



Phyllotaxis as a Dynamical Self Organizing Process Part III: The Simulation of the Transient Regimes of Ontogeny

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In two previous articles [Douady & Couder (1996a,b)] two iterative systems were defined, based respectively on hypotheses developed by Hofmeister (1868) and Snow & Snow (1952). It was shown that in the latter model all the variety of the spiral, whorled and multijugate patterns observed on botany could be obtained as steady regimes of the iteration. In this third article, several of the characteristic transient evolutions observed during the ontogeny are revisited. In the framework of the iterative system of Snow & Snow these evolutions can be reproduced, provided realistic initial conditions and time variations of the parameters are imposed.

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1. Introduction

In the first two parts of this work [Douady & Couder (1996a,b)] we investigated two iterative systems based on the principles proposed respectively by Hofmeister (1968) and by Snow & Snow (1952). We were mainly concerned with the steady regimes of these systems and did numerical simulations involving a very large number of successive iterations. Within this limit we showed that in the first system the formation of the spiral phyllotactic patterns could be obtained and understood. In the second we recovered the spiral modes but found new possibilities of pattern formation corresponding to the whorled and multijugate phyllotactic modes. We demonstrated that the system was controlled mainly by one control parameter: the logarithm of Richards' (1951) plastochrone ratio G in Part I and van Iterson's (1907) ratio Γ in Part II. We also discussed the role of the conicity of the apex, defined by the parameter $1/N$.

In itself, the investigation of the steady modes that we carried through was necessary for the understanding of the underlying principles of organization. In real plants, however, complete growth from seedling to final flowering only involves the formation of a limited number of elements (leaves, sepals, petals, etc.), so our previous results could be thought of as

an idealization with limited validity in botany. The complex situation created by the competition between different types of organization makes it important to examine the specific types of growth evolutions that exist during the ontogeny. The actual structure of the plant will result from the initial conditions and from the time evolution of van Iterson's parameter $\Gamma(t)$. As it will turn out, some modes that were defined as unstable can be observed in reality if the number of elements is limited.

There is a second reason to specifically investigate the transients: very generally, the most interesting problems in pattern formation are the breakings of symmetry. The transients are the regimes of the system during which they are broken. As we will see, these breakings of symmetry occur through archetypes of behaviours so that direct comparison with various botanical data is possible.

2. Running the Simulations

The simulations are done using the same technique as in Part II. The only difference is that instead of looking for the permanent regimes of the iterative system, we sought to reproduce the ontogeny of real plants. There is such a variety of possible transients

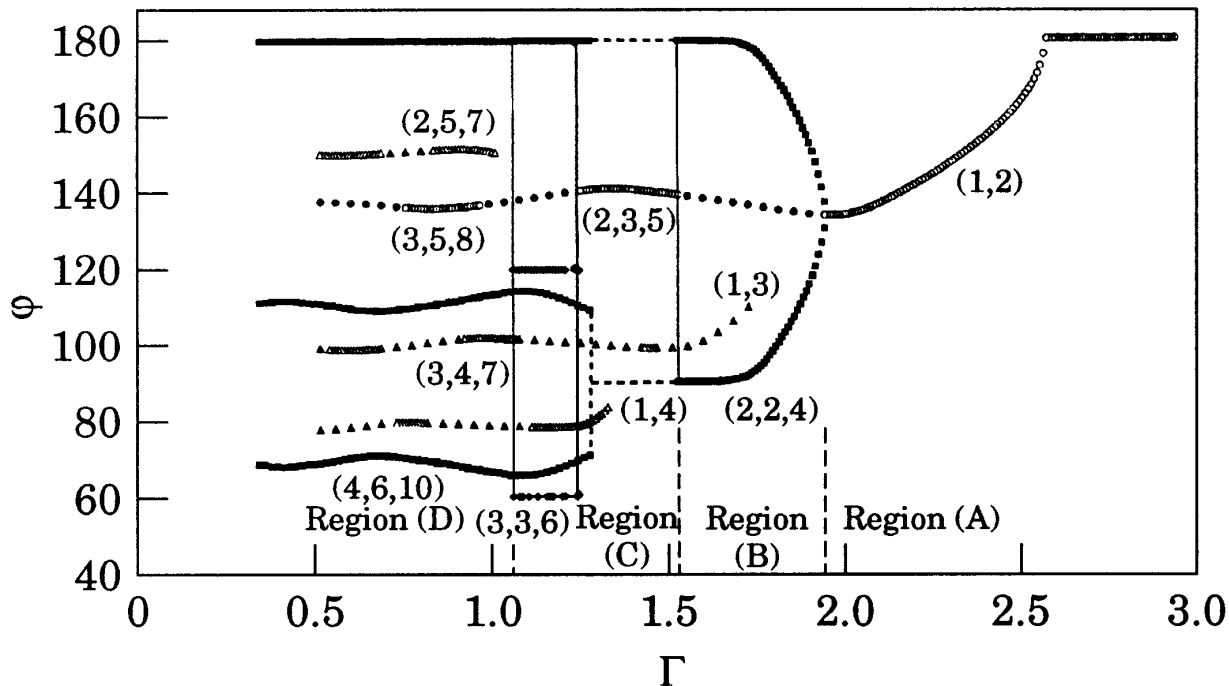


FIG. 1. The $\phi(\Gamma)$ diagram obtained with a conicity parameter $1/N=3$ and a stiffness $\alpha=8$ showing the different regions in which transient regimes are investigated here. The circles (○) are the solutions of the main Fibonacci branch. In the regions where the patterns are unstable the points are further apart and drawn in grey. The black squares (■) represent the decussate and bijugate modes. The triangles (△) are the first three accessory spiral branches corresponding to the series (1, 3, 4, ...), (1, 4, 5, ...) and (2, 5, 7, ...) respectively. Four ranges of values of Γ are defined in this diagram: (A) In the range $\Gamma > 2$ ($\omega > 122^\circ$) only the distichous or the spiral (1, 2) exist. (B) In the range $2 > \Gamma > 1.52$ ($122^\circ > \omega > 90^\circ$) there is coexistence of two different types of organizations: the main spiral and the decussate mode. (C) In the range $1.52 > \Gamma > 1.07$ ($90^\circ > \omega > 62^\circ$) there is a large number of possible modes: the spiral mode of the main series (2, 3, 5), two spiral modes of secondary series: (1, 3, 4) and (1, 4, 5), the trimerous whorls (3, 3, 6) and the bijugate modes (2, 4, 6). (D) is the domain $\Gamma < 1.07$ ($\omega < 62^\circ$) located below the limit of existence of the trimerous whorls. With the exception of the branch corresponding to the series (2, 5, 7, ...) the new possible organizations in this range were not shown here in order to maintain the clarity of the diagram.

that we limited ourselves to what we thought were the most interesting archetypes. There are two situations in which the formation of the successive botanical elements forms an almost steady regime of the iteration. This occurs in the vegetative growth because of the repeated formation of the leaves along the stem. It can also occur after floral initiation in the case of e.g. compositae where there is formation of a large number of florets. We will thus mainly examine the different types of transients leading to these two regimes.

2.1. SIMULATIONS OF VEGETATIVE MODES

In the investigation of vegetative growth we limited ourselves to the case where the conicity parameter is $1/N=3$ and the stiffness $\alpha=8$. The results obtained in Part II for this case are recalled in Fig. 1, which summarizes the various possible steady regimes. As it turns out, the various behaviours observed during transients are defined by the imposed temporal evolution $\Gamma(t)$ of van Iterson's parameter and by the symmetry of the initial conditions.

Figure 2 summarizes the types of $\Gamma(t)$ that have been used. It was stated in Part I that the growth of the seedlings or of new stems always starts at large G .

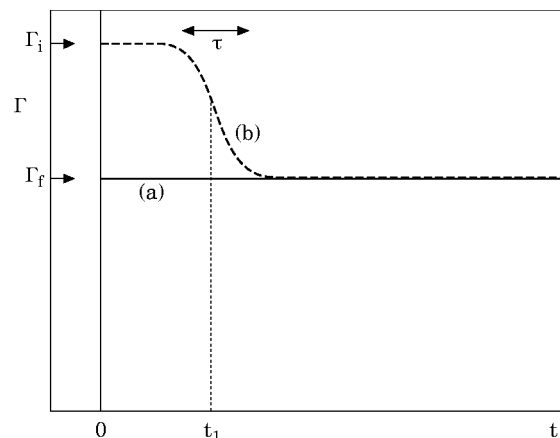


FIG. 2. Two types of the time evolutions $\Gamma(t)$ used in the present study of the vegetative modes. (a) The final value Γ_f is imposed directly. (b) It is reached through a tunable transient which leads from an initial value Γ_i to Γ_f . Both the time t_1 around which the transition occurs as well as its duration τ can be chosen at will (see text).

This general phenomenon is observed but has no particular interpretation in Hofmeister's model. In contrast, the corresponding decrease of Γ is easy to understand in the formulation of Snow & Snow. It simply corresponds to the fact that a new stem starts growing by the initial constitution of an apical meristem. During this process the apex forms from a small number of cells, thus having a very small initial size R_0 . On the other hand, the lateral primordia can only form with a minimal size d_0 which, roughly, appears to be fixed. As a result the growth always starts with a large ratio Γ . The initial decrease of this parameter simply corresponds to the initial increase of the diameter of the apex. Γ will then stabilize and remain approximately constant during the whole vegetative growth.

We thus imposed various $\Gamma(t)$ dependence going from an initial value Γ_i to a final constant value Γ_f . We particularly used the smooth variation provided by the law:

$$\Gamma(t) = \frac{(\Gamma_i + \Gamma_f)}{2} - \frac{(\Gamma_i - \Gamma_f)}{2} \tanh \frac{(t - t_i)}{\tau} \quad (1)$$

With this dependence the transition is defined by t_i , the time at which it occurs and by τ its duration (Fig. 2). We will examine successively transients leading to values of Γ_f located in different ranges of values of Γ labelled (A), (B), (C) and (D) in Fig. 1. As seen in Fig. 1, in these successive regions of decreasing values of Γ the number of branches corresponding to different possible organizations increases. In the case where several possibilities exist we will discuss the reasons why an organization belonging to a given branch is preferentially selected in botanical reality. This selection is related to the second ingredient of these simulations: the initial symmetry imposed on the system. In our simulations we will do so by imposing a number of initial elements placed in specific positions. For instance, two opposite initials can simulate the existence of two cotyledons at the start of the growth.

