

Virtual phyllotaxis and real plant model cases

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Abstract. Phyllotactic pattern results from genetic control of lateral primordia size (physiological or physical) relative to the size of organogenic lateral surface of shoot apical meristem (SAM). In order to understand the diversity of patterns and ontogenetic transitions of phyllotaxis we have developed a geometric model allowing changes of the above proportion in a computer simulation of SAM's growth. The results of serial simulations confirmed that many phyllotactic patterns (including most esoteric ones) and ontogenetic transitions known from real plant model cases can be easily obtained *in silico*. Properties of virtual patterns often deviated from those of ideal mathematical lattices but closely resembled those of the natural ones. This proved the assumptions of the model, such as initiation in the first available space or ontogenetic changes in primordia size, to be quite realistic. Confrontation of simulation results with some sequences of real phyllotactic patterns (case study *Verbena*) questions the autonomy of SAM in its organogenic activity and suggests the involvement of unknown signal positioning primordia in a non-random manner in the first available space.

Additional keywords: *Magnolia*, ontogenetic transitions, pattern formation, SAM, *Verbena*.

MAGNOLIA

Sleepy flower on the leaf

Creamy-white ivory

Sweet to dizziness

Fragrant thing

Maliciously mysterious Universe

Strange visitor among us, humans

(Maria Pawlikowska-Jasnorzewska 1924)

Introduction

Phyllotaxis is the distribution of lateral organs in plants. The organ primordia are initiated iteratively (Hofmeister 1868) on the organogenic surface of the shoot apical meristem (SAM). The regularity of phyllotactic patterns has always intrigued scientists. Today there is still no exaggeration in quoting Darwin's famous statement and saying, that both phyllotactic diversity and, especially, ontogenetic transitions of phyllotaxis remain an 'abominable mystery' in plant biology. The phylogenetic aspect of the diversity is that phyllotactic patterns can be species specific. Having the status of a diagnostic feature in plant taxonomy, they fall into two major categories: whorled – achiral patterns, and helical – chiral patterns. Within one category there are many types of patterns: the decussate or tricussate in the first one, the main Fibonacci, Lucas and many others in the second. The ontogenetic aspect of phyllotactic diversity is that the pattern often changes together with the developmental phase of plant's growth. From the biological point of view it is, however,

the ontogenetic, qualitative changes of phyllotaxis, which occur for no apparent reason and are not associated with the developmental switch of plant organ identity, that are truly challenging. The ontogenetic transitions between the patterns are qualitative when the category or the type of pattern changes, or quantitative when, especially in chiral patterns, there is a progressive change in phyllotactic order (expression) i.e. in the numbers of contact parastichies (Adler 1974, 1977).

The mechanism positioning the primordia of leaves, flowers or flower parts on the organogenic surface of SAM has not yet been fully elucidated. It is undoubtedly genetically controlled (phylogenetic aspect) but also flexible enough to assure the plant's phenotypic plasticity (ontogenetic transitions).

The latest developments in plant biology point out the role of auxin, transported acropetally, in the superficial cellular layer of SAM (Reinhardt *et al.* 2000, 2003; Heisler *et al.* 2005). The polarity of the cells transporting the hormone alters periodically in the vicinity of emerging primordium, with the flux of auxin

being once oriented towards the primordium tip and, after a while, away from it, towards the tip of the apex itself. A spacing mechanism is created by the feedback of the hormone on its own transport. Its component is a primordium acting as a sink, competing with others for the hormone and inhibiting the formation of similar structures in its close vicinity. The efficiency of a sink can be measured by the size of the inhibition field, within which, the auxin concentration is below the level required for the formation of a new sink. New elements emerge in the first available space between already existing neighbouring primordia, as postulated earlier by Snow and Snow (1931, 1952). This space is created by the constant and continuous addition of new cells in a process of SAM's apical growth. Based on these concepts two new models of phyllotaxis have recently been introduced (Jönsson *et al.* 2006; Smith *et al.* 2006a). We still do not know though what kind of signal changes the polarity of the cells and reorients the flux of auxin. Moreover, it is still uncertain to what degree the SAM is autonomous in positioning organ primordia and what role the signals, which flow acropetally from differentiated tissues play in this process (Larson 1977; Banasiak and Zagórska-Marek 2006).

Phyllotactic patterns result from genetic control of lateral primordia size (physiological or physical) relative to the size of organogenic lateral surface of the SAM. It is reasonable to assume that the change in one of these parameters alters the ratio and thus brings up a change in phyllotaxis. The aim of this study was to find, in a computer simulation, the causes of phyllotactic transitions known from plant model cases. The principles affecting the direction of phyllotactic transitions and, thus, the quality of the emerging patterns were of particular interest.

