4a+4,\ldots\rangle,\ a \geq 2,$$

it is impossible to arrive at the term +1 by applying the above described approach. That is why we shall explain the procedure on a concrete example.

Let us assume a phyllotactic pattern (7, 12) with seven parastychies going to the left and 12 parastiches going to the right. The picture of the phyllotaxis-representing sequence is the following:

$$\begin{array}{c|c} & 12 \\ 7 & \\ & 5 \\ 2 & \\ & 3 \\ -1 & 1 \end{array}$$

Calculating the terms of the sequence by successive subtraction, we obtain the term (-1), which stands on the left side of the vertical axis O. Since the parastichies are real, their number is positive, which necessitates the transfer of the negative term to the right of the axis O and the change of its sign. Thus we get a right generative spiral of the pattern. Figure 2 shows a schematic representation of the pattern (7, 12) with seven parastichies going up to the left and 12 to the right. It is obvious from the scheme that we have parastichies 2 and 7 going up to the left and parastichies 1, 3, 5 and 12 going up to the right. For normal phyllotaxis (Fig. 1), the slope of the parastichies has the following arrangement: 1<2<3<5, where the slope of the generative spiral (1) is the slightest. For anomalous phyllotaxis (Fig. 2), the ar-

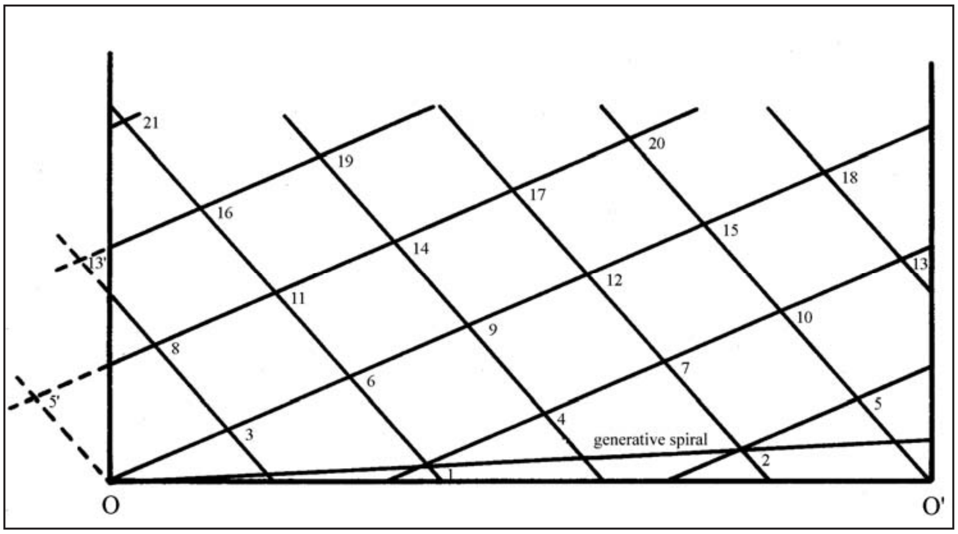

Fig. 1. Cylindrical representation of spiral phyllotaxis.

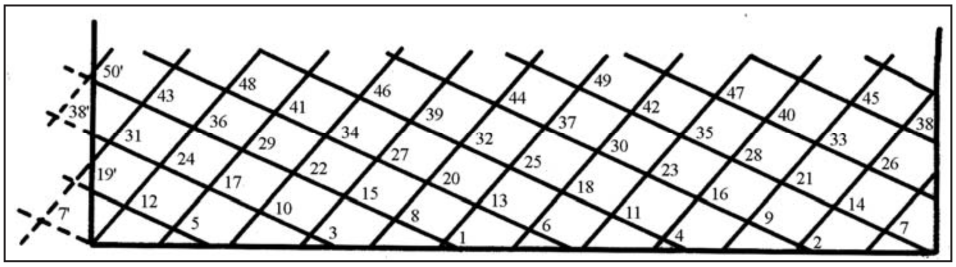

Fig. 2. Cylindrical representation of phyllotactic pattern (7, 12).

rangement is disturbed. The slope of the corresponding parastichies with the pattern (7, 12) looks as follows: 1<3<2<5<7<12. The latter is supported by the following data on the slope of the parastichies expressed in degrees: parastichy 1 – 0.53°, parastichy 3 – 2.56°, parastichy 2 – 2.76°, parastichy 5 – 11.01° , parastichy 7 – 23.88°, and parastichy 12 – 50.53° .