2.2. SIMULATIONS OF INFLORESCENCES

The second type of transition corresponds to the flower initiation. During this process there is usually a decrease in both the conicity (the apex becomes flatter) and $\Gamma(t)$. We could easily, in our simulation, impose a continuous change in conicity. The effect of conicity is essential only at large Γ , however, we do not think that its variation is an important parameter for most of the transients we will consider. So we limited ourselves to the investigation of the effect of various types of decrease of $\Gamma(t)$ at constant conicity.

More refined transients would be necessary only if a quantitative comparison with specific botanical measurements was to be done. We mainly investigated the case where there is no conicity ($1/N=1$) and stiffness $\alpha=8$. The steady regimes of this case were given in Fig. 10 of Part II (Douady & Couder, 1996b). We will discuss in Section 4 the $\Gamma(t)$ dependence used to simulate the transition to floral growth.

3. The transient regimes creating the vegetative modes

3.1. THE GROWTH INTO REGION A: DISTICHOUS GROWTH OR FORMATION OF (1, 2) SPIRALS

We will first examine all the cases where the value Γ_f of the vegetative regime is in region A of Fig. 1, (i.e. is larger than the threshold value of decussate growth). In this case there is only one possible organization at each value of Γ . The phyllotaxy will inevitably be distichous if Γ_f is above the first bifurcation and a (1, 2) spiral if it is below. We will examine successively by which transients this latter organization is reached respectively in the cases where there is initial axisymmetry, initial asymmetry or initial two-fold symmetry.

No initial conditions

In some particular cases, it is possible that an adventitious bud emerges directly from a stem without being linked to a previous leaf. In this case, it can be assumed that it corresponds to an initial condition without any previous elements.

Whenever Γ is above the decussate threshold, the second primordium will grow in a position distichous to the first one. If Γ is above the spiral threshold it will continue distichous growth, if it is below symmetry breaking will occur at the formation of the third primordium. This process is identical to that observed in the physical experiment shown in Fig. 6 and explained in Fig. 7 of Part I (Douady & Couder, 1996a). This process determines the direction of winding of the generative spiral. It will also generate a further growth in the main Fibonacci series which is the only path for an initial growth in region (A).

Asymmetrical initial conditions

Most adventitious buds however, grow with asymmetrical initial conditions. It has long been noted (Bravais & Bravais, 1837, 1839) that the first leaf is determined by the position of the subtending leaf and of the stem. But these two elements play an asymmetrical role and the first leaf appears to be more strongly repelled by the stem than by the subtending

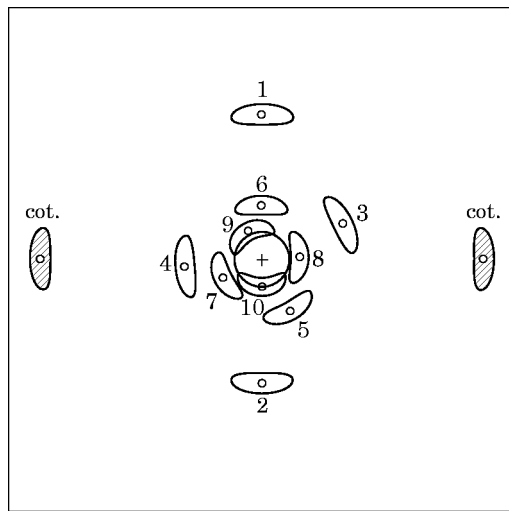


FIG. 3. Simulation of a transient leading to spiral growth in a dicotyledon seedling. This disposition was obtained in a simulation with $1/N=3$ and $\alpha=8$. A transient where $\Gamma(t)$ was decreased from $\Gamma_i=2.25$ to $\Gamma_f=1.9$ (or from $\omega=140^\circ$ to $\omega=115^\circ$) in five particles was used to speed up the transition. Two symmetries are successively broken: the first is the non-simultaneous formation of elements $n^\circ 1$ and 2 (the simultaneous formation is not possible as Γ is above the threshold for decussate mode). The second is the choice for element $n^\circ 3$ to be on the right or left of $n^\circ 1$, which gives the direction of the winding of the generative spiral.

leaf. This asymmetry of the initial conditions of growth of the adventitious buds also exists for plants normally presenting decussate phyllotaxy: it has been observed by Weisse (1894) that the adventitious buds of a decussate stem can be spiral. Had the effect of the stem and of the subtending leaf been identical, the adventitious bud would have started directly in a decussate state (see below).

If the first leaf of the new shoot is only repelled by the main stem, it will grow in the position opposite to it. The second leaf will have the position of the third in the previous case, either starting a distichous growth or a spiral one depending on the value of Γ . Such dispositions are observed in, e.g., poplar trees (*Populus nigra*). Further growth will be identical to that described above.

If the first leaf of the new stem is repelled unequally by the stem and by the subtending leaf, then it will be this first leaf that will be able to break the symmetry and start a spiral growth.

Initial two-fold symmetry

In the initial growth of a dicotyledon seedling, the presence of two identical cotyledons gives an initial two-fold symmetry to the system. If the parameter does not have the value corresponding to the range of existence of the decussate mode there will be transition towards a spiral mode. This transition is well documented in botany. For instance Medford

et al. (1992) give a section of the position of the first four primordia in a seedling of *Arabidopsis*. In order to reproduce this transition in our simulation, we placed two initial elements in a symmetrical position and, after a transient, reached a value for the control parameter in the range of spiral growth above the value for the decussate mode. In this situation there is a characteristic behaviour which is clearly observed in Fig. 3. Both the first two elements form at right angles to the cotyledons as in a decussate mode. They do not, however, form simultaneously. In the case shown in Fig. 3, the first one appeared on the upper side of the figure and the second on the lower side. This has already broken the symmetry in time. It is easy to see that the different available positions for the formation of the third primordium are no longer the positions at right angles to the previous two elements, but closer to the older one (Fig. 3). The third element has the choice between two positions to the right and left of the element $n^\circ 1$. This will again break a symmetry and select the direction of the winding of the spiral pattern. The fourth primordium is close to the position it would have had in a decussate mode, but the pattern has in fact started to spiral. These positions of the third and fourth primordia are typical of the transients observed in many seedlings (e.g. Medford *et al.*, 1992). The position of the particles are also in very good agreement with those drawn by Lyndon (1990) (see his fig. 12-1).

The reverse transition from a spiral mode to a distichous mode

In general, during the growth of a plant the phyllotactic order tends to increase, because of a decrease in $\Gamma(t)$. Reverse evolution of the phyllotaxy is, however, observed in several cases where a chemical treatment is applied to the plant. This was first observed by Schwabe (1971) after a treatment of *Chrysanthemum* by Tri-iodobenzoic acid. More recently, Marc & Hackett (1991) found that Gibberelin applied to *Hedera helix* L. could induce a reverse transition from a spiral to a distichous growth. They demonstrated clearly the relation of this transition in which the divergence angle grows from 140 – 180° , with an increase of the sustaining ω as well as with an increase in radial displacement (or of the plastochrone ratio). If we impose in our simulation an increasing value of $\Gamma(t)$ we find a similar return to the distichous mode. It is worth noting that a similar treatment of other plants can lead to opposite effects. In *Xanthium*, Maksymovych & Erickson (1977), using gibberelic acid, obtained an increase of the phyllotactic spiral order from (2, 3) to (3, 5) and demonstrated

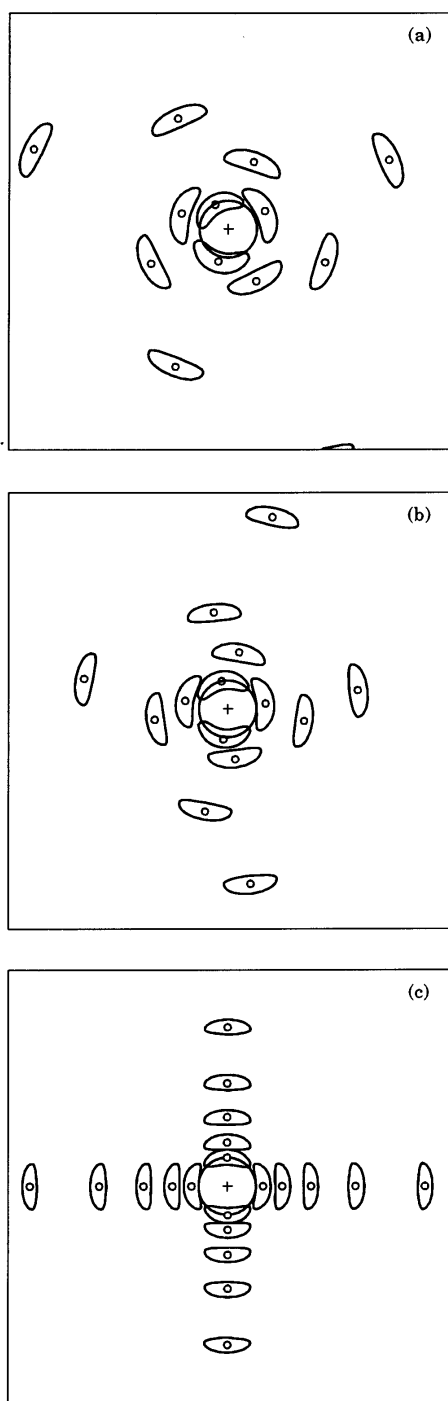


FIG. 4. The patterns obtained with folioid elements ($1/N=3$) and stiffness $\alpha=8$ for three values of Γ in the range of the continuous transition from the spiral (1, 2, 3) to the decussate structure (2, 2) structure. (a) $\Gamma=1.9$ ($\omega=115^\circ$): the pattern is a normal spiral mode (1, 2, 3). (b) $\Gamma=1.87$ ($\omega=113^\circ$) The pattern has become an anomalous spiral mode in which the time intervals δt are no longer exactly equal and the divergence takes successively a normal and an anomalous value. The pattern can also be seen as a decussate pattern in which the positions of the elements oscillate around their ideal position. (c) $\Gamma=1.56$ ($\omega=93^\circ$) The pattern is a decussate mode, two elements appearing simultaneously at 180° from each other.

the link of this evolution with a decrease of both the plastochrone ratio and the conicity.

