INITIAL TRANSITIONS, ORDER AND DISORDER IN PHYLLOTACTIC PATTERNS: THE ONTOGENY OF *HELIANTHUS ANNUUS*. A CASE STUDY

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ABSTRACT

The variability of the phyllotactic organization of *Helianthus annuus* L. is investigated. Specimens exhibiting the various possible phyllotactic modes (Fibonacci spirals, Lucas spirals, bijugate spirals etc...) were selected. The transitions from the initial decussate growth to these organizations, were characterized and shown to correspond to only a few archetypes. The possible transients from a decussate mode were then investigated in the model of self organization introduced by Douady and Couder (1996a, b, c). They are shown to exhibit the same phenomenology as the observed ones. These various transients have a very different probability of occurrence which explains the difference of their frequency in plants. Finally the imperfections of the observed dispositions, which affect mainly the plastochron, are also investigated. The model provides an interpretation of this apparent disorder: after a transition the system optimizes the regularity of the parastichies but in doing so it disturbs the plastochron and the divergence. It is only when very large external disturbances affect the system that a real disorder is generated. In these latter cases the parastichies themselves disappear.

KEY WORDS: morphogenesis, phyllotaxis, ontogeny, *Helianthus annuus*, vegetative growth.

I. INTRODUCTION

I-1. Motivations for revisiting phyllotactic measurements on mature plants

Ideally the aim of the study of phyllotaxis is to understand the disposition of the leaves, bracts, florets etc..., during the whole ontogeny of a plant. The early works on phyllotaxis such as those of Schimper (1830) and Braun (1835) or those of Bravais and Bravais (1837a, b; 1839), Weisse (1897) and Schoute (1922, 1925, 1936, 1938) were carried out by measuring the position of the leaves, bracts or florets around the stems of mature plants. These observations provided the classification of all the existing modes of phyllotaxy. They also led to two important questions:

- 1) Whereas a given species has a dominant type of organization, exceptionally some specimens exhibit other types of phyllotaxy. There is, up to now, a lack of understanding as to what leads to the formation of these exceptions.
- 2) The phyllotactic patterns are not necessarily perfect. Their possible disorder had important consequences in the history of phyllotaxis. Ever since Bravais and Bravais, (1837) most of the investigators of phyllotaxis have been trying to characterize perfect modes of growth such as, for instance, the Fibonacci spiral modes. This approach usually led them to disregard the defects of the patterns. In turn this trend induced radical reactions from other investigators

who, having observed the imperfection of real patterns, were tempted to criticize or even reject the ideal models. For instance Schoute (1938), having observed the occurrence of whorled leaves in an otherwise spiral organization, suggested the existence of a specific binding factor. Similarly the imperfections of the spiral modes stimulated the work by Plantefol (1948). He observed that in the vegetative region of many plants one of the sets of parastichies appeared more regular than the other. This led him to propose a model in which only the parastichies of one direction (which he called "foliar helices") had a dynamical role. The problem is that in neglecting the other set of parastichies the necessary link with the Fibonacci organization is lost.

Both problems, the selection of the modes and the imperfect order, are linked with the dynamics of formation of the patterns in the apical region. Most of the recent works on phyllotaxis have concentrated on observations and measurements in this region and have provided precise data. In particular the geometrical dispositions of the primordia around an apex were characterized at several stages of the growth. In such works as those of Williams (1975) Maksymowych and Erickson (1977), Meicenheimer (1982 and 1987), the divergence angle ϕ_n between successive leaves was measured and the change in time of this angle was shown to be related to

the change of the radial spacing of the primordia as measured by the plastochron ratio a_n . This parameter was defined by Richards (1951) as the ratio of the distance to the apex of two consecutive primordia $a_n = r_{n-1}/r_n$.

However the problem of the mode selection and that of the disorder are difficult to solve by observations of the apex only. The ideal observation would be to record, during the entire growth of a specimen, both the formation of the primordia at the apex and the resulting position of the leaves, bracts etc. along the elongated stem. Unfortunately, except in a few recent experiments (Green et al. 1991), the observation of the apex is usually destructive so that the later growth of the plant cannot be observed.

For these reasons the aim of the present article is to return to measurements on mature plants because they offer two major advantages for a comparison with models:

- 1) All the leaves, bracts, ray florets and florets of a specimen can be observed in sequence so that the whole history of the development of the plant's phyllotaxy can be studied.
- 2) Exceptions to the normal phyllotaxy are rare, however it is easy to select these exceptions by superficial observation of a large population of mature plants. It would be a difficult task to examine the apices of large numbers of plants so as to observe the exceptional transitions precisely when they occur.

There is an obvious difficulty in the comparison of the measurements of the position of the leaves of mature plants with the results of a model concerned with the dynamics of formation of the primordia around the apex. It will be shown here that only a few simple hypotheses are needed to relate the measurements and the simulations. This will permit the analysis of the various possible transients which are at the origin of the variability of the sunflowers' phyllotaxis. Also the disorder observed in the specimens will be compared with that in the simulations.

1-2. *Helianthus annuus*

Because of the high spiral orders they reach in their inflorescences the phyllotaxy of the Asteraceae has been widely investigated and was well documented by Bravais (1837), Weisse (1897), Church (1904) and Schoute (1938), Hernandez and Palmer (1988) and Ryan et al. (1991).

Weisse (1897) was the first to undertake an extended statistical work on the organization of capitula of *Helianthus annuus* L. He found that out of 141 specimens, 133 were organized in the main Fibonacci series and 6 in the Lucas accessory series. Similarly, Schoute (1938) examined 319 specimens of *Helianthus annuus*. Among them 262 were organized in the main Fibonacci series (1, 2, 3, 5, 8, 13, ...), 46 followed the Lucas secondary series (1, 3, 4, 7, 11, ...), 9 had a bi-jugate organization 2(1, 2, 3, 5, 8, 13, ...) and finally 2 followed the second accessory series (1, 4, 5, 9, 14, ...). These studies pointed out the continuity of the phyllotaxy: sunflowers with inflorescences following the Fibonacci or the Lucas series have respectively a Fibonacci or a Lucas spiral organization of their vegetative leaves.

It is emphasized that the very first leaves of the stem of dicotyledonous plant always grow in the opposite decussate position and it is through a transition that the spiral phyllotaxy appears. Studying 200 specimens Codaccioni (1955) showed that the destabilization of the decussate mode occurs at the second, third or fourth node respectively in 25%, 43% and 25% of the specimens. Immediately after the transition, even a superficial observation of the stems shows that the ordering

of the leaves is imperfect. Schoute (1938) measured the positions of all the leaves of several specimens. These were the same measurements that have been performed for the present work. For some spirally organized specimens he observed that there was frequently quasi simultaneous formation of two, three or four leaves. His interpretation was that there existed a binding factor leading to the formation of what he called imperfect binding whorls. It will be demonstrated here that it is not necessary to invoke a specific factor to understand these patterns.

1-3. Theoretical model

In a recent work (Douady and Couder 1996a, b, c) the minimum dynamical model necessary to the generation of the phyllotactic orders was sought. The rules for the formation of a new primordium put forward by Hofmeister (1868) and by Snow and Snow (1952) were investigated. Those based on the Snows' rules were shown to be more general and sufficient to generate all the spiral, whorled and multijugate modes observed in botany, as well as irregular patterns. It is the ability of this model to reproduce the real transient which will be investigated here.

1-3-1. The basis of the iterative system

The basic hypotheses of the model can be summarized in the following way:

- The stem apex is axisymmetric; its shape can be approximated by a plane or a cone.
- The primordia are either circular or transversely elongated.
- The primordia are formed at the periphery of the apex and, due to the growth, they move away from the apex with a radial velocity $V(r)$.
- A new primordium appears when and where an available space of azimuthal size l_1 has become available at the periphery of the apex of radius R_0 .
- There is no later reorganisation leading to changes in the angular positions of the primordia.

These hypotheses form the basis of a dynamical iterative system in which the repeated formation of interacting elements creates the order.

Note that all the parameters of the botanical reality will be characterized here by a symbol without a prime. Each of these parameters has a counterpart in the numerical simulation which will be named by the same symbol but with a prime.