The model

The physiological size of primordia may have nothing to do with their real geometric size. However, in the models of phyllotactic pattern formation and the pattern's subsequent transformation, it is convenient to have the primordia (or their inhibition fields) shown as circles tightly packed on a circular, cylindrical, paraboloid or conic surface representing organogenic surface of growing SAM (Williams and Brittain 1984; Battjes and Prusinkiewicz 1998; Zagórska-Marek 1999, 2000; Smith *et al.* 2006b; Hellwig *et al.* 2008).

In order to understand the emergence of various patterns and their ontogenetic transitions, we have simulated SAM's growth using a special computer program written by Marcin Szpak (Zagórska-Marek and Szpak 2006). In our geometric model we assumed:

- (1) an infinite cylinder of a constant width as simulation space,
- (2) primordia as circles of a changing radius, and
- (3) primordia emerging in the first available space (in lowest possible position between the two neighbouring, already existing primordia).

The following abbreviations of simulation parameters have been used throughout the paper.

- (1) R, the radius of the circle representing organ primordium,
- (2) IP, the initial phyllotactic pattern,

- (3) PA, the angle of parastichy intersection in the initial phyllotactic pattern,
- (4) DR, the deviation rate, i.e. the change in the radius of subsequent primordium, expressed as percentage of the previous value of R (in case of continuous change in R),
- (5) DS, the percentage change (in case of discontinuous change in R), and
- (6) DM, the deviation minimum, i.e. the limit of the change in R, expressed as percentage of the initial value of R.

In interpreting the results of simulations, we have identified the emerging phyllotactic pattern by counting its contact parastichies and writing down their numbers in the opposed parastichy pair formula (Adler 1974, 1977). The numbers were supplemented with *s* and *z* indexes, which allowed identification of pattern

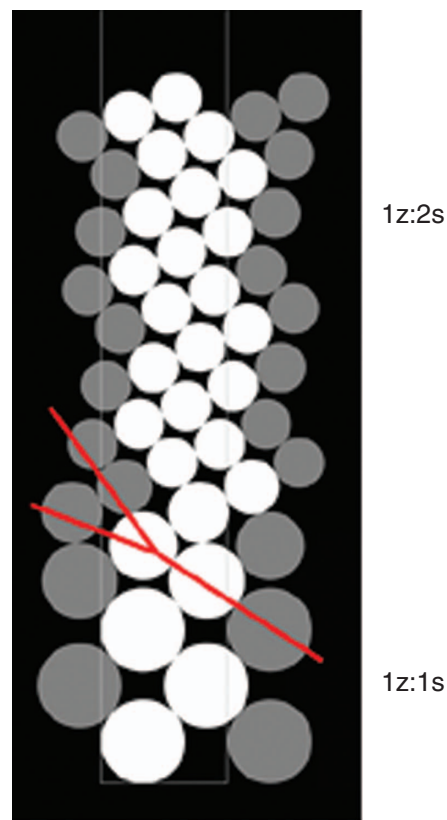


Fig. 1. Fast, yet continuous decrease in R (radius of the circle representing organ primordium) transforms the initial distichous pattern via dislocation (red bifurcation of one parastichy) into spiral, 1 : 2 main Fibonacci phyllotaxis. The 6th pattern element is initiated in the available space big enough to accommodate two sites of initiation. The selection of either left or right position by newly forming primordium determines a chiral configuration of the emerging pattern. Here, the primordium is shifted to the left. In opposite case, the Fibonacci pattern would develop in a form of a mirror-image of the one shown here. Here, and in all subsequent figures, the simulation space is visualised as a rectangular frame (split-open surface of cylinder). For better identification of phyllotactic pattern the same primordia at each level are shown on the opposite sides of the frame as grey and white counterparts. The numbers of the conspicuous parastichy pair identifying the emergent phyllotactic pattern are supplemented with (*s*) and (*z*) indexes of parastichy orientation to the left and to the right, respectively. This allows recognition of pattern chirality.

chirality. s was used when orientation of parastichies on the organogenic surface viewed from the outside was to the left, z , when it was to the right. Besides the contact parastichies tangent to each other, thus, being the most conspicuous, there are also many other secondary helices in each phyllotactic pattern. Their numbers belong to the mathematical series associated with the pattern (as the 1, 2, 3, 5, 8... series with the main Fibonacci pattern). They are inconspicuous but may become visible when the order (expression) of phyllotaxis changes. Their numbers and orientation are also informative, helpful in pattern identification. The list of patterns identified in nature and of the mathematical series attributed to them (based on secondary connections between the pattern elements) has been provided in earlier papers (Zagórska-Marek 1985, 1994).