3.2. THE GROWTH INTO REGION B: THE COMPETITION BETWEEN THE FIBONACCI SPIRAL AND THE DECUSSATE ORGANIZATIONS

Transients leading to the vegetative value Γ_f can lead in region B where there is coexistence of two main modes: the spiral mode (2, 3) of the main series and the decussate (2, 2) mode. Since the early studies of Schimper (1830), Braun (1831, 1835), Dutrochet (1834) and Bravais & Bravais (1837, 1839) the relationship between the whorled modes and the spiral ones has been a much debated question. Our results in Part II (Douady & Couder, 1995b) exhibit the coexistence of the two types of organizations. We have shown that the main factor that determines which of them is most stable is the shape of the apex. The stability of the decussate mode is strongly increased by the effect of conicity. This seems to be confirmed by a rapid review of published data about decussate apices.

Historically, one of the reasons for the apparent complexity of the problem of the relation of the spiral with the decussate mode is the existence of various types of imperfect whorled modes. Schoute, in a series of four articles (1922, 1925, 1936, 1938), specifically investigated the relationship between perfect whorls and imperfect ones. He demonstrated that a continuous deformation of the spiral pattern could lead to the decussate one. This is reflected in our simulations by the continuity of the transition from the mode (1, 2, 3) to the mode (2, 2). A result of this continuous transition is that these imperfect whorls are observed in the simulation as forming steady regimes in a finite range of values of Γ .

The formation of the vegetative decussate modes from two cotyledons

In cases where the conicity conditions are met, the transients leading to a decussate mode depend on the symmetry of the initial conditions. Obviously the situation of a seedling where there is initial two-fold symmetry caused by the presence of two cotyledons is ideal for growth in the decussate mode. If the growth parameter is in the range where this mode is selected, then there is direct formation of a perfect and stable decussate mode.

The formation of the vegetative decussate modes from an asymmetrical situation and the oscillating decussation

In contrast, if the initial situation does not have two-fold symmetry, the formation of the decussate

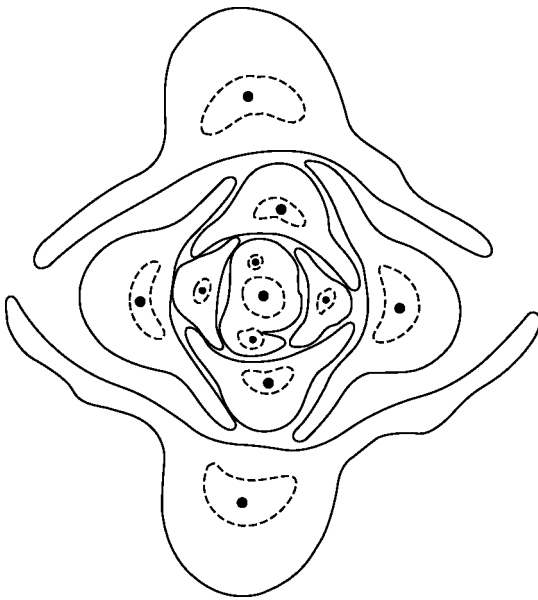


FIG. 5. The "oscillating decussate" mode as observed in a cut of an apex of *Epilobium hirsutum* [After Fig. 9(a) from Snow & Snow (1935)].

mode occurs through a bifurcation and a transient regime is observed. This is the situation observed when the initial growth is spiral and can also be the case for the axillary buds if the influence of the stem and of the subtending leaf are asymmetrical. Strict decussation can thus be reached.

As shown in Fig. 1, however, the transition from a spiral structure (1, 2, 3) to a decussate mode (2, 2) is not abrupt, but intermediate states exist in a finite

range of values of Γ . If the parameter is in this range it is possible to obtain a steady regime of what can be called an imperfect decussation. Figure 4 shows three patterns obtained for decreasing values of Γ in this region of transition. For the larger value [Fig. 4(a)] the pattern is a spiral mode. For the intermediate value [Fig. 4(b)] it can be described either as a spiral mode having a disturbed set of parastichies or as a decussate mode in which the positions of the successive primordia oscillate around their normal positions. Finally, the third pattern [Fig. 4(c)] corresponds to the perfect decussation.

Snow & Snow (1935), in some transients between an unstable spiral and a decussate mode, found a type of organization that they called "oscillating decussation". Their drawing of the apical disposition of the primordia is reproduced in Fig. 5. A comparison with Fig. 4(b) shows that this pattern is identical to that which we obtained.

Such imperfect modes have more often been described in botanical literature by the resulting disposition of leaves around a mature stem. An early drawing of an imperfect decussate mode as observed in *Acer campestre* was drawn by Dutrochet (1834). It clearly shows that the leaves of the same whorl do not have their insertion strictly at the same height. This shift has a very characteristic evolution in the successive pseudo-whorls. Bravais & Bravais (1839) also described anomalous decussation in *Oxalis corniculata*, where they found that the angle of two leaves of the same whorl could be smaller than 180° (they say 137.5°), while the

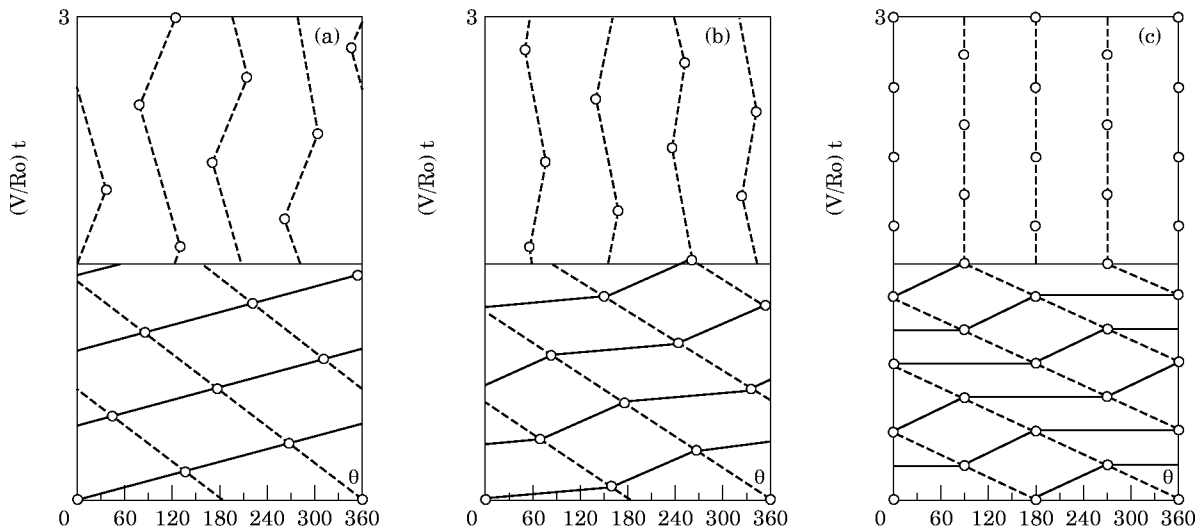


FIG. 6. The positions of the leaves as they would be observed on a cylindrical stem if they retained the angular and time repartition found in our simulation in the three cases shown in Fig. 4 [(a) $\Gamma=1.9$ (b) $\Gamma=1.87$ (c) $\Gamma=1.56$]. In order to visualize the continuous deformation permitting this transition, two types of link between the elements are drawn on each pattern. In the lower part of the patterns the links are drawn with the conventions used for a spiral mode, here the generative spiral (continuous line) and the parastichies of order two (dotted lines). Note how the generative spiral loses its meaning in the decussate situation. The transition is thus seen from left to right as a transition from a perfect spiral mode to a very distorted one. In contrast, in the top part of the patterns the links were drawn to exhibit the decussate character. We go from left to right, from a very distorted decussation to a perfect one.