1-3-2. Numerical simulation

How the rules of Snow and Snow (1952) were implemented in numerical simulations is described in Douady and Couder (1996b, c). The simulations are done in a radial configuration, the plane projection of a cone, sketched in Fig. 1. The elements are formed at the periphery of a central circle of radius R'_0 . With time they move away radially with a velocity $V'(r')$. Each element generates a repulsive potential. A new element is created on the circle when the potential due to the previous elements is, in this point, below a threshold value. It was shown that this is equivalent to the appearance of a new element when a space of minimum azimuthal size l'_1 is formed at the periphery of the circle. The parameter which controls the phyllotaxy is $\Gamma' = l'_1/R'_0$ the ratio of the size of the primordium at its formation to the radius of the apical meristem (see Fig. 1). This parameter is very similar to that used by van Iterson (1907) in his geometrical analysis of phyllotaxy. The simulations show that, in general, for a given

Fig. 1. A typical pattern obtained in the numerical simulation showing the relevant parameters. The radius of the central region is R'_0 . The primordia are represented by one of their isopotential lines. A primordium at its formation is characterized by its azimuthal and radial sizes l'_1 and l'_2 . Van Iterson's parameter Γ' is defined as $\Gamma' = l'_1/R'_0$. In the present set of simulations a given primordium grows in size as it moves away radially. The velocity at which the elements move away from the center is V' and the time interval between the formation of two elements is the plastochrone $\Delta t'_n$. The distance of the primordium of order n to the center is r'_n . The ratio $a'_n = r'_{n-1}/r'_n$ is Richards' (1951) plastochron ratio. If the apical region grows exponentially the relation of the plastochron ratio can be written as $a'_n = \exp(G'_n)$ where $G' = V'\Delta t'_n/R'_0$ (Douady and Couder 1996a). The divergence angle is ϕ'_n . Note that each of the quantities defined in this numerical pattern has a correspondent in a real apex where it is named with the same symbol but without a prime.

value of Γ' there is spontaneous formation of one of several possible steady regimes of the iteration. The patterns are defined by the relative position of the elements given by the divergence angle ϕ'_n and by the plastochron, the time interval $\Delta t'_n$ separating the formation of two consecutive elements. Whereas the divergence determines the relative azimuthal positions of the elements, the plastochron determines their relative radial positions. The latter can be characterized by the ratio of the radial displacement of the elements during one period to the radius of the central region $G'_n = V'\Delta t'_n/R'_0$ (Douady and Couder 1996a, b, c). This parameter is related to the plastochron ratio $a'_n = r'_{n-1}/r'_n$ (Fig. 1). If the apical region grows exponentially the relation of a' with G'_n is simply:

$$a'_n = r'_{n-1}/r'_n = \exp(V'_0 \Delta t'_n / R'_0) = \exp(G'_n) \quad [1]$$

For each mode of organization ϕ'_n and G'_n are related to each other but it is Γ' , van Iterson's parameter, which determines both these quantities.

In the present study the variant of this simulation (Douady and Couder 1996b) has been selected in which the elements increase in size as they move away from the central circle. The repulsive interaction between the elements can be chosen at will. Its important characteristic is how fast it decreases with distance. This is defined in Douady and Couder (1996 b)

Fig. 2. Diagram of the steady values of the divergence angle ϕ' as a function of the parameter $\Gamma' = l'_1/R'_0$ as obtained in a simulation with a conicity $N' = 1/3$, a stiffness $\alpha' = 3$ and with primordia growing in size as they grow older.

The open circles correspond to the main Fibonacci branch, the open squares to the first secondary branch (following the Lucas series). The open diamonds to the second secondary branch (1, 4, 5, ...). The black diamonds represent the two values of ϕ' in the range of existence of the opposite decussate modes and the three values of ϕ' in the bijugate spiral modes. The black triangles are the three fold whorls.

The growth of sunflowers starts in a range of values of Γ' corresponding to the decussate mode and their later change leads to a decrease of Γ' . The four main possible developments correspond to transitions to the main Fibonacci branch (a), to the Lucas branch (b), to the bijugate spirals (c) and to the trimerous whorled modes (d).

by a "stiffness parameter" α' chosen here to be $\alpha' = 3$. Finally the plane of computation is the projection of a conical apex; the conicity parameter which gives the ratio $N' = l'_2/l'_1$ was chosen here to be $N' = 1/3$.

Simulations of the steady regimes of the iterative system for these values of the parameters were done first. The resulting values of divergence angle ϕ' as a function of Γ' are plotted in Fig. 2. The open circles correspond to solutions where only one single element forms at each period. These are the distichous and spiral modes. The spiral solutions form in Fig. 2 a series of separated branches. Only one of these branches exists for all values of Γ' . Along this main branch ϕ' converges scillingly towards $\phi = 2\pi(1-\tau)$ when Γ' tends towards zero (Douady and Couder (1996a, b). Correlatively the parastichy order of the spiral patterns undergo successive transitions of the type (i, j) to (j, i+j) which build up the successive Fibonacci orders. For decreasing Γ' there is an increasing number of independant secondary branches having a structure similar to the main branch. Along them the parastichies are organized in Fibonacci-like series with different initial terms such as the Lucas series (1, 3, 4, 7, 11, 18...), the second accessory series (1, 4, 5, 9, 14...) etc...

In the other modes, drawn in Fig. 2 in black symbols, several elements are formed simultaneously. These are the phyllotactic whorled and multijugate modes. In the $\phi'(\Gamma')$ diagrams their ranges of existence are characterised by the fact that ϕ' is multi-valued. For instance, in the decussate range the divergence is 180° or 90° depending on whether the two successive elements are in the same whorl or not.

Figure 2 displays the characteristics of steady regimes of the iteration. In the real growth of plants a limited number of primordia is generated and the parameter $\Gamma' = l'_1/R'_0$ varies

with time. A set of simulations (Douady and Couder 1996c) aimed at investigating some of the possible transient regimes of the system has already been performed. This work demonstrated that the high order Fibonacci organizations were naturally obtained whenever there was continuity of the growth with a continuously decreasing Γ' . A second result was that even if there was a certain disorder in the iterations the resulting patterns remained practically normal. The aim of the present article is to perform a direct comparison of measurements done on plants with simulations obtained with the iterative model.

II. MATERIAL AND METHODS

II-1. Botanical measurements

II-1-1. Collection of the specimens

The sunflower plants (*Helianthus annuus* L.) were chosen from three fields located near Guerande (Brittany, France). They were collected in the second half of August 1994; at that time their growth was complete and their seeds ripe. The aim was not to repeat a statistical analysis of the repartition of the various phyllotactic modes. This required selecting just several samples of the different modes of organization and finding what type of development lead to their formation. The position of all the leaves and of a few bracts of 21 specimens was measured. Twelve of them ($n^{\circ}1, 2, 3, 4, 6, 7, 13, 14, 16, 17, 18, 21$) were chosen at random and nine were selected because they presented, at first sight, a specific interesting feature.

In the randomly chosen plants, 11 had an inflorescence with parastichies ordered in the main Fibonacci series and one ($n^{\circ}1$) had a bijugate head. As for the selected plants four ($n^{\circ}9, 10, 12, 20$) had parastichy order in the Lucas series. Two specimens ($n^{\circ}5$ and 15) had a bijugate inflorescence. Specimen $n^{\circ}19$ had an initial transition from decussate to trimerous whorls, followed by formation a Fibonacci spiral. The stem of specimen $n^{\circ}8$ revealed a very large scar near the ground and a perturbed phyllotaxy. Finally, specimen $n^{\circ}11$ had a fasciated stem and two heads opposite to each other.

II-1-2. Measurements

The successive leaves in order of their formation are labelled with increasing numbers. The height h_n above the ground of all the leaves of formation order n was measured on all the specimens with an accuracy of ± 3 mm. The angular position θ_n of the leaves was also measured. In a few cases the stem was slightly twisted near the head. In these cases this effect was estimated by the general twist of all the vascular strands and the angles corrected accordingly. The accuracy of the measurements was estimated to be $\Delta\theta = \pm 5^\circ$. This precision was judged sufficient: due to the extension of the leaf bases it is doubtful that the position of the leaves could be defined with better accuracy. The divergence $\varphi_n = \theta_n - \theta_{n-1}$ between one leaf and the next, could either be deduced from the measurements of θ_n or measured directly.

II-1-3. The display of the results

A) The height h_n of the successive leaves is first plotted as a function of their formation order n . This is done in Fig. 3 for specimen 16 which had a very regular Fibonacci organization and for specimen $n^{\circ}10$ which had irregularly spaced leaves on the stem. It is remarkable that the two plots $h_n(n)$ are still similar, both being on the average, monotonous and linear in the range of vegetative growth.

Fig. 3. Plot of the height h_n of the successive leaves as a function of their formation order n (black dots: specimen $n^{\circ}16$, open diamonds specimen $n^{\circ}10$). The elongation is initially small. In the vegetative regions the plot exhibits on the average a linear dependence suggesting a constant factor of elongation.

B) Plots $h_n(\theta_n)$ give a reconstruction of the disposition of the leaves on the stem. For this representation to be realistic the ratio of the length to the width of the representative strip is chosen to be the same as the ratio of the height to the perimeter of the stem. With this rule a $h_n(\theta_n)$ plot reproduces the real aspect of the unrolled stem. An artifice is used to make the structure more visible. In the plane representation of a cylinder the peripheral periodicity is lost. It is possible to recover this periodicity by repeating the pattern. In Fig. 4 three identical patterns are presented next to each other so that $-2\pi < \theta < 4\pi$. Naturally only the central strip $0 < \theta < 2\pi$ represents reality.