Let us examine another instance of anomalous phyllotaxis: the pattern (9, 16), where 16 parastichies going up to the left and nine parastichies going up to the right. The sequence representing the phyllotaxis will look as follows:

16	
	9
7	
	2
5	
3	-3
1	-1

After calculating the terms of the sequence, we get the term (-3), which is positioned to the right of the vertical axis. We transfer this term to the left of the axis and change its sign to the positive, at the same time calculating the difference between the last term to the right (2) and to the left (3), which again results in a negative term (-1). We transfer it to the left of the axis and change its sign. Thus we establish that the generative spiral in this case is left-oriented.

For patterns of normal phyllotaxis with two, three or more generative spirals, (J>1), direction is established following the above-described model for normal phyllotaxis. For example, the pattern (6, 4) can be recorded as 2(3, 2). Determining the direction of the generative spiral (3, 2), we determine the directions of the two spirals in the pattern (6, 4).

Determination of the rise (*r*)

Let us examine the triangle OA_mA_n (Fig. 3), where the vertex O coincides with the zero primordium (A_0), while the vertexes A_n and A_m respectively with the primordia which determine the phyllotactic pattern

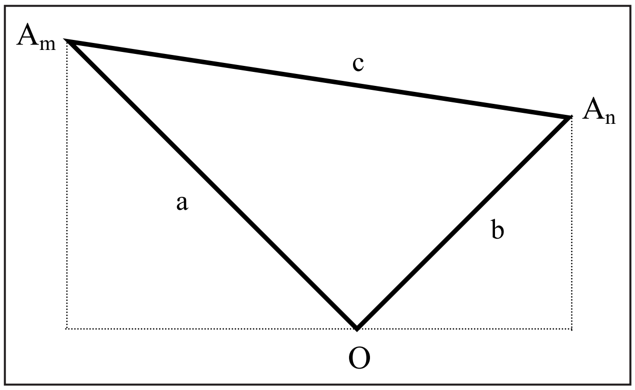

Fig. 3. Phyllotactic triangle of pattern (n, m).

(*n, m*), $n<m$. The rise (*r*) has to be calculated on the basis of three given legs of the triangle – *a*, *b* and *c* and the pattern (*n, m*) of the phyllotaxis.

Knowing that the point A_n rises above the zero level at a distance *nr*, and the point A_m at a distance *mr*, the following equation can be postulated:

$$\sqrt{a^2-(mr)^2}+\sqrt{b^2-(nr)^2}=\sqrt{c^2-(mr-nr)^2} \tag{1}$$

Solving the equation for *r* gives:

$$r=\frac{1}{2}\sqrt{\frac{(a+b+c)(a+b-c)(a+c-b)(b+c-a)}{mn\left(c^2-a^2-b^2\right)+a^2n^2+b^2m^2}} \tag{2}$$

Determination of angle (*γ*) of the intersection of the opposed parastichies in the conspicuous parastichy pair

Angle *γ* in the phyllotactic triangle of the pattern (*n, m*) appears to be the angle at the vertex *O* (Fig. 3). With the three given legs of the triangle, angle *γ* can be calculated by the following equations:

$$\cos\gamma=\frac{a^2+b^2-c^2}{2ab},\quad \gamma=\arccos\frac{a^2+b^2-c^2}{2ab} \tag{3}$$

Determination of the bud radius (*R*)

Let us look at a cylindrically represented phyllotaxis (Fig. 4) in an unrolled cylindrical surface plan. We assume that radius *R* of the cylinder is also the radius of the bud. The ordinate of primordium 1 is *r*, called rise. The distance *OO*' = *2πR*. The phyllotactic triangle determined by the three most closely positioned primordia has the legs *a*, *b* and *c*. Radius *R* has to be determined with known *a*, *b*, *c* and *r*.