Results and discussion

The assumption that the size of primordia is subject to ontogenetic change appeared to be particularly fruitful. The

model, in testing, produced an almost infinite number of transitions, with many resulting patterns of primordia spacing, more or less regular. The changes we had been applying were abrupt or continuous, quick or slow, with the radius decreasing or increasing.

Continuous change

The continuous decrease or increase in the radius of pattern elements (R) typically changed an order (expression) of the initial phyllotactic pattern, which is quite a common condition in many plants. We have investigated this case assuming the initial pattern (IP) as distichous, with the expression 1 : 1. This pattern, the first in monocots, where there is only one cotyledon in the embryo, often extends to the vegetative zone of the main axis, as exemplified by grasses. In dicots, as they possess two cotyledons, the IP should be decussate (see the case study *Verbena* below). In the simulation the continuous decrease in R (Fig. 1), caused transformation of the initial 1 : 1 distichous

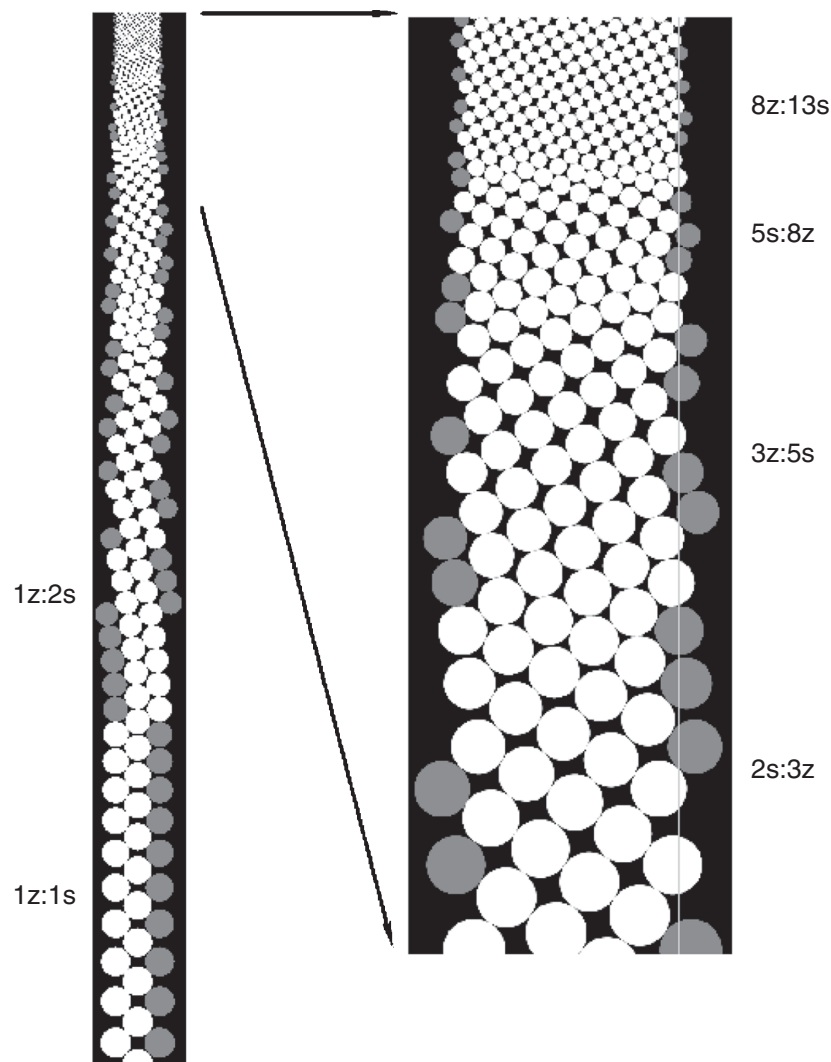


Fig. 2. Slow, continuous decrease in R (radius of the circle representing organ primordium) brings up at first a qualitative transition, similarly as in Fig. 1, and then a cascade of changes in phyllotactic order (numbers of conspicuous parastichies).