C) The data provide the successive values of the divergence angle φ_n and the distance in height Oh_n separating successive leaves. Both can be plotted as a function of h_n (Figs 6 and 7). In the region where the elongation is constant or slowly variable the latter plot reflects the fluctuations of the plastochron.

II-2. The simulations of the initial transient and of the vegetative growth

The simulations that were performed for this work explored transients meant to simulate the initial growth of the sunflower seedling and the build-up of the vegetative region. The later development during the flower initiation was not addressed here as it was already investigated in Douady and Couder (1996c).

The technique of the numerical simulations has been given elsewhere (Douady and Couder (1996b)). They were performed on McIntosh computers MIIIfx, Quadra 950 and Quadra 840 av. The program was written in Think Pascal.

II-2-1. Imposed $\Gamma'(\tau')$ variation

The main problem is to impose in the numerical simulation realistic time variations of the parameters. The conicity of the apex was here assumed to be constant and the development due to a decrease of the parameter Γ' . Such initial decreases of Γ' are described in many botanical cases (see Williams 1978) and are mainly due to the increase in size of the apex. During the later vegetative growth the phyllotaxy remains steady, meaning constant values of the parameters.

A smooth variation of $\Gamma'(t')$ has been used leading progressively from an initial value Γ'_i to a final value Γ'_f located below this range, and given by the relation:

Figs 4-7. Results of the measurements performed on specimen n°16.

Fig. 4. Positions of the successive leaves on a $h_n(\theta_n)$ diagram, the first two elements being the cotyledons. The central region ($0^\circ < \theta < 360^\circ$) corresponds to the actually measured positions. The diagram is made periodic by repeating the same positions h in the ranges ($-360^\circ < \theta < 0$) and ($360^\circ < \theta < 720^\circ$). The total height of the stem was $h = 90$ cm and its perimeter varied from $2\pi R = 5$ cm at the bottom to $2\pi R = 3$ cm at the top. Neglecting the tapering the scales of the diagram $h_n(\theta_n)$ were chosen so that it represents the pattern observed on the stem. This plot permits the direct observation of the generative spiral.

Fig. 5. $h_n(\theta_n)$ has been compressed vertically so as to exhibit a (2, 3, 5) spiral mode in the vegetative region.

Fig. 6. The successive values of the divergence angles $\phi_n(h_n)$ as a function of the height showing the transition from a decussate to a spiral mode. In the latter the average value of the divergence is $\langle \phi_n \rangle = 135.9^\circ$ but the instantaneous value fluctuates around this value.

Fig. 7. The successive values of Δh_n as a function of h_n . The elongation being a slowly evolving function the observed fluctuations of Δh_n are due to the irregularity of the plastochron.

$$\Gamma'(t) = ((\Gamma'_i + \Gamma'_f)/2) - ((\Gamma'_i - \Gamma'_f)/2) \tanh((t' - t'_1)/\tau') \quad [2]$$

Where $\tanh$ is the hyperbolic tangent. This time dependence, shown in Fig. 8, is meant to represent the reduction of Γ' during the initial build up of the vegetative region of the stem.

The parameters in (2) are chosen in order to produce realistic patterns. Since most specimens had an initial decussate growth the value of Γ'_i was chosen in the range of stability of this organization (except in one case see §III-1-2). The decrease of Γ' starting from the decussate range can lead, as shown in Fig. 2 to transitions to one of several organizations which exist at smaller values of Γ' . They are the Fibonacci the Lucas, and the bijugate spirals or the tricussate mode (labelled a, b, c, d respectively in Fig. 2). The numerical investigation of the steady regimes (see Douady and Couder 1996c) have shown that these modes are not equally stable in different ranges of values of G' . For instance immediately below the decussate range (for say $\Gamma' \sim 1$) the most stable mode is a Fibonacci mode (2, 3, 5). The Lucas, tricussate and bijugate modes are stable only for smaller values (in the vicinity of $\Gamma' \sim 0.85$). When the formation of a given organization is to be simulated we impose a value of Γ'_f in the range of maximum stability of this particular organization.

Finally in relation (2) the transition is also characterized by t'_1 the time at which it occurs and τ' the duration of the transition (Fig. 8). A first approximation of the time t'_1 is chosen so that the number of decussate whorls before the transition coincides with that of the specimens. Both t'_1 and τ' are then empirically finely tuned to reproduce the observed transitions. The total number of iterations is chosen to be of the same order as the typical number of leaves (approximately 30) of the specimens.

II-2-2. Measurements and display of the results

The formation of a pattern can be observed directly on the computer screen in real time (Fig. 10). Each primordium is represented by one of its isopotential lines so that the visual aspect of the pattern is that of the projection of an apex.

For comparison with the botanical data one may wish to have other representations. For this purpose the angular position and time of formation of the successive elements are also recorded. For reasons explained in the appendix (§A-1) this is done as a function of a time t'' easily deduced from the computer time t' . The position of a particle of order of formation n is thus defined by its time of formation t''_n and by the angle θ'_n at which it forms on the periphery of the central circle.

II-3. Comparison of the measured with the simulated patterns

The problem with this comparison lies in the different variables used in the two cases (see Figs 1, 10 and 11). It can be summarized as follows. The relative position of two successive leaves is defined from the botanical measurements by their distance in height, $\Delta h_n(h_n)$ and their divergence $\phi_n(h_n)$. The whole resulting spatial pattern can be drawn by plotting $h_n(\theta_n)$.

In the simulation the relative position of successive elements is given by the plastochrone $\Delta t''_n$ (t''_n) and by the divergence $\phi'_n(t''_n)$. The advection velocity being equal to unity, the former gives the relative radial positions of the elements. As for the spatial pattern given by the computation, it is a polar plot $t'_n(\theta'_n)$ (Fig. 10).

The comparison of these two sets of results is possible using two hypotheses:

Figs 8-9.

Fig. 8. The time change $\Gamma'(t')$ used in our simulations. The initial growth occurs at a value Γ'_i in the decussate range. It then undergoes a transition to a value Γ'_f which corresponds to the steady regime of vegetative growth. The transition occurs at a time t'_1 and lasts during a time τ' . The values chosen here are those used in the simulation shown in Figs 10-15.

Fig. 9. Plot of the height h_n of the successive leaves of specimen n°16 (Fig. 4) as a function of the time of formation t''_n of the corresponding elements in the numerical simulation (Fig. 12). This curve is well defined and can be fitted by equation [6]. This fit was used to ascribe a height h'_n to the elements generated by the simulation so as to perform the comparison displayed in Fig. 11.

- 1) The angular position of the leaves around the stem is that of their initial formation as primordia around the apical meristem.
- 2) After its initial formation in the apical region, the pattern is elongated due to the growth of the stem. Here we need only a hypothesis on the total effect of the elongation. The working hypothesis is that when the growth is completed, parts of the stem which are near to each other have undergone a similar stretching. This is in agreement with models of growth such as Cusset's (1991) and with the results of Wetmore and Garrison (1966) who studied the time evolution of the elongation in *Helianthus*. A consequence of this hypothesis is that where two leaves are observed to form a node their formation was quasi simultaneous. It is not that the elongation failed to occur between them.

The plots $h_n(n)$ shown in Fig. 3 support this hypothesis. It is realistic to assume that the phyllotaxy is steady in the vegeta-

Figs 10-11. Computed and observed transients leading to a Fibonacci order.

Fig. 10. An initial breaking of the opposite decussate symmetry was obtained in the simulation. The imposed change of $\Gamma'(t')$ led from an initial value $\Gamma'_i = 1.38$ located in the decussate range to a final value $\Gamma'_f = 0.95$ located below it. It was characterized by $t'_i = 0.7$ and $\tau' = 0.3$. Two elements (1 and 2) were imposed initially. Placed symmetrically, they simulate the influence of the initial cotyledons. The numbers show the order of formation of the elements. When underlined they correspond to elements having formed by pairs. The initial growth is decussate. Its first destabilization occurs with the shifted positions of elements 9 and 10. The later elements form one at a time. The element 11 is observed to appear with equal probability either to the right or to the left of element 7. Here it formed to the right and this position fixed the direction of winding of the later spiral growth.

Fig. 11. The same transition from the decussate mode to a Fibonacci spiral as observed (in a $h_n(\theta_n)$ diagram) on the first leaves of the specimen n°16 (open circles). The positions of the successive elements of the simulation shown in (a) are also plotted (black triangles). For this purpose an artificial height $h'_n(\theta'_n)$, was ascribed to each of them using the procedure discussed in the appendix. The similarity of the mode of destabilization is clearly observed.

tive region of the middle region of the stem. This means that Γ has a constant value and that the primordia appear, on the average, at constant time intervals. On the irregular specimen n°10 the leaves are not evenly spaced on the stem but the plot $h_n(\theta_n)$ is still, on the average, monotonous and linear in the range of vegetative growth. This suggests that the local irregularities of h_n are due to an initial irregularity of their time of formation and not to uneven stretching. This will be con-

firmed by the more precise comparison with the numerical model.