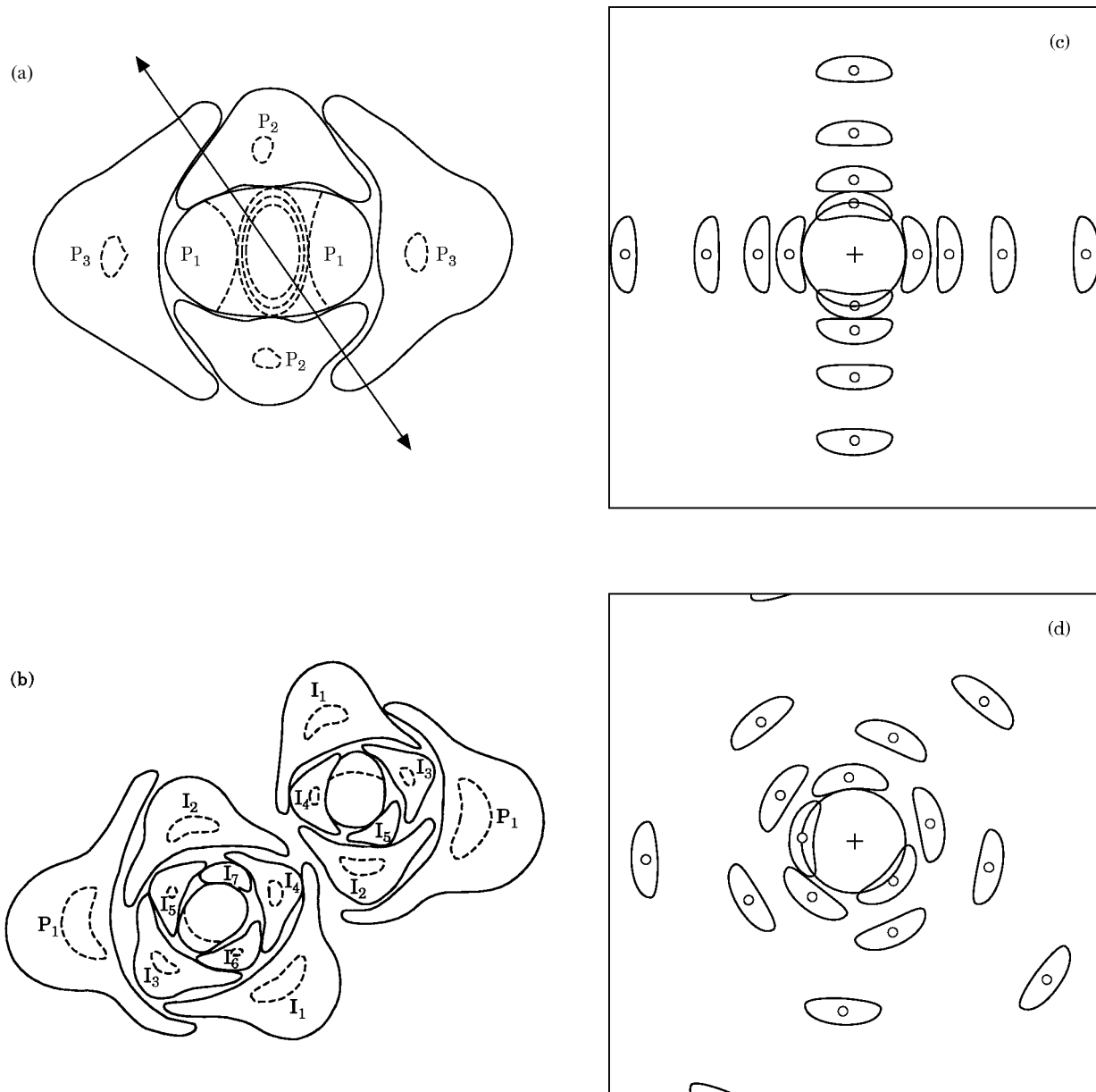


FIG. 7. The experiment of Snow & Snow: (a) A cut of a normal decussate apex of *Epilobium hirsutum*. The microsurgery operation consisted of slitting this apex diagonally along the arrow. [From Fig. 2, Snow & Snow (1935)]. (b) One of the results of this operation was the formation of two independent stems with spiral phyllotaxy [from Fig. 4(a), Snow & Snow (1935)]. (c and d) Two patterns obtained at the same value $\Gamma = 1.64$ ($\omega = 97.8^\circ$) for $1/N = 3$, $\alpha = 8$ showing the coexistence of two different phyllotaxies, depending upon the initial imposed symmetry. (c) With symmetrical initial conditions a decussate mode (2, 2) is obtained. (d) With asymmetrical initial conditions a spiral mode (2, 3) grows.

angle with the first leaf of the next mode was 85° (instead of 90°). They observed the same dispositions in the prophylls of many dicotyledons such as *Chrysanthemum indicum*, *Fragaria*, and *Ranunculus*. For comparison with these data we have assumed that the primordia formed on the model apices shown in Fig. 4 have matured and are now arranged on a cylindrical stem. We assume that the secondary elongation of the stem is constant and that the angular positions of the elements do not change

throughout the maturation. We then obtain the disposition of the leaves by placing them according to their successive divergence angle on a strip of width 2π representing the unrolled cylinder, the height of their insertion along the z axis being proportional to their time of formation. The new drawings [Fig. 6(a–c)] show the position of the leaves around a stem that would be observed for the three cases shown in Fig. 4. The intermediate pattern [Fig. 6(b)] can be described as a spiral mode in which successive parastichies have

slid relative to each other. It can also be described as a decussate mode in which the positions of the successive primordia oscillate around their normal positions. Comparison of Fig. 6(b) with the drawings of Dutrochet (1834) and those of Schoute (1938) shows the identity of the disposition of the successive imperfect whorls found in the simulation with the botanically observed ones.

The coexistence of the decussate and the spiral modes: the interpretation of an experiment by Snow & Snow

A decisive experiment from a conceptual point of view was carried out by Snow & Snow (1935). They initiated a series of works in which they analysed the effects of perturbations created by microsurgical operations of the apex. In particular they chose *Epilobium hirsutum*, a plant normally having a decussate phyllotaxy, and slit the apex diagonally [Fig. 7(a)]. It resulted in the growth of two independent shoots. In each of these shoots, the usual symmetry imposed by previous elements had been broken so that a spiral growth ($i=2$, $j=3$) was observed in most cases [Fig. 7(a)]. Richards (1951), re-examining the drawings of the apices cuts in the article by Snow & Snow (1935), showed that this change in the phyllotaxy occurred even though there had been no change in the plastochrone ratio. This demonstrated the possibility of obtaining either decussate or spiral phyllotaxy under the same conditions by a simple change of the symmetry of the initial conditions. We investigated this possibility in the case ($1/N=3$, $\alpha=8$) where we chose a value $\Gamma=1.64$ ($\omega=97.8^\circ$) in the range of existence of the decussate mode. We performed two simulations. In the first we imposed two initial elements opposite each other playing the role of cotyledons and obtained the decussate growth [Fig. 7(b)]. In the second we reproduced the position of the remaining primordia in half of the slit apex by imposing two initial elements, separated by a plastochrone and at 90° from each other. With these initial conditions we obtained a (2, 3) spiral phyllotaxy [Fig. 7(c)]. Richards (1951), discussing the Snows' result, remarked that if, after the operation, the plant was left to grow for long enough, a return to the decussate disposition was observed. In our simulation the spiral mode is also a transient and a return to the decussate mode is observed if a large enough number of iterations is done. This reflects the fact that for the chosen values of the parameters the decussate phyllotaxy is the most stable mode [see Part II (Douady & Couder, 1996b)]. In other terms, the conicity and the plastochrone ratio fix the most stable phyllotactic mode but a different

organization can be observed transitorily, if it is forced by the initial conditions caused by the "history" of the plant.

3.3. THE TRANSIENT REGIMES LEADING BELOW THE REGION OF DECUSSATION (REGION (C))

Because of the high phyllotactic orders they reach in their inflorescences the compositae have been widely investigated. In particular Weisse (1897) and Schoute (1938) did extended statistical works on the observed organizations of capitulae of *Helianthus annuus*. The former found that out of 141 specimens, 133 were organized in the main Fibonacci series and 6 in the Lucas accessory series. The latter examined 319 specimens and found most of them in the main series, 46 in the Lucas series, nine in a bijugate organization and two in the second accessories series starting with (1, 4, 5).

Measurements on various specimens of *Helianthus annuus* confirm the previous observations: in each specimen there is a continuity of the phyllotaxy. The specimen having capitulae in the Fibonacci, Lucas or second secondary series have leaves disposed along the stem with divergence angles ϕ near 140° , 99° and 80° , respectively. Similarly, specimens with bijugate inflorescences also have bijugate leaves. This means that the transition to a given branch of solutions occurs early in the growth. The variety of the phyllotactic modes of the inflorescences reflects the variety of possible transitions at the beginning of the vegetative growth.

The possibility for sunflowers to reach several types of organization derives from the fact that their seedlings initially grow in the decussate mode and that the decrease of Γ leads to a value Γ_f which is in region (C) of the $\phi(\Gamma)$ diagram of Fig. 1. In this zone five possible organizations exist. The first one is the spiral (2, 3, 5) of the main Fibonacci branch. The second and third are two spiral modes (3, 4) and (1, 4, 5) situated, respectively, on the first and second accessory series. The fourth is the bijugate organization 2 (1, 2). The fifth is the trimerous (3, 3) whorled mode. A transition to a value of Γ_f situated in region (C) can thus lead in principle to one of these five modes of organization. It is remarkable that all these organizations are actually observed in sunflowers. In the first four cases the initial transient will fix the whole phyllotactic system of the plant. The statistical results point to the fact that their respective initiations do not have similar probabilities. As we will see below, this is observed in our simulations as only a few of the possible transients can lead to the rarer of these organizations. Finally, we can note that the fifth possibility, the transition to a trimerous

mode, is occasionally observed along sunflower stems but that in this case the later decrease of Γ leads to a return to a spiral mode. [The transition from a trimerous whorled mode to a trijugate pattern, which is, in principle, possible as the transition from a decussate to a bijugate mode (see below), has not been observed]. A detailed analysis of the transient modes observed in *Helianthus annuus* will be given elsewhere (Couder, unpublished).

The simulation of the transient leading from a decussate mode to one of the spiral modes

We started these simulations with two initial opposite elements and applied various types of evolutions of $\Gamma(t)$ from an initial value $\Gamma=1.6$ ($\omega=95.2^\circ$) in the decussate range (B) to $\Gamma=1.2$ ($\omega=70.2^\circ$) in the range (C). The results showed that in a large majority of cases there was a transition from a (2, 2, 4) mode to a (2, 3, 5) mode and thus a return to the main Fibonacci branch. The high probability of this transition is related to the fact that the mode (2, 3, 5) is among the stablest in this range [as it is very close to a hexagonal piling, see Part II Douady & Couder (1996b)].

The transition to a lucas series

We examined transients leading to a slightly smaller value of Γ_f . We systematically repeated these simulations, changing step by step the values of the time of occurrence and of the duration of the transient [t_1 and τ in eqn (1)]. As above, the usual evolution of the pattern is a transition to the main spiral branch. Exceptionally, however, for very specific values of the parameters other transitions were obtained. These included transitions to the bijugate mode to be examined below, transition spirals of the Lucas series (3, 4, 7), and even transitions to the second accessory series (4, 5, 9). The specificity of the required time evolution of $\Gamma(t)$ needed to trigger these transitions seems to be the explanation of their scarcity in nature. These transitions will be examined in Couder (unpublished).