The area of the cylindrical surface allotted to each primordium is

S = *2πRr*. On the other hand, this area is *S* = *ab.sinγ*, or $S=2\sqrt{\frac{p}{2}\left(\frac{p}{2}-a\right)\left(\frac{p}{2}-b\right)\left(\frac{p}{2}-c\right)}$, where $p = a+b+c$ and *γ* is the angle of intersection of the opposed parastichies of the conspicuous parastichy pair. Thus the bud's radius can be derived from the following equations:

$$R=\frac{ab.\sin\gamma}{2\pi r},\ \text{or}\ R=\frac{\sqrt{\frac{p}{2}\left(\frac{p}{2}-a\right)\left(\frac{p}{2}-b\right)\left(\frac{p}{2}-c\right)}}{\pi r} \tag{4}$$

Determination of the linear divergence (a_x)

Linear divergence (a_x) is the abscissa of the primordium 1 (Fig. 4). Given the three legs of the phyllotactic triangle (*a, b* and *c*), phyllotactic pattern (*n, m*), $n<m$, radius of the cylinder (*R*), and rise (*r*), the linear divergence (a_x) has to be determined.

Let us look more closely at the triangle with vertexes *O*, *O*' and A_{nm} (Fig. 4). This triangle has been named the *opposed parastichy triangle* of the opposed parastichy pair (*n, m*) (Adler 1998). The leg $OA_{nm} = mb$, while the leg $O'A_{nm} = na$. In order to determine linear divergence, we have to perform the following procedure.

We shall draw the opposed parastichy triangle for the particular phyllotactic pattern. On the leg OA_{nm} of the triangle, *m* steps are inserted and *n* steps on the leg $O'A_{nm}$. At the end of each step the number of the primordium is written: for example, on the leg OA_{nm} the first primordium after the zero is A_n, the second is A_{2n}, and so on, while on the leg $O'A_{nm}$ the first primordium is A_m, the second is A_{2m}, etc., and at the vertex we have the primordium A_{nm}. Then the direction of the generative spiral is determined (on Fig. 4 it is right-oriented). Thus, having once determined the opposed parastichy triangle, we then choose two primordia with the closest possible numbers standing on the right and left legs of the parastichy triangle respectively. If their numbers are successive, then the divergence between them is one, if the difference in their numbers exceeds 1, then there are as many divergences between them as is the difference between their respective numbers.

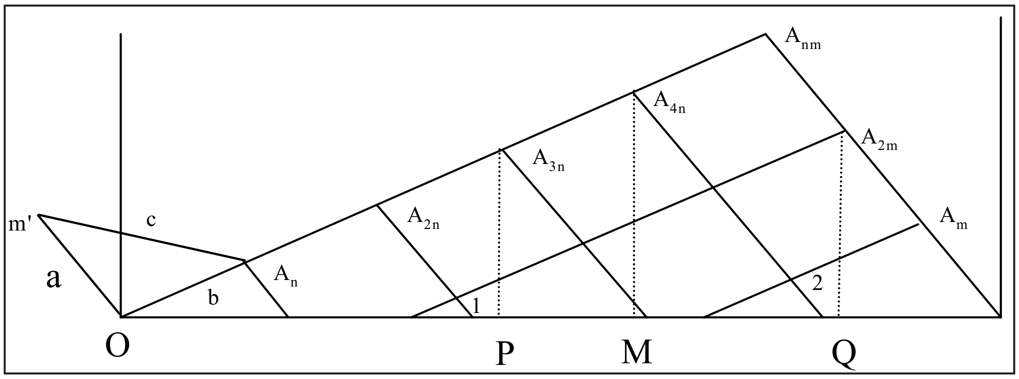

Fig. 4. Cylindrical representation of spiral phyllotactic pattern (n, m).