The distance in height between two successive leaves is thus assumed to be related to the time interval which separated their formation by a relation of the type:

$$h_n - h_{n-1} = k(t) (t_n - t_{n-1}) \quad [3]$$

A constant k is a very good approximation in the vegetative region but $k(t)$ varies in the transient regimes. It increases during the initial formation of the stem and will decrease during the floral development. The variation of $k(t)$ with time can be estimated by a method described in §II-3-3 and in the appendix (§A-2). It will be used in the quantitative analysis of the transients.

II-3-1. Comparison of the results: Representation of the phyllotactic patterns

The plot $h_n(\theta_n)$ shown in Fig. 4 gives a reconstruction of the disposition of the leaves on the unrolled stem. The elongation has stretched the pattern so that the parastichies that existed during the pattern formation near the apex have disappeared. We can assume that in the vegetative apex the pattern must have been the Fibonacci mode located just below the decussate range. In this range of values of Γ' it has three sets of parastichies (2, 3, 5). It is simply a change of the vertical scale of the plot $h_n(\theta_n)$ which leads to this disposition (Fig. 5). Though they represent the same data, the visual aspect of the patterns of Fig. 4 and 5 is remarkably different. While in Fig. 4 an irregular generative spiral was the most visible feature, in Fig. 5 much more regular parastichies of order 2, 3 and 5 can easily be drawn.

This may appear a trivial result. The vertical compression of a cylindrical helical lattice is known to generate changes of nearest neighbours and thus of parastichy order. Bravais and Bravais (1837) have demonstrated that if the angle of divergence is equal to the ideal irrational value $\Phi = 2\pi(1-\tau)$ the compression generates successive transitions from a parastichy order (i, j) to the next $(j, i+j)$ with the Fibonacci rule of transition (see Fig. 4 in Rothen and Koch 1989).

This property however is specific to an ideal lattice where the vertical distance of the elements is constant and where the divergence angle φ_n is always equal to Φ . Here, where the lattices are imperfect, the result has a different meaning. It is remarkable that it is with the rate of compression chosen above that the $h_n(\theta_n)$ plot exhibits the most regular parastichies order. This can be understood in the following way. The patterns resulting from self organization optimize the parastichy order, but are not ideal. The various scales chosen for the $h_n(\theta_n)$ plots reveal the differences with the ideal pattern. The vertical stretching amplifies the irregularities of the plastochron, while too large a vertical compression reveals the irregularities of the angles. The difference of φ_n with the ideal angle $\Phi = 2\pi(1-\tau)$ then dominates and the pattern again appears disordered. In the case shown in Figs 4-5 it was not possible, for instance, to obtain regular parastichies of order 8 by a larger compression. A more refined procedure to operate the compression is to relate directly the measurements to the simulation. It is presented below in §II-3-3, in Fig. 9 and in the appendix and will be used in the analysis of the transients.

II-3-2. Comparison of the results: display of the simulated patterns

A) From the data it is possible to plot $t''_n(\theta'_n)$. The radial velocity of the elements being equal to unity, t''_n is a

measure of the radial distance. This plot is thus a cartesian representation which can be considered as an unrolled cylindrical pattern. The horizontal and vertical scales of $t''_n(\theta'_n)$ are first chosen to correspond to the azimuthal and radial distances r'_n of the primordia in the radial pattern. The parastichy order is thus unchanged (Fig. 12). We can also stretch the $t''_n(\theta'_n)$ plots vertically. In the approximation of a constant elongation the stretched pattern (Fig. 15) exhibits the disposition of the leaves that would have resulted from the growth of this "numerical apex" into a stem. A comparison with the botanical pattern $h_n(\theta_n)$ becomes possible.

B) We can also plot the evolution of the divergence angle ϕ'_n and that of the plastochrone $\Delta t''_n$ as a function of their time of formation t''_n (Figs 13 and 14).

II-3-3. An attempt at quantitative comparison of the results

The assumption of a constant elongation is not valid during the transients. In order to make a quantitative comparison of the transitions a more refined representation of the elongation is needed. To do so has to be selected a transition which reproduces the main characteristics of a given specimen. Then the plant should be related to its simulation by plotting the vertical position h_n of the n^{th} leaf as a function of the time of formation t''_n of the n^{th} element in the simulation (Fig. 9). These plots give well defined curves that appear to be very similar from one specimen to the other and which can be accurately fitted by a simple mathematical relation (see the appendix). Each element of the simulation is thus ascribed the height h'_n that it would have reached during the later growth of a plant. Then the positions $h'_n(\theta'_n)$ are compared with the $h_n(\theta_n)$ positions in the plant.

III. RESULTS

The results will be presented, for each possible phyllotactic mode, as a systematic comparison, of the botanical data with the simulation. In each case the questions of the transients from a decussate mode to this particular mode and that of the regularity of the patterns will be addressed successively.

III-1. The formation of the Fibonacci series organization

III-1-1. Observation

Eleven specimens had a normal Fibonacci organization after the initial destabilization of the decussate region. Their characteristics are summarized in Table

1. Two others ($n^{\circ}8$ and 19) acquired a Fibonacci organization at a late stage of their growth and will be discussed separately.

Only two modes of initial transitions were observed in the studied specimens.

A) The characteristics of the first type of transition can be observed in Figures 4-7 which summarize the results for specimen $n^{\circ}16$. The transition is best observed on the compressed pattern (Fig. 5). The initial growth is decussate (2, 2, 4) with two sets of two parastichies and one set of four orthostichies. The first two non-decussate leaves, which form, are still approximately simultaneous but no longer opposite to each other. The next leaf is observed in different specimens in one or the other of two possible symmetrical positions. This determines the direction of the spiral.

B) In the second type of transition the first leaves which are not decussate remain opposite each other but do not form simultaneously. The next leaf then appears by itself, displaced

either to the right or the left of its normal position, determining the direction of the winding of the generative spiral. This type of transition appears similar to the initial transitions, observed in the apical region, in *Epilobium* (Meichenheimer 1982) and in *Linum usitatissimum* (Meichenheimer 1987). However in these cases the non simultaneity of the first pair was not remarked. This is not surprising since the shift can be very small.

The Fibonacci specimens were usually more regular than the others. In all cases a parastichy of first order (generative spiral) could be recognized along the stem, though it was not always very regular. Figure 6 shows the evolution of $\phi_n(h_n)$ the divergence angle for the specimen $n^{\circ}16$. In the decussate region two values are observed corresponding to the divergence between two leaves of the same whorl ($\pm 180^{\circ}$) and two leaves of successive whorls ($\pm 90^{\circ}$). After the transition to a spiral mode the divergence ϕ_n fluctuates slightly around an average value $\langle \phi_n \rangle = 135.9^{\circ}$. In 1 Fig. 7 we have plotted Δh_n has been plotted as a function of h_n . In a perfect steady spiral mode Δh_n should be constant. Even though specimen $n^{\circ}16$ was one of the most regular, Δh_n is found to fluctuate strongly.

The later development of this specimen is not shown on the figure. It led to the build-up of an inflorescence in which the bracts had parastichies (8, 13) and the florets parastichies (55, 89) at the periphery of the inflorescence. This development was continuous and corresponded to the results of the models presented in Douady and Couder (1996a, c) for the formation of the inflorescences of Asteraceae.

III-1-2. Simulation and discussion

A) The transients

When a slow decrease of Γ' is imposed in the simulation from a value in the decussate range to a value located immediately below this range the usual development is a transition from the decussate (2, 2, 4) mode to the normal spiral branch (2, 3, 5). Fig. 8 shows the imposed variation of Γ' (from $\Gamma'_i = 1.38$ to $\Gamma'_f = 0.95$) which generated the results shown in Figs 10-15 corresponding to a Fibonacci growth similar to that of specimen 16.

Fig. 14 shows the detail of the transition as observed in the radial geometry of the computation. The position of the first two elements was initially imposed to simulate the existence of the cotyledons. The initial growth is decussate and the first observed destabilization of this disposition is the formation of two simultaneous elements ($n^{\circ}9$ and 10 in Figs 10-11) which are displaced symmetrically towards each other. The next element ($n^{\circ}11$) then appears by itself in either of two possible positions located symmetrically with respect to the position of element $n^{\circ}7$. The choice of its position will determine the direction of winding of the whole spiral pattern. This pattern is very similar to the drawing by Williams (1975) of the transition from a decussate organization to a spiral mode (2, 3, 5) observed in *Linum usitatissimum* (Figure 4.1.7 of the reference).

This type of transition corresponds to that observed in specimen $n^{\circ}16$. In order to compare the simulation to the measurements the procedure described in §II-3-3 and in the appendix has been used. To each element of order n an artificial height h'_v has been ascribed the elongation function chosen so as to obtain the best fit with the botanical data. The superposition (Fig. 11) of the numerical $h'_n(\theta'_n)$ with the actual $h_n(\theta_n)$ of the leaves of specimen 16 demonstrates the excellent agreement of the angular positions of all the successive elements.