THE TRANSITION TO THE BIJUGATE MODES

We had shown in Part II (Douady & Couder, 1996b) that there existed a whole continuous branch of bijugate modes built on the model of the main Fibonacci branch but having two generative spirals. The $\phi(\Gamma)$ dependence of these modes is shown in Fig. 1. In the low Γ region the bijugate organization is stable and this branch is easy to follow during a steady decrease of the parameter. The same is not true in the region where there should be transition from

decussate to the (2, 4) spiral mode. In this range of values of Γ there is a gap in which these solutions are unstable and where a transition to the main spiral mode (2, 3) normally occurs. This instability however does not prevent the observation of the bijugate branches: for fast decreases of Γ that are compatible with botanical ones (e.g. a decrease from $\Gamma=1.55$ to $\Gamma=1.21$ in 10 particles) the instability does not have time to grow and the gap of instability is crossed. The formation of two opposite elements at each period is thus maintained and the system develops into a bijugate spiral that can then be observed down to very low values of Γ (see below, Section 4.1). It is worth noting that in plants, as the unstable region is crossed, the two opposite elements are not usually formed exactly simultaneously. This transition from a decussate mode to a bijugate one, rare in sunflowers, is more likely to appear in the inflorescence of plants which have usually decussate leaves. Such bijugation is found systematically in *Dipsacus silvestris* Mull.

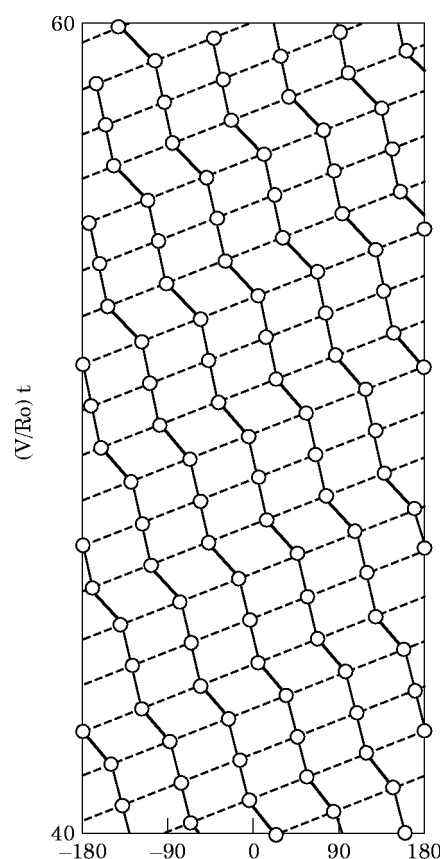


FIG. 8. The transient mode between the spiral mode (2, 3) and the tricussate mode (3, 3) in the case ($1/N=1$, $\alpha=8$) for $\Gamma=1.5$. Positions of the leaves as they would be observed on a cylindrical stem if they retained the angular and time repartition found in the simulation. Note that the distortion affects only one of the sets of parastichies (of order 5), while the other set (of order 3) is unperturbed.

The transition to the trimerous whorled mode

If the transition to the trimerous organization is an exception in *Helianthus annuus*, it is common in the vegetative region of many other plants. This transition has many similarities with the transition to the decussate mode investigated above.

In a perfect trimerous mode, the angle between leaves of the same node is 120° . It was first observed by Bravais & Bravais (1839) that these modes could be imperfect. Two of the angles of a node are larger (they say of the order of 137.5°) and the third one is smaller (of the order of 85°). They also observed that the position of this smaller angle in successive whorls formed a spiral around the stem and this observation suggested a relation with the spiral mode. We examined the transition region between the spiral mode (2, 3) and the tricussate window. For $1/N=1$ and $\alpha=8$ it corresponds to the region around $\Gamma=1.5$ [see Fig. 11 of Part II (Douady & Couder, 1996b)]. In our simulations, in contrast with the transition to the decussate mode, it does not form a steady intermediate regime but allows a slow transition from one mode to the other. Figure 8 shows the resulting position of the leaves around a stem during such a transition. This disposition is identical to that described by Schoute (1938) after Bravais (1839).

We can remark on Fig. 8 (as previously on Fig. 6) that the imperfect spiral modes are characterized by the perturbation of only one of the sets of parastichy while the other remains undisturbed. This is a general feature of the disturbed spiral patterns. It was probably this characteristic that led Plantefol (1948) to single out one of the parastichy sets, which he called the foliar helices, and to disregard the other. Unfortunately, in doing so the link of the system with the Fibonacci series vanishes.

Transition from a decussate to a trimerous whorled mode

In the stems of many plants a transition between two whorled modes of successive order can be seen. The transition can involve the existence of several intermediate anomalous nodes [e.g. in vervain (*Lippia citriodora*)] or can be extremely fast: direct transitions from (2, 2) to (3, 3) are observed in the first whorl of leaves in rose laurel (*Nerium oleander*). We sought to reproduce such transitions by imposing different types of evolutions of $\Gamma(t)$ leading from the range of stability of the decussate mode to that of the tricussate mode. These transitions are possible but only for such specific values of τ and t_1 in relation (1), so they should be rare events. The direct transition from a whorled mode to another is difficult because

the symmetry of the initial mode does not create favourable initial conditions for the next. For this reason it is surprising that in some species such transitions are frequent and rapid, being completed in approximately two or three whorls. This probably points to a limit of validity of our model and will be discussed in Section 5.

4. The formation of high order modes in floral initiation (region D)

4.1. THE TRANSIENT LEADING TO THE FORMATION OF HIGH ORDER SPIRAL MODES

In the simulation of the first article (Douady & Couder, 1996a) we showed that varying the value of the control parameter $G(t)$ led naturally to the formation of high order spirals and could explain the structure of, e.g., sunflower heads. This was also in good agreement with the continuity of the phyllotaxy along the main Fibonacci branch clearly demonstrated by measurements of $\phi(\langle G \rangle)$ done on cuts of apices by Williams (1975) in flax (*Linum Lusitanum*), by Erickson & Meicenheimer (1977) on the evolution of $\phi(\langle G \rangle)$ in *Xanthium* during floral evocation, or by Maksymovych & Erickson (1977).

The diagrams $\phi(\Gamma)$ that we obtain with the Snows' criterium, however, always show at low Γ transitions to whorled modes of high order. We must, therefore, examine whether the possibility of having a continuous transition to high order spirals still exists. The main factor of stabilization of the spiral modes is the fact that the growth creates a rapidly varying $\Gamma(t)$ (through both an increase in the size of the apex and a decrease in the primordia size). There is an important difference between the spiral modes and the whorled modes from this point of view. As shown in Part II (Douady & Couder, 1996b) there is no continuity from a whorled mode to another. Each corresponds to a given symmetry and this symmetry has to be broken before the next whorled mode is reached. This process requires a minimum number of primordia (as pointed out above for the transition from the decussate to the tricussate mode). In contrast, as discussed in Part I (Douady & Couder, 1996a), the spiral growth undergoes smooth transitions from one Fibonacci mode (i, j) to the next $(j, i+j)$. If the plant's growth produces a constant decrease of Γ , the system will not remain long enough in a given range of values of Γ to allow a transition to a whorled mode.

In order to produce a realistic transient representing the growth of a sunflower, we imposed, in the case of $1/N=1$ and $\alpha=3$, a specific evolution of $\Gamma(t)$.

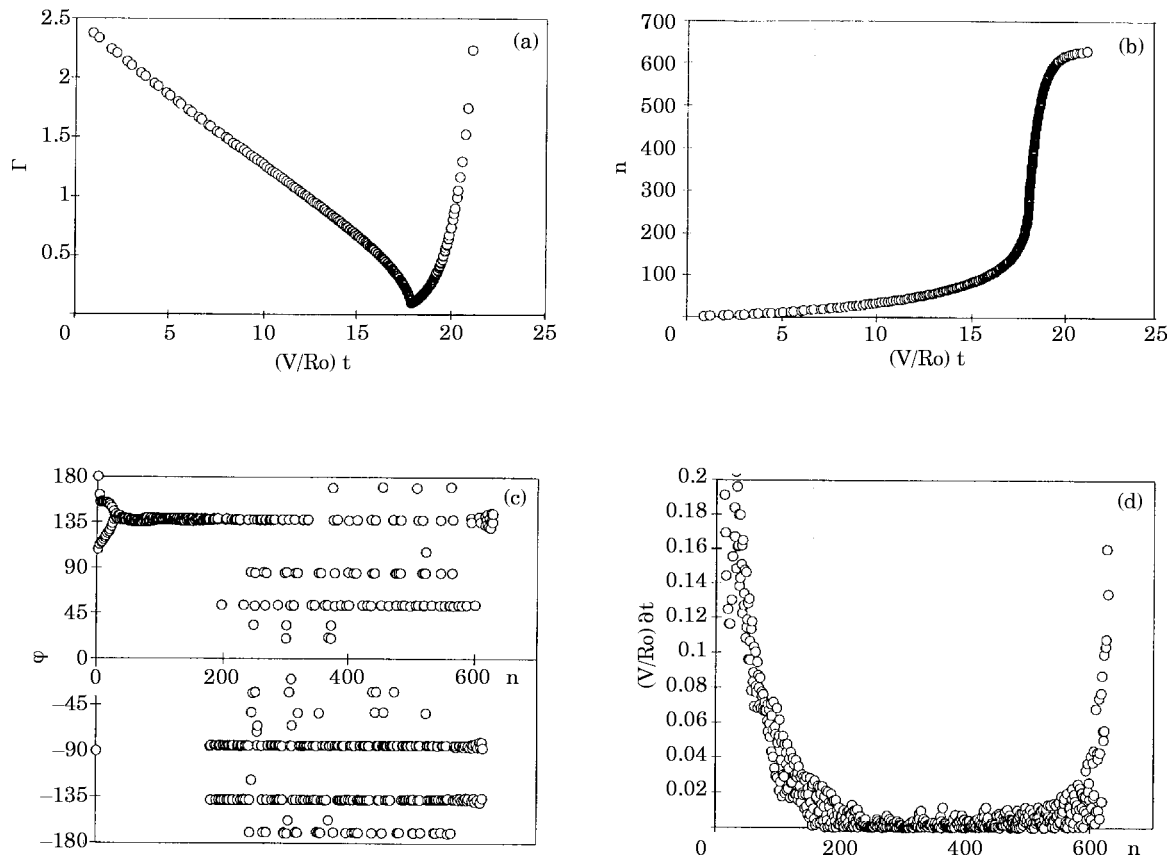


FIG. 9. Simulation of the build-up of the inflorescence of compositae with the Snow & Snow type of simulation. (a) The imposed parameter $\Gamma(t)$ is first a decreasing function of time (from $\Gamma = 2.4$ to $\Gamma = 0.096$) so as to simulate the transition from vegetative to floral growth. $\Gamma(t)$ then increases back (from 0.096 to 2.2) simulating the terminal growth of the centre of the inflorescence. (b) The resulting number of elements as a function of (adimensionalized) time. The decrease in Γ lasted 250 particles and the increase 380 particles. (c) The obtained divergences $\phi(n)$ showing the initial decussate mode ($\phi = 180$, and $\phi = \pm 90$), then the evolution into a spiral. In the region of small Γ (or G) the presence of many permutations is observed. They are similar to those observed in Part I (Douady & Couder, 1996a). (d) The resulting plastochrone ratio $G(n)$. The permutations in the orders of appearance correspond to fluctuations of G close to zero. This is different to the situation in Part I (Douady & Couder, 1996a) where G was imposed and therefore regular (In Part I Γ , if it had been measured, would have been similarly fluctuating).