Let us assume that we have chosen the primordia $A_{3\mathrm{n}}$ and $A_{2\mathrm{m}}$ (Fig. 4). Their projections along *OO*' are the points *P* and *Q*. The distance *PQ* will encompass one or several divergences. Determination of the distance is performed in a direction coinciding with the direction of the generative spiral: in this case $A_{3\mathrm{n}}$ is positioned lower than $A_{2\mathrm{m}}$ and the direction fully coincides with that of the generative spiral. If we have chosen primordia $A_{2\mathrm{m}}$ and $A_{4\mathrm{n}}$, the measurement of the distance between the points *Q* and *M* is performed in the direction of the generative spiral, starting from point *Q*. Thus the difference $4n - 2m$ will determine the number of divergences, which as a common distance will include the sum of the segments *QO*' and *OM*. These two segments can easily be calculated, if it is known that $O'A_{2\mathrm{m}} = 2a$, $QA_{2\mathrm{m}} = 2mr$, $MA_{4\mathrm{n}} = 4nr$, $OA_{4\mathrm{n}} = 4b$.

Thus $QO' = \sqrt{(2a)^2 - (2mr)^2}$ and $OM = \sqrt{(4b)^2 - (4nr)^2}$.

In the previous example the segment *PQ* can be determined on the basis of the following equation:

$PQ = OO' - OP - QO'$, where $OP = \sqrt{(3b)^2 - (3nr)^2}$.

The distance $OO' = 2\pi R$, where the radius *R* is a known value. Generally, the distance *OO*' is assumed to be 1 and then $a_{\mathrm{x}} < 1$.

Determination of the angular divergence (*d*)

After the linear divergence (a_{x}) has been determined, the transition to angular divergence is given by the following expression:

$$d = \frac{a_x}{2\pi R} 360 \qquad (5)$$

Discussion

Application of the above-described methodology to the buds of *Pinus mugo* allows determination of the direction of the generative spiral, the rise, the angle of intersection of the opposed parastichies in the conspicuous parastichy pair, the radius of the bud, and the linear and angular divergences.

According to the fundamental theorems of Jean (1994), the angular divergence of each particular phyllotactic pattern can vary within set limits. A comparison of the real values of the angular divergence with the theoretically set limits of phyllotactic patterns with greater frequency of occurrence is shown in Table 1.

It is obvious from the data in Table 1 that the real values of the angular divergence fall within the theoretically set limits. Of all 125 cases, only one deviates from the theoretically set limits: with the pattern (8, 13) the real value of the divergence has been calculated as 138.64°, while the theoretical value amounts to 138.46° – the real value is higher by 0.18° than the theoretically possible one. This discrepancy is probably due to the rounding of calculations, or to imprecise determination of the linear dimensions of the input measures. Despite this fact, a difference of 0.1 % as in this particular instance is fully acceptable and can be neglected. This gives grounds for the conclusion that the proposed method for practical assessment of the parameters of the phyllotactic pattern described above gives real and precise results.

Table 1. **Real and theoretically determined values of the angular divergence (*d*°) for different phyllotactic patterns of buds from *Pinus mugo*. The theoretically determined values of the angular divergence are according to Jean (1994).**

Phyllotactic pattern	Real divergence			Theoretical divergence	
	minimal	maximum	mean ± s.e.[1]	limit angle	interval
(8,5)	136.96	138.76	137.64 ± 0.28	137.51	135 – 144
(8,13)	136.69	138.64	137.54 ± 0.07	137.51	135 – 138.46
2(3,5)	67.59	69.63	68.59 ± 10.7	68.75	60 – 72
(11,7)	98.93	100.30	99.57 ± 0.25	99.50	98.18 – 102.86

[1] s.e. – standard error

Douady & Couder (1996) have developed a computer model of the phyllotaxis. In computer simulations, the following parameter has been adopted $\Gamma = l/R$, where *l* is the width of the primordium in an orthoradial direction and *R* is the radius of the apex (in our case the radius of the bud). One of the results of their study was the conclusion that the phyllotactic patterns arise at a fixed meaning of the parameter *Γ*.

Distribution of the phyllotactic patterns of the buds as a function of the parameter *Γ* is seen in Fig. 5. It is obvious from Fig. 5 that the separate models arise at a fixed interval of the value of parameter *Γ*. The more complex the pattern is (the complexity of the pattern is expressed by $m+n$), the smaller the values of the parameter are. These data correspond to the theoretical model of Douady & Couder (1996), which supports further the conclusion that the method is adequate.