It can be seen that the appearance of element $n^{\circ}11$ is the critical event. It corresponds to the formation in the pattern of

Figs 12-15. The Fibonacci pattern obtained in the numerical simulation after the transient shown in Figs 10-11.

Fig. 12. The scales of this $t''_n(\theta'_n)$ diagram were chosen to correspond to the radial and azimuthal distances of the radial patterns of the simulation. As a result the parastichies observed here are the same as in the simulation. At the transition one of the parastichies sets of order 2 is undisturbed. A dislocation mediates the transition from two to three of the order of the other set of parastichy.

Fig. 13. The successive values of the divergence angle $\phi_n(t'_n)$. It shows some fluctuations around an average value $\langle \theta'_n \rangle = 140.8^\circ$.

Fig. 14. The successive values of $\Delta t'_n$ as a function of t'_n . As for the botanical specimen of Figs 4-7 there is a strong irregularity of the plastochron.

Fig. 15. A generative spiral can be drawn on the vertically dilated $t''_n(\theta'_n)$ diagram

a dislocation of the type investigated in the context of cylindrical lattices by Harris and Erickson (1980) and described in botanical cases by Zagórska-Marek (1994). An extra parastichy is generated in one of the sets of parastichies of order 2 of the decussate pattern. Simultaneously the orthostichies bend to the left to become parastichies and they also present one dislocation so that their number changes (4 → 5). Altogether a transition from (2, 2, 4) to (2, 3, 5) is thus obtained.

The second type of transition, where the destabilization occurs by the non simultaneous formation of two elements, was also investigated. The simulations show that this transition cannot be obtained starting from a value of Γ' located in the decussate range. It rather characterizes the transition to a spiral organization of the plants having an initial growth with a value of Γ'_i located above the decussate range. This transition will be described with reference to Fig. 3 of Douady and Couder (1996c) where it was shown and discussed. With such a Γ'_i the existence of an initial pair of opposite leaves is forced by the two cotyledons, but their formation cannot be simultaneous (see elements 1 and 2 of the quoted figure). The following element ($n^{\circ}3$) appears by itself displaced to the left or the right, a transition in which the symmetry is broken. Element $n^{\circ}4$ then forms in the position it would have had if the mode had been decussate. But it is single and located on the spiral initiated by element $n^{\circ}3$.

B) The disturbances of the numerical pattern

The simulated pattern of Fig. 12-15 are very similar to the plots obtained in specimen $n^{\circ}16$ shown in Fig. 4-7. The divergence has a similar average value and weak fluctuations around this value. The most interesting feature concerns the plastochron. In both the plots of $\Delta t'_n$ (from the simulation) and those of $\Delta h'_n$ (from the plant) very large fluctuations are observed. This confirms that it is not necessary to invoke an uneven elongation of the stem to explain the irregularities of Δh_n .

III-2. Lucas series organizations

III-2-1. Observation

Four of the collected plants ($n^{\circ}9$, 10, 12, 20) had an organization following the Lucas series. After initial leaves in the decussate position the symmetry breaking led directly to a Lucas mode of low order and the later build up of the inflorescence generated an increase to a parastichy order (7, 11) for the bracts and to (29, 47), (47, 76) or (76, 123) for the florets. The inflorescences appeared perfectly regular in all cases but this was not the case for the stems.

The only specimen where a regular generative spiral could be found was $n^{\circ}9$. In the case of $n^{\circ}12$ a very irregular generative spiral could still be recognized but several pairs of leaves of the spiral region appeared quasi simultaneously. In the case of specimens $n^{\circ}10$ and 20 no generative spiral could be found. Average divergence angles were measured (except for $n^{\circ}20$). They are close to the ideal value of the Lucas branch $\Phi_L = 99.5^\circ$. The complete results of the measurements of one of the irregular plants ($n^{\circ}10$) and the transient observed in the most regular one ($n^{\circ}9$) will be presented here.

Figures 16-19 give for specimen $n^{\circ}10$ the elongated and compressed $h_n(\theta_n)$ patterns as well as the $\phi_n(h_n)$ and $\Delta h_n(h_n)$ dependences. The absence of a regular generative spiral is clearly seen in Fig. 16. If the elements are linked in their order of formation, the corresponding line moves up generally to the right (anticlockwise winding). However there are two instances where the line reverses to the opposite direction of winding. These anomalies are also easy to observe in the plot of $\phi_n(h_n)$ (Fig. 18). The average value of the divergence is

$\langle\phi_n\rangle = 100.9^\circ$ but the plot exhibits two sequences of three anomalous values of the divergence (-160° , -100° , -160°). They are due to two permutations in the order of formation of two successive elements. The corresponding sequence of divergence values are thus simply $2\langle\phi_n\rangle - 2\pi$, $-\langle\phi_n\rangle$, $2\langle\phi_n\rangle - 2\pi$. In spite of these anomalies the compressed $h_n(\theta_n)$ pattern (Fig. 17) exhibits parastichies (3, 4) which are only weakly disturbed.

III-2-2. Simulation and discussion

A) The transition

The diagram $\phi'(\Gamma')$ shown in Fig. 2 suggests that the second way out of the decussate mode is a transition to the main secondary branch (1, 3, 4) (labelled as (b) in Fig. 2). Once this jump has taken place the later development will follow this branch smoothly so that the inflorescence will have parastichy orders in the Lucas series. Transitions to the Lucas mode occur in the simulation for slightly larger decrease of Γ' than in the previous case. For instance the results shown in Figs 22-25 were obtained for a transition from $\Gamma'_i=1.3$ to $\Gamma'_f=0.85$. However we should point out that the range of values of t'_1 and τ' for which the pattern undergoes this particular transition is extremely narrow. In particular it only occurs for well chosen values of the time t'_1 around which the decrease of Γ' occurs. The specificity of the $\Gamma'(t')$ laws necessary to induce this transition probably explains the scarcity of the Lucas organizations in nature.

The detail of the transition to a Lucas spiral corresponds to an archetype shown in Fig. 20 as it results from the simulation. At first this transition is somewhat similar to the first type of transition leading to the Fibonacci order. Two elements of the same whorl appear approximately simultaneously (see the positions of elements $n^{\circ}9$ and 10 respectively in Fig. 10 and Fig. 20). But being nearer to each other than in the previous case they leave space for the formation of two (instead of one) elements on the other side of the apex (elements $n^{\circ}11$ and 12 in Figs 20-21). From then on the elements will wind up into a generative spiral with a divergence angle of the order of 100° . In terms of dislocations the transition from (2, 2, 4) to (1, 3, 4) means that a parastichy has disappeared in one direction and one has formed in the opposite direction. For simplicity the latter only is drawn in figures 17 and 22. As for the initial orthostichies they simply bend to become parastichies. The initial destabilization measured on specimen $n^{\circ}9$ corresponds exactly to the process found in the simulation as can be seen by the quantitative comparison of $h'_n(\theta'_n)$ with $h_n(\theta_n)$ shown in Fig. 21. The same destabilization was observed on specimen $n^{\circ}12$. Note that elements $n^{\circ}14$, 15 and 16 appear almost simultaneously; comparison between several transients show that interventions in their order of formation are frequent and generate perturbations in the later pattern.

B) The anomalies

As in the botanical specimens, the Lucas patterns obtained in the simulations are less ordered than the Fibonacci ones. Figures 22-25 show the characteristics of a pattern obtained in the simulation after the transient discussed above. The divergence (Fig. 23) fluctuates around an average value $\langle\phi'_n\rangle = 101.7^\circ$ and exhibits two sequences of anomalous values due to permutations in the order of formation of the elements as observed in the plant. The plastochron is very irregular (Fig. 24).

The imperfections of the patterns resulting from a self organization process were first observed by Veen and Lindenmayer (1977) in the simulation of a reaction-diffusion model.

Figs 16-19. The positions $h_n(\theta_n)$ of the leaves of the Lucas series specimen n°10 which had a (47, 76) inflorescence.

Fig. 16. The pattern on the stem appeared disordered as seen on $h_n(\theta_n)$. Approximately at mid-height there is one instance where there is simultaneous formation of two elements. Such a disposition is similar to Schoute's (1938) binding whorls. Above and below there are two other instances in which the formation of two elements is interverted. If the elements are linked in their order of formation, the resulting line runs back and forth around the stem and does not form a spiral.

Fig. 17. After a vertical compression, the pattern appears more regular and parastichies of the mode (3, 4) can easily be recognized. The transition from the decussate mode (2, 2, 4) can be seen as one of the sets of parastichies of order 2 becoming of order 3 by a localized dislocation and the set of orthostichies becoming the parastichies of order 4 of the new pattern.