During the growth from seedling to the border of the inflorescence $\Gamma(t)$ first decreases before increasing again during the completion of the inflorescence from border to centre. The time dependence $\Gamma(t)$ shown in Fig. 9(a) was chosen to first decrease as $(t - t^*)^{1/2}$, before increasing again as $\exp(t)$. These particular laws were chosen because they produce a smooth variation of $\Gamma(n)$ close to that used in Part I (Douady & Couder, 1996a). Figure 9(b) shows the total number of elements as a function of time and Fig. 9(c) the resulting divergences $\phi(n)$. After a period of decussation the pattern undergoes a transition to a regular spiral pattern characterized by a convergence of ϕ towards Φ . When the parameter Γ becomes very small the angle between successive elements ϕ is observed to take successively several values. This corresponds to the process described in Part I and is caused by a disorder in the time of formation of the elements. It is worth noting that in Part I the

periodicity was imposed so that this disorder could only result in strict permutations of the order of formation. Here there is no imposed periodicity, so there are also wide fluctuations of the times of appearance. This is clearly seen in Fig. 9(d) which shows the observed values of $G(n)$: in the range of small G the observed fluctuations are caused by this disorder. It is worth noting that in the presence of such permutations, linking the elements in their order of formation leads to running back and forth around the apex so that there is no more generative spiral. Inspection of the geometry of the resulting pattern (Fig. 10), however, shows that it is only weakly disturbed and that the parastichies are still easy to observe. The pattern obtained in this simulation is as close as that obtained in Part I to the actual structure of a sunflower head.

We can generalize this remark to other secondary spirals of the pattern. Let us consider a mode, say

(5, 8), which has been built through the sequence of transitions $(1, 2) \rightarrow (2, 3) \rightarrow (3, 5) \rightarrow (5, 8)$. These previous states have contributed to its organization so that it remains possible, if the system has not been affected by noise, to draw on the pattern regular spirals of order 1, 2, 3 as well as the actual parastichies (the classically defined generative spiral being amongst these, the spiral of order 1). But these spirals which are a memory of the previous states have lost their dynamical role as they link elements that are spatially too far away from each other to have a direct influence on the position of each other. In reality the system is submitted to noise and when it reaches high order modes these artificial spirals vanish. The generative spiral is actually the most fragile and is the first to disappear. This does not affect the existence of the dynamically active parastichies. In other terms, in the range of small Γ , the formation of the parastichy do not result from global interactions but rather from local ones induced by nearest neighbours interactions. This is in agreement with the ideas of Church (1904) who believed in a dominant role of the parastichies.

As noted above, the system can undergo, in the early stages of the build-up of the vegetative spirals, a transition to another organization. In these cases the system will remain on the same branch of solutions during its later evolution. So, during the further decrease of Γ , as in the botanical reality, we will obtain for instance a Lucas inflorescence from an initial Lucas vegetative mode or a bijugate inflorescence from a bijugate vegetative mode. A pattern of

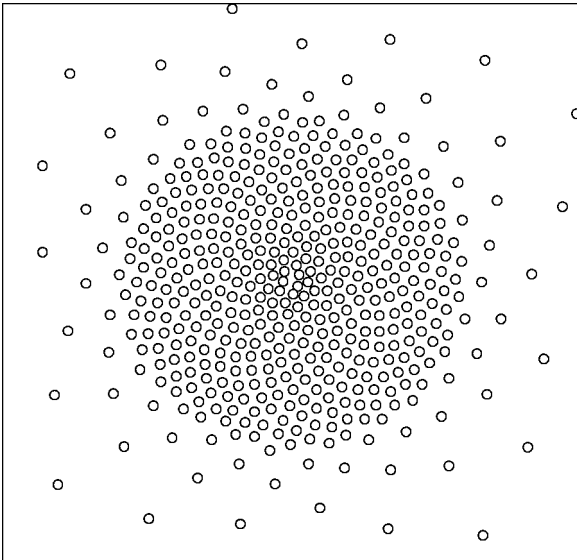


FIG. 10. Aspect of the pattern resulting from the transient described in Fig. 9. The maximum order of the parastichies at the periphery is (34, 55). As in Part I, in spite of the disorder in the time of formation of the elements [Fig. 9(c)], the resulting pattern appears regular.

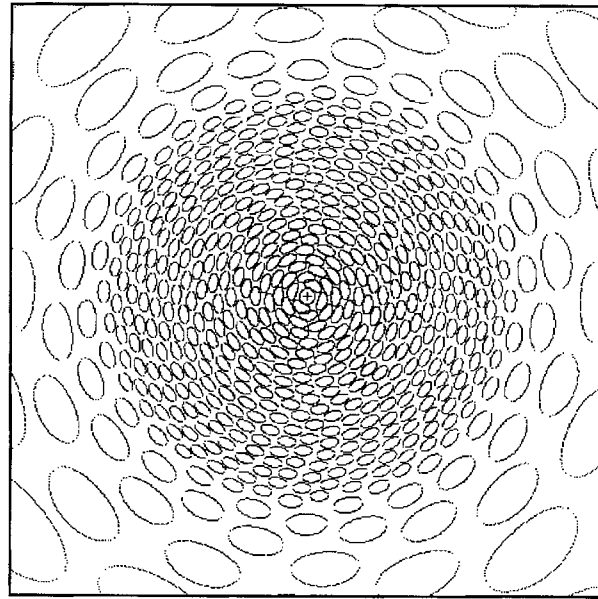


FIG. 11. A bijugate inflorescence obtained in the simulation with $(1/N=3, \alpha=8)$. This value of conicity was chosen because of the possibility of having a stable decussate initial mode in the vegetative range. The simulation was started in this mode and a time dependence $\Gamma(t)$ of the type used for Fig. 9 was then applied. In spite of the existence of an unstable region (see Fig. 1) the system can still undergo a transition from decussation to bijugation and the winding proceeds on the bijugate branch. The maximum phyllotactic order at the periphery of the inflorescence is (26, 42). As soon as the mode had become bijugate, the conicity could have been reduced, and the pattern would have remained bijugate. This would have produced elements more in the shape of the primordia in a compositae inflorescence.

this latter type obtained starting from an initial decussate mode is shown in Fig. 11.

4.2. TRANSIENT REGIMES CREATING HIGH ORDER WHORLED MODES (I, I) OR SPIRAL MODES OF THE ACCESSORY SERIES (I, I+1)

In the preceding sections we have shown that the continuity of the various spiral branches is essential in allowing the system to evolve continuously on a given branch, even though, transitorily, it may not be in the most stable mode for the local value of Γ . Now we can ask the reverse question: are the most stable modes sometimes observed?

As shown in Fig. 4(b) of Part II, if, in our simulation, the previous iterations have led to the formation of a whorled mode (3, 3), a continuous decrease of Γ will produce a sequence of successive transitions $(3, 3) \rightarrow (3, 4) \rightarrow (4, 4) \rightarrow (4, 5) \rightarrow (5, 5)$. In this sequence, the natural transition from a whorled mode (i, i) generates the spiral mode $(i, i+1)$ of an accessory series. Two such successive modes (5, 5) and (5, 6) are shown Fig. 12(a) and (b). These modes were obtained in Part II (Douady & Couder, 1996b) by iterations involving an extremely

large number of elements, a situation which is botanically unrealistic.

Reviews on the variety of observed phyllotactic modes can be found in Williams (1975) and Jean (1994). They show that the occurrence of the modes (i, i) and $(i, i+1)$ is frequent in inflorescences and flowers. Typical examples of such modes were first listed by Church (1904). He observed transitions between them in e.g. *Echinopsis tubiflora*, *Raphia ruffia*, *Lycopodium Selago*. Similarly, the survey done by Fujita (1938) gives a distribution of the pattern frequencies in a hundred species of angiosperms. It shows an important incidence of spiral orders that he calls "other accessory series". These spiral orders are precisely those in which the two parastichy orders differ by a unity e.g. (3, 4) or (4, 5), etc. Fujita states that they are particularly frequent in the families Salicaceae and Araceae.

It is worth noting that the various types of corn (*Zea mays*) cobs can be analysed as having such types of phyllotaxy. They always exhibit an even number of parallel rows of seeds. The number of these rows ranges from 8 to 22, depending on the cobs, the growth conditions, and the maize variety. It is remarkable that whenever the number of rows is 8, 12, 16 or 20 these rows form orthostichies. But with 10, 14 or 18 rows the structure is weakly spiralled. This difference is easy to understand taking into account the fact that the element is formed of two neighbouring seeds. Take the case where 12, 16 or 20 rows are observed. These are in fact whorled phyllotactic modes (3, 3, 6), (4, 4, 8) or (5, 5, 10). Because of the tightness of the packing the successive whorls form 6, 8 or 10 orthostichies. Each primordium forming two seeds, 12, 16 or 20 rows are seen by the eye. Similarly the cases with 10, 14 or 18 rows correspond to spiral arrangements of the pairs of seeds with parastichy order (2, 3, 5), (3, 4, 7) and (4, 5, 9) respectively. A detailed analysis of this type of phyllotaxy will be given elsewhere (Douady, unpublished).