According to Jean (1990, 1994), phyllotaxis is governed by the general and simple morphogenetic principles such as: optimal design, minimal entropy production, simple laws of packing efficiency. For the last principle, Douady & Couder (1996) and Douady (1998) showed that when the system is unstable and has reached the point of bifurcation, it chooses the pattern with higher compactness of packing. The studies of Douady & Couder (1996) show that for spiral phyllotaxis the compactness of packing is higher for patterns with lower complexity (the patterns represented by the smaller terms of the Fibonacci-type sequence). Meanwhile, when the pattern changes from lower to higher complexity, the compactness of packing shows a cyclic path of alternation.

The compactness of packing of the phyllotactic patterns of the buds of *Pinus mugo* is represented by the parameter $\rho = l^2/2\pi Rr$. Figure 6 reflects the changes in the compactness of packing (ρ) as a function of parameter Γ for the different phyllotactic patterns represented by the Fibonacci sequence. It is obvious from Fig. 6 that the compactness of packing changes cyclically with the change in the values of parameter Γ, with a marked tendency for an increase in the compactness of packing parallel to an increase in the values of Γ, i.e. when the pattern displays low complexity, the compactness of packing is higher. Moreover, the maximum compactness of packing is attained, when the pattern *(m, n)*, $n<m$ is transformed into the pattern *(m, m+n)*, i.e. at the border values of parameter Γ for the two patterns. In the concrete example in Fig. 6 these are the values of Γ from 0.46 to 0.52, where we actually observe a transition from (8, 5) to (8, 13) (Fig. 5). These data are thoroughly congruent with the theoretical model of Douady & Couder (1996), which once again supports the conclusion about the precision and accuracy of the proposed method for practical assessment of cylindrically represented spiral phyllotaxis.

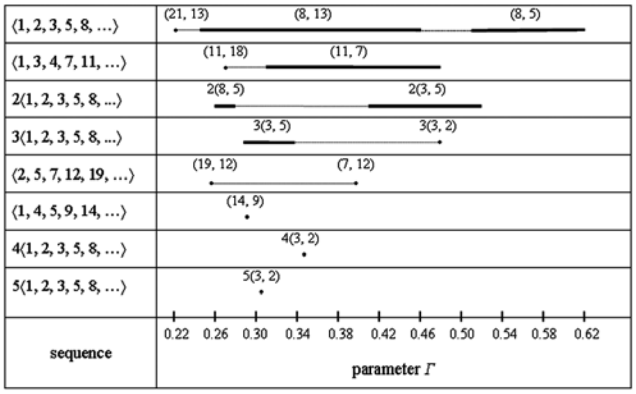

Fig. 5. Phyllotactic patterns of the buds as a function of the parameter Γ.

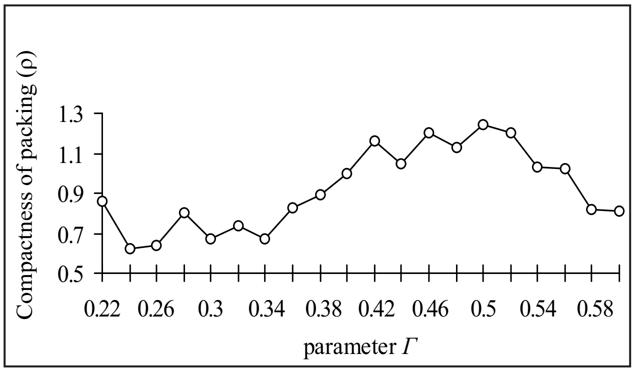

Fig. 6. Compactness of packing (ρ) as a function of the parameter Γ – mean values by intervals of the parameter Γ at 0.02 for the Fibonacci sequence.

Conclusion

The proposed method for practical assessment of cylindrically represented spiral phyllotaxis complements the existing methods and gives objective results with minimum input data: the conspicuous parastichy pair and the distances between the three closest positioned primordia. The angular characteristics typically difficult for measuring with real objects have been avoided to be taken into consideration. The results obtained from the assessment of really existing in nature phyllotactic patterns correspond sufficiently to the fundamental theorems of Jean (1994), as well as to the theoretical model of Douady & Couder (1996).

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