Fig. 18. The evolution of the divergence angle $\varphi_n(h_n)$. The average divergence is of the order of 100°. Two anomalies characterized by a sequence of values $\varphi_p = -160^\circ$, $\varphi_{p+1} = -100^\circ$, $\varphi_{p+2} = -160^\circ$ are observed. They are due to permutations in the elements' order of appearance.

Fig. 19. The successive values of Δh_n as a function of h_n showing the strong irregularity of the plastochron.

The disturbances of the iterative system involving permutations in the formation order were described in detail by Douady and Couder (1996). They showed that permutations occur with increasing frequency when the parastichy order increases, but that these anomalies are more and more difficult to observe on the resulting patterns. The observation of such permutations on specimen n°10 is, to our knowledge, the first botanical confirmation of this effect.

These defects are not due to a random process but to the proximity of a transition involving the formation of parastichies with dislocations. The resulting perturbations subsist in several rows of the parastichies during the growth of the pattern. A regular pattern may be obtained after a large number of iterations.

III-3. Bijugate organizations

III-3-1. Observation

The head of specimen n°5 had an organization $(68, 110) = 2(34, 55)$ at the periphery of its inflorescence. It is shown in Fig. 26 where the bijugate organization of the last two pairs of leaves can be observed. The three specimens (n°1, 5 and 15) which had bijugate heads also had bijugate stems. They were all very similar so we limit ourselves to describing specimen n°5.

In all three cases the leaves' disposition on the stem appeared different from the ideal. The bijugate mode is usually described as a spiralling decussate mode in which two leaves form simultaneously opposite each other, each pair forming at an angle (different from 90°) from the previous pair. This is not what is observed here. Figures 27-28 show the position of the leaves of specimen n°5. The formation of the leaves of most pairs is non simultaneous (Fig. 30). Furthermore the measurements of the divergence (Fig. 29) show that the two leaves of the same pair are not opposite each other.

But the pattern, once compressed (Fig. 28), is bijugate and very ordered. The initial transition can be seen as a transition from a decussate mode $(2, 2, 4)$ to a bijugate mode $(2, 2, 4)$. This transition is progressive: the orientation of the parastichies changes and the orthostichies bend to become parastichies. There is no need in this transformation for dislocations and none are visible.

III-3-2. Simulation

A) The transition

The diagram $\phi'(\Gamma')$ shows that below $\Gamma' = 0.95$ bijugate spiral organizations are stable solutions of the iterative system. The transition to a bijugate organisation (labelled (c) in Fig. 2) is thus the third possibility of transition from the decussate pattern. However, between the decussate and the bijugate organizations, there is a gap of values of Γ' for which both are unstable. For these values of Γ' the return to the Fibonacci branch is the normal development: this gap can be crossed only if the decrease of $\Gamma'(t')$ is fast enough.

This type of transition was relatively easy to obtain in our simulation and Figs 31-32 show a typical result. The numbering of the successive elements was chosen so as to permit comparison with the transients of Figure 10 and 20. The main characteristic is that when a pair of elements (n°9 and 10) destabilizes they both shift in the same winding direction, instead of sliding towards each other as they did in the previous transitions. The next two elements (n°11 and 12) shift in the same direction so that the four orthostichies become four parastichies and the pattern becomes spiral. The comparison of the numerical result with the positions of the leaves of the

Figs 20-21. Computed and observed transients leading to a Lucas series spiral.

Fig. 20. The initial breaking of the opposite decussate symmetry as it was obtained in the simulation. The imposed change of Γ' leads from an initial value $\Gamma'_i = 1, 3$ located in the decussate range to a final value $\Gamma'_f = 0.848$. The characteristic times are $t'_1 = 1$ and $\tau' = 0.3$. The numbering of the elements was chosen so as to permit comparison with the previous case. The destabilization of the decussate mode corresponds again to the shifted positions of elements 9 and 10. The position of the next element (n°11) to the left or the right of 7 again determines the direction of winding of the spiral. The difference with Fig. 14 is that Γ'_f being now smaller, the element n°11 does not inhibit the formation of element 12 on the other side of 7. This initial transition led to the Lucas mode but it is difficult to obtain a regular pattern and a tricussate mode can also be reached after such transients.

Fig. 21. The transition from a decussate mode $(2, 2, 4)$ to a spiral mode $(1, 3, 4)$ as observed in specimen n°9 (open circles) in a cylindrical $h_n(q_n)$ diagram. The positions $h'_n(\theta'_n)$ of the successive elements of the simulation shown in (a) are also plotted (black triangles).

Figs 22-25. The Lucas pattern obtained in the numerical simulation after the transient shown in Fig. 20.

Fig. 22. With the scale of the radial patterns the diagrams $t''_n(\theta'_n)$ the pattern appears regular with parastichies of order 3 and 4.

Fig. 23. The successive values of the divergence angle $\phi'_n(t''_n)$. It tends towards an average divergence $\langle \phi'_n \rangle = 100^\circ$. Two interversions of the order of formation similar to those of specimen 10 (Fig. 18) are observed.

Fig. 24. The time intervals separating the formation of consecutive elements.

Fig. 25. Once vertically stretched the pattern looks like specimen 10. In particular it exhibits pseudowhorls similar to those observed in Fig. 16 and of the type described by Schoute. No generative spiral can be drawn.

Fig. 26. Photograph of specimen n°5 which had a bijugate inflorescence ((68, 110) i.e. 2. (34, 55)). Two pairs of leaves can be seen: they form quasiwhorls but the leaves of the same pair are not exactly at the same height.

plants n°5 and 15 (Fig. 32) shows the identity of the transition.

B) The anomalies

At first sight the transition from a decussate to a bijugate mode appears the smoothest. As it does not involve any defect it leads to the formation of remarkably regular parastichies (Fig. 33). However, once stretched (Fig. 36) the pattern appears far from the ideal bijugation as the simultaneity of the formation of the pairs is not maintained. It is precisely when the system crosses the range of values of Γ' for which both decussate and bijugate patterns are unstable, that these distortions are observed. They are the precursors of the return to the spiral organization that would occur if the system remained in the unstable range. These disturbances were observed in all the simulations. They are entirely similar to those observed on the bijugate specimens.

III-4. Transition to a trimerous whorled mode

III-4-1. Observation

A fourth possibility labelled (d) in Figure 2 is a direct transition from the decussate mode to a trimerous whorled mode. This transition was observed on specimen n°19 shown in Figs 37-38. The leaves formed three nearly perfect whorls before a return to a Fibonacci spiral mode. It is interesting to note that a reasonably regular lattice is obtained by compression (Fig. 38).

III-4-2. Numerical simulations

In the numerical simulation the transition to trimerous whorls was observed for a time change of $\Gamma'(t')$ very similar to that giving rise to the Lucas organization.

III-5. The strongly disturbed plants

III-5-1. Observation

Specimen n°8 had, between its first and second pairs of leaves, a very deep scar covering a third of the stem's perimeter. As a result the positions of the leaves on the stem were disordered. In the present case the pattern remains entirely disordered whatever the compression applied to the $h_n(\theta_n)$ plot and no regular set of parastichies is observed (Fig. 39). This specimen only recovered a Fibonacci organization of its bracts and of its inflorescence.

Another specimen (n°11) had a weakly fasciated stem. At the flower initiation the tip had split, leading to the formation of twin heads. The photographs of Figs 41-44 shows that, as Janus in the myth, this plant had two faces practically opposite each other. The stem was fasciated on most of its length and its splitting was located only 5 cm below the heads. The fasciation generated a disorder of the position of the leaves and no parastichy order could be seen on the compressed $h_n(\theta_n)$ plots. After the splitting both heads recovered axisymmetry. The phyllotaxy of one of the inflorescences was very regular with a parastichy order (54, 87) at its periphery (Fig. 43). This is a trimerous Lucas mode 3 (18, 29), a very rare organization indeed. As for the second head (Fig. 44) the numbers of spirals in each direction were approximately 70 and 91 but though the pattern was ordered on most of the surface, there remained a sector in which the elements were disordered so that there was no global parastichy order.

These observations can be understood in the following way. After the splitting the two apices recovered axisymmetry at a time when the new primordia were future bracts. At this point the phyllotaxy is (8, 13) or (13, 21) on normal specimens, meaning that the value of Γ was very small ($\Gamma \sim 0.2$). In contrast with the normal situation, for both heads the system lacked previous ordered elements. As a result one of the heads restabilized on a secondary branch of the diagram. The other reached a local order on most of its surface but failed to reach a regular global mode.

This is similar to a result obtained by Hernandez and Palmer (1988). These authors performed a circular cut around the apex of a flowering sunflower. The following regeneration of the capitulum led to a disordered pattern.

III-5-2. Simulation and discussion

Disordered patterns or rare phyllotactic modes are obtained in our simulation when it starts directly at a small value of Γ' with incoherent initial elements. When the number of iterations is small the system does not have time to organize itself and chaotic patterns are obtained on which no parastichy order can be found (Figure 40). Around an individual element the local order is not very different from what it would be in an organized pattern; the density of the packing, without being optimum, remains high. The resulting pattern thus has the same relation to the organized patterns that an amorphous solid has to a crystalline solid.