We must therefore examine whether or not such organizations can be reached in transients of the type that occur during flowering initiation. We must first remark that in the formation of flowers there are often interversions in the order of formation of the elements. For instance there are cases where the primordia of stamens appear between the already formed primordia of petals and carpels. This process, which is a common occurrence as shown in Sattler's atlas of floral organogenesis (1973), is not represented in our model: acropetal order of formation is necessary for coherence with our hypotheses.

Even with this limit the simulation of flower formation is more difficult than that of the compositae inflorescences for the reason that during the floral initiation there are strong changes in the apex shape and in the primordium sizes. As the total number of elements is often small (in contrast with the case of the compositae) the transients are more rapid. We found that a specific difficulty shows up during very fast transients. The same type of problem is evident in simulations which are started abruptly at a small value of Γ . After the formation of the first element in a random position the space left for the formation of the second element is much wider than necessary. In the model we have used hitherto, the second particle is then placed at the absolute minimum, i.e. opposite the first element in the middle of the available space. The process is then repeated and, for very small Γ , it is clear that this procedure systematically favours the whorled modes with an order which is a power of two: (4, 4), (8, 8) etc. The other whorled modes will be hard to reach.

This drawback of the simulation derives from the fact that placing an element at the absolute minimum energy can create a waste of space: if an available space is large enough for two elements, placing one in the middle inhibits the formation of the second. This is in contradiction with the main assumption on the dynamics, which is to create as many elements as possible in the available space.

We can note that this problem did not exist in the previously investigated slow transients because the space made available at each step was never large enough to allow for the formation of two elements. We thus brought a slight modification to the algorithm to be used specifically in the situations of rapid transients. When the available space is too large, the minimum potential is also much lower than the required threshold value. In such cases the programme searches for the two positions on each side of this minimum where the potential is equal to the threshold. A new element is then formed at random in one of them. For a simulation started directly at a small value of G , the second particle is thus not placed opposite the first one, but on its side, right or left, and the process is repeated as long as there is a large enough space. In this manner, when Γ is in the range where a whorled mode (i, i) is most stable, this mode will directly be obtained, although it will initially be imperfect (the elements are placed at the same time, but not at regular angular positions). It will then rapidly grow into a perfect whorled pattern [Fig. 12(a)]. If the value of Γ is just between the intervals where the whorled modes $(i+1, i+1)$ and (i, i) are selected, then an imperfect whorl

of i elements will first be observed. After this first whorl, there will be a continuous transition toward the most stable spiral mode [Fig. 12(b)], which is $(i, i+1)$ as shown in Part II.

The proximity of the modes (i, i) with $(i, i+1)$ corresponds to the observation reported by Fujita: the species quoted to present the modes $(i, i+1)$, are those known to usually present whorls of various order (e.g. from 3–5 in *Lysimachia punctata*). Correlatively, once a mode, say (i, i) , is formed a small change of Γ is sufficient to induce a transition to $(i, i+1)$. Such transitions are common in corn cobs. They were also studied in *Magnolia* flowers by Zagorska-Marek (1994) and by Meicenheimer *et al.*

(1989), who showed that this evolution of the pattern was mediated by the formation of a crystallographic dislocation.

We tried to reach those modes in the presence of initial elements. The simulation shows that it is very difficult, if not impossible. The problem is similar to that of reaching a whorled mode (3, 3) from a decussate mode (2, 2). The presence of pre-existing elements which breaks the axisymmetry of the system, acts as a hindrance to the formation of the whorled modes. In rapid transients, the system remains in the spiral family, or may jump to another solution but which will be closely related to the one that has been left. Our simulation seems to suggest, therefore, that in the cases where the flower directly builds up perfect whorled modes it occurs after a complete interruption of the generation of primordia by the apex. In other terms, in these cases there may exist a discontinuity between the vegetative growth and the flower build-up. This would be in agreement with a remark by Lyndon (1978). Studying *Silene*, he stated (1357): “The effect of the leaves on the positioning of the sepals seems to be small or non-existent”.

5. Discussion and conclusions

Our model was built up to be as simple as possible. It has obvious limitations because of the approximations we made. We now discuss these together with the results we obtained.

5.1. CONTINUOUS VERSUS DISCRETE MODELS, PHYSIOLOGY OF THE GROWTH

The complete problem of phyllotaxis would be that of the dynamics of a continuous system (the apical meristem) and would include three questions about the stability of the central region of the apex, the formation of the primordia and the nature of their interaction. A prerequisite to solving this problem would be to know the nature of the underlying physiological process at work in the apex growth. This process is not identified with certainty yet, but its main characteristics are that it creates well-defined, finite size primordia and gives them a short range repulsive (or inhibiting) interaction. We can notice that two of the main hypotheses have these necessary characteristics.

The generation of patterns by reaction–diffusion processes was initially proposed by Turing (1951) on a theoretical basis. It is only recently that the Turing instability has been obtained experimentally by de Kepper *et al.* (1991) in a chemical system. Finite size circular domains are observed to form and to organize into periodic lattices. There is an inhibiting

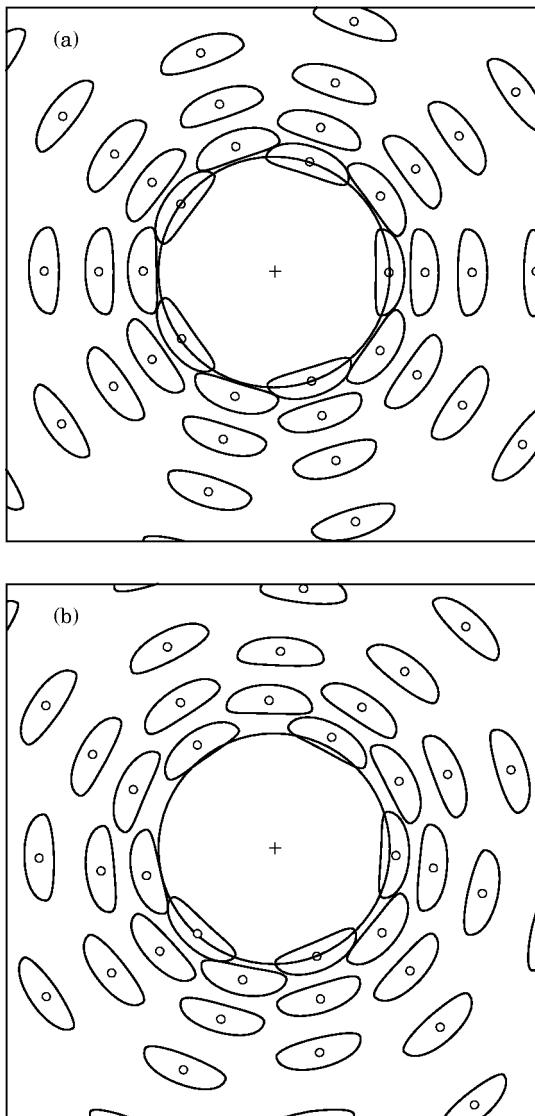


FIG. 12. (a) A whorled mode (5, 5) obtained in the simulation with $1/N=3$ and $\alpha=8$ at $\Gamma=0.76$ ($\omega=43.9^\circ$). (b) An accessory spiral mode (5, 6) obtained in the simulation with $1/N=3$ and $\alpha=8$ at $\Gamma=0.73$ ($\omega=42.1^\circ$).



FIG. 13. Photograph of the region of a stem of *Abelia* showing a leaf of anomalous shape at the node where a transition from a three fold to a four fold whorled mode occurs.

interaction between these elements which is short range, being limited by the diffusion. Such a process is thus able to generate the formation of finite primordia and to explain their short range interactions.

On the other hand, the buckling instabilities put forward by Green (1992) lead to the formation of wavy surfaces having finite size bumps. These bumps have a repulsive interaction with their first neighbours so that such a process also meets the prerequisites. We believe that it will be difficult to decide between these models by phyllotactic studies only.

The formation of finite size identical elements and their interaction justifies the transformation of the actual continuous problem (the time evolution of the shape of the whole apex) into a discrete iterative one. This approximation was implicitly used in many of the previous works on phyllotaxis. The substitution of a discrete system for a continuous system is also a classical simplification used in nonlinear physics.

The discretization of the primordia does, however, create limitations that we can examine. There are botanically observed situations which cannot be modeled in that way. These are all the cases where the formation of individual primordia is not observed to be the first destabilization of the apex. Scanning electron micrographs of apices of *Acacia longipedunculata* (Rutishauser & Sattler, 1984) and horsetails (*Equisetum hyemale*) (Gifford & Foster, 1989) clearly show that in these species, instead of isolated primordia, the meristem first generates successive rings. It is only at a later stage that the rings break up into individual primordia. At this time the interaction between the rings has already become weak, so there is a relative independence between them. Successive whorls with a variable number of leaves are thus observed. We can note that such a sequence of successive destabilizations would be possible in a reaction diffusion process as well as in a buckling instability.

More generally, the hypothesis of identical primordia appears to introduce a hindrance of rapid transients leading from a whorled mode to another. Such direct transitions from a decussate to a tricussate mode are observed, for instance, along the stems of rose laurel (*Nerium oleander*). Our model fails to realistically produce these rapid transitions. We believe that the discretization of the time appearance of the primordia may be too strong an assumption for the modeling of such cases. In our simulation a primordium appears abruptly. Whatever the physiological process, there must be a typical time of formation of the primordium. If this

time is short compared with plastochrone our model is a good approximation. If it is comparable to the plastochrone, then the primordia may influence one another during their appearance. This process could be important for the whorled modes, where the primordia of the whorl appear nearly at the same time. More generally it could also contribute to dampening the defects and to shortening the duration of the transitions from one mode to another.

Correlatively, the hypothesis of identical elements may be too strong: there is botanical evidence of plasticity of primordia. Figure 13 shows a region of a stem of *Abelia* where the phyllotaxy undergoes a transition from trimerous whorls to tetramerous whorls. This transition lasted two periods. The photograph shows that one of the three leaves of the intermediate node is anomalous, being almost split in two. Observation of several stems having such transitions show anomalous twin leaves covering all the range of shapes leading from a single leaf to a pair of leaves. An anomalous leaf almost certainly grows from a primordium which has an anomalous azimuthal elongation. This suggests that the transition between two whorled modes can be mediated by an increase in the azimuthal size of part of the apex and the splitting into two of the corresponding primordium. This cannot occur in our model where we have assumed all the primordia to have the same shape.

5.2. COMPARISON WITH BOTANICAL DATA AND POSSIBLE IMPROVEMENT OF THE DISCRETE MODEL

Within the discrete model possible improvements could be brought about by more quantitative comparisons to botanical measurements. Ideally a very good fit would require a comparison with the whole evolution of the various quantities $\Gamma(t)$, $\phi(t)$, $\delta t(t)$ and $G(t)$ during ontogeny. The possibility of observing the same apex continuously could permit the acquisition of such data. If the data were available, a fine tuning of the simulations could then be done to make them as close as possible to botanical reality. Several parameters could be adapted:

(i) In most of our simulations, the characteristics of the particles (and particularly the repulsive field they create) did not change with time. In botany the primordia grow in size as they are advected away. Depending on the nature of the interaction, it is conceivable that their repulsive or inhibiting influence could either increase or decrease with time. If the interaction results from a contact pressure or from a buckling instability the repulsion is likely to increase

with the size of the primordia. In contrast, several authors considered that the inhibition, caused by the diffusion of a chemical produced by the primordia, could decay with time. Our assumption that the potential created by one element does not change with time was the simplest and a compromise between the two cases. As reported in Section 4.5 of Part II (Douady & Couder, 1996b) we performed a few simulations with primordia having either increasing or decreasing sizes. The results were qualitatively the same but the precise value of the thresholds was slightly affected.

(ii) Similarly the stiffness of the interaction could be determined as it leads to shifts of the thresholds. Our results suggest that the realistic interaction is probably stiff so that each primordium is only sensitive to its nearest neighbours. Long range interactions tend to inhibit the formation of the whorled modes. Within the limits of a discrete model the potential cannot be too stiff, however, because in the piling of hard disks any localized disturbance propagates to infinity in the pattern.

5.3. THE RESULTS OF THE DISCRETE MODEL

We used very general hypotheses. The robustness of our results, which are only weakly dependent on the interaction law and geometry, as well as their correspondence with actual botanical arrangements, is the reason why we think they can be botanically relevant. They are entirely compatible with previous results obtained by, e.g., van Iterson (1907) and Williams & Britain (1984) in geometrical models and by Mitchison (1977) for a diffusion model. They are, however, more general because they are compatible with any repulsive or inhibiting interaction of the primordia. Furthermore they bring about a link between several approaches that were proposed previously.

Phyllotaxis generates quasi-crystallographic radial pilings of finite size elements around a central region also of finite size. Four factors can be used to define the pattern: the divergence angle ϕ and three length scales: the radius of the apex R_0 , the orthoradial size l_1 of the primordia at their formation, and the length VT over which the elements drift away from the center in one period. The ratio of these length scales provide two-dimensional numbers, G and Γ . The former is linked with Richard's plastochrone ratio, the latter with the sustaining angle ω . The three quantities ϕ , G and Γ are not independent: the nature of the iterative system that generates the pattern differs by the assumptions about which quantity is imposed by the physiology. In Hofmeister's system the periodicity (and thus G) is imposed: Γ and ϕ result

from the dynamics. In the Snows' system the primordia size (and thus Γ) is imposed: G and ϕ result from the dynamics and define the pattern. As pointed out above, in this latter case when the seedling becomes a plant there is a natural decrease of $\Gamma(t)$ because of the growth of the size of the apex.

In the two types of simulations the dynamic of phyllotaxis is dominated by the trend of the system to generate the densest patterns. For this reason our results are closely linked with the possible pilings analysed by van Iterson (1907). This is also why the shape of the apex and that of the primordia have a role in the selection of the phyllotactic modes. The differences between our results and those of a purely geometric approach are caused by the fact that the iterative system brings in a selection principle amongst the patterns. Some of them, although geometrically possible, are not dynamically generated because in these cases the position for a new primordium is not optimal, i.e. does not correspond to the largest space. This selection is important: at all the bifurcations leading from a spiral mode (i, j) to another, the selected transition [to $(j, i+j)$] is that corresponding to the construction of the Fibonacci series. This is an essential ingredient of the interpretation of the formation of Fibonacci type of series during the ontogeny. The simulations of the Snow & Snow hypothesis also show that the whorled and spiral modes can be obtained with the same type of dynamic. Actually the whole variety of the observed botanical patterns can be obtained, including most of the characteristic transients.

In very general terms the difficulty in understanding phyllotaxis comes from the relation between local order and global order. The existence of high order Fibonacci modes seems, at first sight, to imply a process of organization in which, at a given time, an element interacts with all the other elements present around the apex. This is wrong: our results, after many others, demonstrate that at a given time the position of formation of an element is determined by its nearest neighbours and thus by the parastichies. We have shown that, because of these growth rules, the system tends to optimize the density of its packing. At a small value of Γ , however, many different systems of parastichies have similar packing efficiencies and can thus keep growing. The rules of appearance of a new element create a local order but they do not lead *by themselves* to an interpretation of the global order of the system. In particular the common selection of the Fibonacci sequence does not result only from them. The selection of this particular global order is to be sought in the ontogeny of the plant. As shown above, the build-up of the high order

Fibonacci patterns starts at the initial stages of vegetative growth and occurs through the successive transitions during a continuous decrease of Γ . During this decrease the parastichy orders change with a sequence of transitions from (i, j) to $(j, i+j)$. This evolution occurs locally: it is linked with the change of the nearest neighbours of an element described on Fig. 8 of Part I (Douady & Couder, 1996a). As the same process occurs all around the apex, the system globally undergoes a transition (i, j) to $(j, i+j)$. It thus follows the main branch of solutions of the $\phi(\Gamma)$ diagram so that at small Γ a high order global Fibonacci pattern is obtained. If all the successive transitions $(1, 2) \rightarrow (2, 3) \rightarrow (3, 5)$ etc were perfect, there would be a memory of the whole sequence of transitions so that the global order would be the ideal one with a constant plastochrone, a constant divergence and a perfectly regular generative spiral. In fact perturbations always occur and the order is usually imperfect. The imperfections affect the time of formation of the elements, even leading to permutations in their formation. In this situation the ideal order as defined by the generative spiral is destroyed. The remarkable asset is that such perturbations are hardly visible on the parastichies. In other terms the Fibonacci order of the parastichies is robust relatively to the loss of global coherence marked by the disparition of the generative spiral. In a forthcoming article (Couder, unpublished) we will show that such permutations are actually of common occurrence in sunflowers.

The role of the ontogeny in the build-up of the global order is demonstrated by the possibility of the system to generate patterns with other global orders. This explains the existence (in e.g. sunflowers) of rare cases where the inflorescence is organized in the Lucas series or in a bijugate mode. Their build-up is always caused by (Weisse, 1894) an early transition to these modes during the destabilization of the initial decussate mode. In its later evolution the system just follows the branch of the $\phi(\Gamma)$ diagram initially chosen.

A contrario, if we start a simulation directly at a small value of Γ there is no particular selection of an organization in the main Fibonacci series. In such simulations the system can remain chaotic or generate one of the several organizations (whorled or spiral) possible at this value of Γ and having a good packing efficiency. We believe that these simulations give a plausible interpretation to the variability observed by Zagorska-Marek (1994) in *Magnolia* flowers. Very rare phyllotaxic orders as well as chaotic patterns are observed in our simulations as in botanical reality.

Generally, when the pattern is disordered it still exhibits a local order on most of its surface, with only a disordered sector.

The other main result of our model is to have obtained, in the same simulations, both the whorled modes and the spiral ones. This has permitted discussion of their relative stability. The main characteristic of the whorled modes is that there is no continuity from one of them to the next. Two results are worth mentioning.

(i) Our model predicts that the whorled mode of lowest order, the decussate mode $(2, 2)$ can only exist with either elongated primordia or with conical apices and short range interaction.

(ii) For small values of the parameter Γ , we observed the whorled modes (i, i) with increasing numbers i of elements in the whorl, separated by secondary spiral modes of the type $(i, i+1)$. These modes are known to exist in flowers, for instance in the female inflorescence of maize. We searched the realistic transients leading to these modes. If the growth starts from an opposite arrangement, they are only selected after a very sharp transient to the final value of Γ . This corresponds to the situation of the maize cobs. In this case only a few previous leaves appear to play a role; after a short disordered transient the pattern reorganizes. Perfect high order whorled modes such as those observed in some flowers are optimally obtained if there is no influence of the previous vegetative organization. This suggests a discontinuity leading the flower to form *de novo*.

5.4. GENETIC DETERMINATION AND SELF ORGANIZATION

In general terms, our results and botanical experiments such as those performed by Snow & Snow (1935) on *Epilobium hirsutum*, suggest that the phyllotaxy of a given specimen is not predetermined, but arises from a dynamical self organization throughout the growth. On the other hand, each species has an archetype of organization so that there exists some genetic determination of its phyllotaxy. There thus seems to be a contradiction between the determination of the phyllotaxy by genetic factors or by self organization.

This contradiction is only apparent. Genetics, in a large sense, by generating the structure and the physiology of the apical meristem, sets in the self organization system and makes it work. This is clearly demonstrated by the existence of mutants of *Arabidopsis* (Medford *et al.*, 1992) where the self organizing system is absent, resulting in a totally disordered growth. Similarly, in mutants with fasciated shoots, the phyllotactic order is affected by

the loss of the normal apical structure. These extreme cases apart, there is still a variability of the phyllotaxy of different specimens of a given species (or even of various branches of the same plant). This is not to be ascribed to mutations: it is simply the signature of self organization. The genetic system does not fix the phyllotaxy directly, rather it determines the system that will generate it. During the ontogeny of a given specimen the response of the plant to the environmental conditions will provide the precise time evolution of the growth parameters as well as the initial conditions. As self organization takes place these particular conditions will give a specimen its specific organization.

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