In some cases the system finds its way to a regular organization: it can do so on any of the branches that exist at the given value of Γ . Very rare phyllotactic modes can thus be obtained. A direct organization of the pattern at a low value of Γ could be responsible for the variability of the patterns in

Figs 27-30. The positions of the successive leaves of specimen (5).

Fig. 27. The relative times of formation of the successive elements is clearly observed on the stem. During the transition from decussate to bi-jugate the synchronous formation of the two elements of a whorl is not maintained.

Fig. 28. Once compressed, the pattern is seen as undergoing a smooth transition characterized by the absence of crystallographic defect. Note however that one of the set of parastichies is more regular than the other.

Fig. 29. Evolution of the divergence. There is a region where the opposite position of the leaves was not maintained.

Fig. 30. Plot of the successive values of Δh_n as a function of h_n . They reflect the large fluctuations of the plastochron. There is a range of values where the elements do not form by pairs

Figs 31-32. Computed and observed transients leading to a bijugate spiral vegetative mode.

Fig. 31. The initial breaking of the opposite decussate symmetry as it was obtained in the simulation. This transient was obtained for Γ' decreasing from $\Gamma'_1 = 1.3$ to $\Gamma'_f = 0.917$ with $t'_1 = 0.9$ and $\tau' = 0.3$. The initial growth is decussate and its first destabilization corresponds to the shifted positions of elements 9 and 10. The difference with the previous cases is that their positions are now shifted in the same direction so that they remain approximately opposite to each other. In this transition the simultaneity of the formation of two elements is not exactly maintained (element 11 has formed before 12). Fig. 32. The transition from a decussate mode (2, 2, 4) to a bijugate mode as observed in specimen n°15 (open circles) and specimen n°5 (open squares) in a cylindrical $h_n(\theta_n)$ diagram. These two specimens had the same direction of winding and the origin of the measured angles was chosen so as to exhibit the similarity of their developments. The positions of the successive elements obtained in the simulation shown in (a) are also plotted (black triangles). The identity of the destabilization is clearly observed.

Magnolia described by Zagórska-Marek (1994) or for the exceptional organizations discussed by Jean (1994).

IV. DISCUSSION

IV-1. Comparison with previous results

Schoute (1938) published the position of the leaves of 8 specimens having various phyllotaxies. It was possible on his drawings to measure the position of the leaves and to reconstruct the initial data. These data have been processed in the same way as presented here. Many characteristics of both sets of measurements coincide. Schoute's Fibonacci plants are the best organized and always retain a generative spiral. His Lucas specimens are very disordered. As for his bijugate specimens they show the same loss of simultaneity of the formation of the pairs of leaves that have been observed in *Helianthus*. There is however a quantitative difference in the initial transients. Most of Schoute's specimens exhibited direct transitions from the decussate mode to trimerous or quadrimerous whorls, followed by a return to a spiral organization. It thus seems that the initial transition corresponded to a larger decrease of $\Gamma(t)$. This difference could come from a difference in the variety of the collected plants or in the conditions of their growth. One can note that with this larger change of Γ' a transition to a spiral mode of the series (1, 4, 5, 9, etc...) becomes possible (Fig. 2). Schoute found such specimens while we did not. A few numerical simulations performed with a larger jump in the value of $\Gamma'(t)$ produced this transition.

Schoute emphasized the simultaneous formation of several leaves in an otherwise spiral growth. This is the reason for which he believed in the existence of a binding factor. This factor does not seem to be necessary: these isolated whorls are simply a manifestation of the above-described fluctuations of the plastochron.

IV-2. Validity of the simulation

Qualitative results have been obtained here which shed light on the possible transients within vegetative growth and on the relation between order and disorder. However, it is not possible to claim that the model at present simulates the botanical reality because of the large number of parameters to which the conjectural values have to be ascribed.

There are first the general parameters of the iterative system such as the conicity and the stiffness of the interaction. Both were shown (Douady and Couder 1996b) to affect the stability of the decussate mode. The stiffness of the interaction represented by α' is unknown and had to be imposed. Furthermore the simulations were all done at a constant and hypothetical conicity. We have investigated the destabilization of the decussate mode as due to a reduction of Γ only. The time changes of apices shapes during the ontogeny as described by Williams (1975) show a reduction of their conicity. This effect could contribute to the transitions out of the decussate mode. In this case (Douady and Couder 1996b) a transition to the Fibonacci spiral mode (2, 3) without a change of Γ is possible. The relative importance in reality of the reduction of Γ and of the conicity can only be estimated by direct measurements at the tip. They will also provide values to the four parameters Γ_i , Γ_f , t_1 and τ of the transients themselves.

Amongst the many transients that have been performed two main differences with reality were observed.

Figs 33-36. The bijugate mode obtained in the numerical simulation after a transient of the type shown in Fig. 31.

Fig. 33. The smooth transition as observed on the $t''_n(\theta'_n)$ plot drawn at a scale corresponding to that of the radial distances in the simulations.

Fig. 34. The successive values of the divergence angle $\phi'_n(t''_n)$. Note that as in the specimen (Fig. 27) there is a region where the opposite position of the elements is not maintained.

Fig. 35. The time intervals separating the formation of consecutive elements. As in the specimen (Fig. 30).

Fig. 36. Elongated $t''_n(\theta'_n)$ plot. The transient region in which the elements do not form by pairs is clearly visible.

Figs 37-40.

Fig. 37. The positions $h_n(\theta_n)$ of the successive leaves of specimen (19) which exhibits a transition from a decussate to a three fold whorl, then a return to the Fibonacci order (3, 5).

Fig. 38. The corresponding compressed pattern showing the transition from parastichy order (3, 3) to (3, 5).

Fig. 39. The disordered pattern $h_n(\theta_n)$ observed on specimen n°8 which had a deep wound in the lower part of its stem. No parastichies are observed but there is still a reasonably homogeneous repartition of the elements.

Fig. 40. A disordered pattern obtained in a simulation started directly at $\Gamma' = 0.95$ with two simultaneous initials located at 55° from each other.

Figs 41-44. Photographs of the Janus-like double head of the specimen n°11.

Figs 41-42. General aspect.

Fig. 43. One of the inflorescences has a very regular phyllotaxy with parastichy order $(54, 87) = 3(18, 29)$ at its periphery.

Fig. 44. The phyllotaxy of the other head is perfectly organized on most of the surface except in a sector (seen on the left) which is disordered.

- The transients led to a bijugate organization more frequently than in reality. This probably indicates that the chosen conicity or stiffness was not optimal.
- Generally the transients were less rapid in the simulation than in reality. This could be due to the intrinsic limitation of the model itself. Its crudest approximation is that it replaces a continuous process (the formation of a primordium) by a discrete one in which a finite size element forms abruptly. It is possible that in a continuous process the transitions would be easier.

More data about development at the apex are now needed if more quantitative simulations are to be done.

V. CONCLUSIONS

Richards (1951) wrote: "The failure of past classificatory systems has been due to their derivation from some particular, and false theory, so that the data collected have little more permanent value than the theory itself; indeed, by a regrettable inversion, the facts of phyllotaxis have frequently been falsified in order to conform with the postulates".

In this work an attempt has been made to avoid this pitfall. First the crude results have been given of the very simple measurements done on mature plants. It is only at a second stage that interpretative assumptions have been made. The first one states, as is classical in phyllotaxis, that the divergence angles are preserved during the growth. The second states that the elongation is a smooth function so that the distance in height of the elements reflects the interval of time which separated their formation.

From a basic point of view the most important results obtained here are related to the disturbed patterns.

In the idealized description of the spiral phyllotaxy the elements are generated at regular time intervals, each element forming at a constant divergence angle from the previous one. In the reality of vegetative growth of sunflowers, this is untrue: the plastochron varies very much and the divergence angle, in spite of having a well determined mean value, also exhibits fluctuations. In several of the observed specimens the irregularity of the plastochron was so large that some leaves formed a kind of whorl, in agreement with the previous data by Schoute (1938). In the most extreme case interventions of the order of formation of the leaves were observed.

Because they were different from the corresponding perfect infinite lattices. However this "disorder" is not the result of a random noise. The very principle of the simulation presented here is an optimization of the position of the newly formed element. This position results from a deterministic process and the noise is weak. The observed irregularities result from the local optimization of the lattice. This is clearly shown by the fact that in all these situations the parastichies obtained after a compression of the pattern are much more regular than would have been expected from the fluctuations of both the plastochron and the divergence.

These irregularities have two different origins:

A) The decrease of Γ at an early stage of the growth induces a change in the piling of the primordia and results in a transition from a decussate arrangement to a spiral mode. The transition itself occurs by the formation of a dislocation which hinders the immediate formation of a perfect spiral pattern and generates later perturbations. It is the cause of Schoute's binding whorls and of our permutations. If the interaction between primordia was very stiff (as the contact of hard disks), the defects would not be eliminated and would propagate through the whole pattern.

B) A second type of disturbance is observed when the system crosses a range of values of Γ for which the existing phyllotactic mode is unstable. In these cases, the irregularities are the precursors of a transition to a more stable mode. This transition can however abort if the unstable range is crossed swiftly enough. Such disturbances are present in the transition from the decussate to the bijugate modes.

A characteristic of the imperfect patterns is that one of the parastichy sets is more affected by the perturbation than the other. This characteristic has been found in both the plants and the simulations. Such observations are probably responsible for the attempt by Plantefol (1948) to give to the most ordered parastichies a specific role.

The results for the disturbed lattices support the hypotheses of Snow and Snow (1952) when they proposed that the formation of a primordium occurred when sufficient space became available. The existing lattice defines the position and time of the formation of the new element. The dynamical reality is thus geometric, and the position of the new element is, in the steady regimes, determined by the existing parastichies. The plastochron, the generative spiral and the divergence are only tools for the description of the lattice, but do not determine the dynamics. At a transition the system minimizes the distortions of the parastichy pattern which exhibits localized dislocations as described by Harris and Erickson (1980). The resulting disturbance of the plastochron and of the divergence can be very large.

The difficulty in understanding phyllotaxis has come from the relation between local and global order. The present results demonstrate that at a given time the position of formation of an element is determined by its nearest neighbours. It has been shown previously (Douady and Couder 1996b) that the system tends to optimize the density of the packing. However, for a given small value of Γ there are many patterns having similar packing efficiency and which can thus keep growing. This means that the rules of appearance of a new element create a local order but do not, by themselves, generate the global order of the system. In particular the usual selection of the Fibonacci sequence does not directly result from it.

The origin of the global order is to be sought in the ontogeny of the plant. The build-up of the high order Fibonacci patterns starts at the initial stages of the vegetative growth and is due to iterations during a continuous decrease of Γ . During this decrease a spiral organization will remain on the same branch of solutions in the $\phi(\Gamma)$ diagram (cf $\phi'(\Gamma)$ in Fig. 2). If the initial transition leads to the (2, 3, 5) mode, a high order Fibonacci pattern will be formed at small Γ (Douady and Couder 1996 c). If the initial breaking of symmetry leads the system to have (1, 3, 4) or (2, 2, 4) parastichy order, other branches of solutions will be followed and, at small Γ , a high order Lucas or bijugate pattern will be reached.

In reverse, if the continuity of the phyllotaxy is accidentally broken at a late stage, the system will start its self organization again directly at a low value of Γ with disturbed initial conditions. The experiments by Hernandez and Palmer (1988) as well as our observations demonstrate that this will result in a long period of chaotic growth. The self organization will provide a local piling with a density similar to that of an organized pattern, but having no global order. The resulting patterns, instead of having a crystal-like order, will look amorphous. After many iterations however the pattern can return to an order which can belong to any of the secondary branches of the $\phi(\Gamma)$ diagram existing at this value of Γ . As a result rare phyllotactic modes can be reached.

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APPENDIX

A-1. The time measured in the simulation

The parameter controlling the growth is the geometrical ratio $\Gamma = l_1 / R'_0$. The iterations themselves determine (Douady and Couder 1996 b) the main two characteristics of the patterns $G_n' = V' \Delta t_n' / R'_0$ and ϕ_n' . It was shown earlier that for regular lattices $G' = \beta' \Gamma'^2$ where β' represents the compacity of the packing. For practical reasons, the length and time scales of the simulation were chosen so that R'_0 and V' are always equal to unity. As a result, in the computation, a change of $\Gamma'(t')$ can only result from a change in the primordia sizes l_1 and the resulting changes of G_n' affect only the time intervals $\Delta t_n'$. As shown by the measurements of Williams (1975), in the botanical reality, the ratio Γ changes mainly because of the increase of the apex radius R_0 . The simulation could have been done with primordia of constant sizes and an apex of varying size R'_0 . In this case for the same G_n' , the time intervals between the formation of successive elements would have been $\Delta t''_n = \Delta t'_n / \Gamma'$ instead of $\Delta t'_n$. This situation is more realistic and for this reason the plots are given as a function of t'' given by:

$$t''_n = \sum_0^n \frac{\Delta t'_n}{\Gamma'(t'_n)} \quad [4]$$

A-2. The problem of the elongation

The quantitative comparison of the numerical transient to the observed one requires an empirical description of the stem's elongation. The first step is to obtain a precise simulation of the phenomenon. The parameters Γ_i , Γ_f , t_1 and τ of equation [2] are chosen as described in §II-2-1 so that the resulting sequence of angles reproduces as closely as possible that of the observed transition which is to be modelled. The problem is now to ascribe to each element the height it would have reached had the apex given rise to a mature stem.

We used the assumption that the distance in height between two successive leaves is related to the time interval which separated their formation by relation (3):

$$h_n - h_{n-1} = k(t) (t_n - t_{n-1}) \quad [3]$$

The function $k(t)$ is not known because we do not know the times t_n of formation of the primordia in the botanical case. Our results however suggest that k is a constant during the vegetative growth. In most of the figures of this article we used this characteristic and compared directly the lattice $h_n(\theta_n)$ of the botanical measurements with the lattices $t'_n(\theta'_n)$ of the simulation. However for the transients a more refined fit is needed. On the patterns measured on plants (Fig. 4, 16, 27 etc...) the first elements are vertically more densely packed than the other. To the contrary in the simulation the first elements are less densely packed than the others (Fig. 13, 25, 36). This means that at the beginning of the growth k is not a constant but a function of time. We cannot determine the botanical $k(t)$ but if the simulation represents reality the times t'_n of the formation of the elements of the simulation are proportionnal to t_n so that there should be a relation of the type:

$$h_n - h_{n-1} = k'(t'') (t'_n - t'_{n-1}) \quad [5]$$

The function $k'(t'')$ can be determined by the plot of the vertical position of the n^{th} leaf h_n as a function of the time of formation t'_n of the n^{th} particle formed in the simulation (Fig. 9). These plots give smooth curves that appear to be very similar from one specimen to another. They can be accurately by relations of the type:

$$h_n = h_0 \ln [\cosh(\alpha t'')] \quad [6]$$

where $\ln(\cosh...)$ is the logarithm of the hyperbolic cosine and where h_0 and α are two fitting parameters. We deduce from the fitting curve obtained with (6) the height h'_n that the element n would have reached had the numerical apex grown into a stem. The resulting h'_n are very close to the corresponding h_n . This is a verification of our hypothesis that the elongation do not undergo rapid fluctuations from one region of the stem to the other. Had it done so relation (6) would have only represented a mean growth and the points representing h_n in Fig. 9 would have been scattered around this fitting curve. The values of h'_n found on the fitting curve would then have been different from the corresponding h_n . Finally we can note that relation (6) was chosen because its derivative gives to $k'(t'')$ a dependence:

$$k'(t'') \propto \frac{dh}{dt''} = \alpha h_0 \tanh(\alpha t'') \quad [7]$$

where $\tanh$ stands for hyperbolic tangent. This is a simplified version of the generally admitted sigmoidal models of the time dependence of the stems' elongation (Cusset 1991).

TRANSFORMACJE PIERWOTNE, PORZĄDEK I ZABURZENIA WZORÓW FILOTAKTYCZNYCH: NA PRZYKŁADZIE *HELIANTHUS ANNUUS*

STRESZCZENIE

Przedmiotem prezentowanych badań jest zmienność organizacji systemu filotaksji *Helianthus annuus* L. Wybrano rośliny o możliwie różnorodnej filotaksji: Fibonacciego, Lucasa, bijugii itp., a następnie opisano transformacje prowadzące do tychże układów od pierwotnej ontogenetycznie filotaksji nakrzyżległej. Wykazano, że odpowiadają one kilku zaledwie archetypom. Przebadano następnie możliwe przekształcenia filotaksji nakrzyżległej z zastosowaniem modelu zaprogramowanego przez Douady i Couder (1996a, b, c). Jak się okazało, odznaczają się one cechami podobnymi do cech opisanych wcześniej transformacji naturalnych. Różne jakościowo przekształcenia, analizowane teoretycznie, mają bardzo zróżnicowane prawdopodobieństwo wystąpienia, co tłumaczy ich niejednakową frekwencję w warunkach naturalnych. Badano również nie-regularności systemu mające przede wszystkim wpływ na plastochron. Model objaśnia ich obecność w sposób następujący: po transformacji system optymalizując regularność przebiegu parastych zmienia plastochron i dywergencję. Jedynie mocne zaburzenia wewnętrzne są w stanie zdeorganizować system do tego stopnia aby nastąpił zanik parastych.

SŁOWA KLUCZOWE: morfogeneza, filotaksja, ontogeneza, *Helianthus annuus*, rozwój wegetatywny.