pattern into 1:2 main Fibonacci phyllotaxis. The decrease systematically widened the available space, to the point when new primordium could be shifted in it either to the left or to the right. It was a moment of symmetry breaking. Random selection of the shift set up the chirality of the emerging pattern, but it did not affect its type – in both situations it was the main Fibonacci pattern. This qualitative transition was accomplished through dislocation (red line on Fig. 1), i.e. by an addition of one parastichy in only one of the two sets of helices making the opposed parastichy pair (*sensu* Adler 1974, 1977). Similar dislocations, associated with qualitative transitions between various patterns, have been described in natural phyllotactic lattices of balsam fir and magnolia (Zagórska-Marek 1985, 1987, 1994). In a simulation, further changes in R caused the continuous rise in order of the chiral pattern (Fig. 2). This case is best illustrated in nature by inflorescences of Asteraceae family. In capitula of *Helianthus*, *Bellis* or *Telekia* (Fig. 3), the numbers of parastichies in the opposed parastichy pair are usually very high. They represent one of the highest expressions of main Fibonacci phyllotaxis known in plant kingdom. Vegetative phyllotaxis in Asteraceae, preceding the formation of inflorescence, is of a much lower order (Couder 1998). Tracing selected parastichies during these ontogenetic changes shows that they visibly change their inclination, and ultimately become inconspicuous. We have observed the same effect in the simulation where IP was the main Fibonacci (Fig. 4) and R was continuously increasing. In this case, the order of phyllotaxis was decreasing. In all our simulations, the width of the organogenic surface was constant. In nature, the changes in order of phyllotaxis are often observed when pattern elements are of the same identity – in coniferous vegetative shoots or in some inflorescences (Fig. 4). It is likely that in these cases they are caused by developmental

fluctuations in a size of SAM's organogenic surface, associated with changing vigor of the shoot, or with determinate character of its growth (as in capitula of Asteraceae).

We noted a dependence of the quality of the emerging pattern on the initial parastichy angle (PA). We have tested the significance of PA in a sequence of simulations by changing its value from 60 to 90° . Other parameters of the simulations were kept constant at the following values: IP , 1:1; DR , 97%; DM , 40%. The emerging pattern was either the esoteric 1, 2, 3, 8, 11... phyllotaxis ($60 < PA > 78.8$) or the common 1, 2, 3, 5, 8... main Fibonacci pattern ($PA > 78.8$). In both these patterns, shown in Fig. 5, the orientation of low order parastichies was identical: $2s:3z$, but 8-parastichies (red asterisks) in a resulting pattern, initially oriented to the left (s), became vertical when $PA = 78.8$ degrees and then flipped to the right (z). The low 2:3 expression causes that the qualitatively different pattern shown in the left simulation in Fig. 5 may be erroneously classified as the main Fibonacci. Its divergence, however, is 129.76, close to the limiting value. The latter, calculated theoretically, equals 132.18, whereas for the main Fibonacci – 137.5. We note that the first pattern, the appearance of which in computer simulations was also reported by Liaw (1998), belongs to the so-called 'impossible' patterns (Jean 1994). It has been reported by Fujita (1937, 1939) as appearing sporadically in *Plantago*, by Zagórska-Marek (1985) as engaged in phyllotactic transitions in *Abies balsamea* vegetative shoots and finally it was documented on scanning electron microphotographs of *Magnolia* floral apices (Zagórska-Marek 1994).

Intrigued by the appearance of this pattern in our simulations, we traced the consecutive divergences in the continuous



Fig. 3. Inflorescence of *Telekia*, representative of Asteraceae family, shows very high numbers of the opposed parastichy pair (*sensu* Adler 1974). Visible spiral parastichies connect the florets densely packed on the flat disc of capitulum.

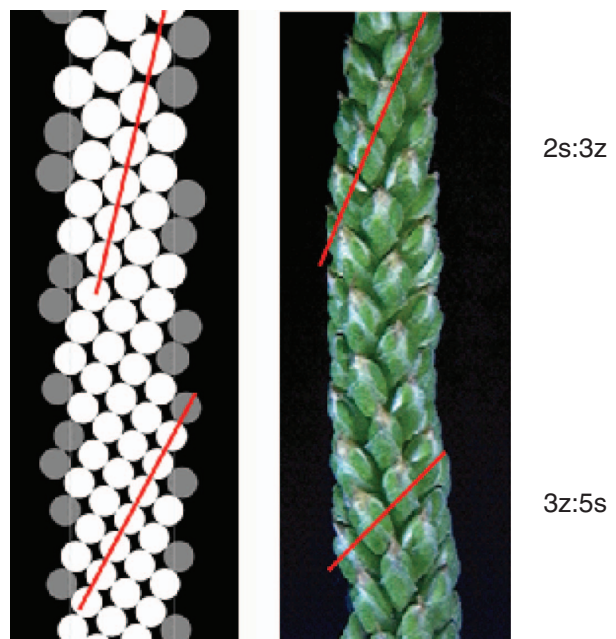


Fig. 4. The continuous increase in R (radius of the circle representing organ primordium) lowers the order of phyllotaxis. A computer simulation (left) is compared with real changes in *Plantago* inflorescence (right). In both situations selected parastichies ($3z$) become steeper (red line) when the expression of Fibonacci pattern changes.

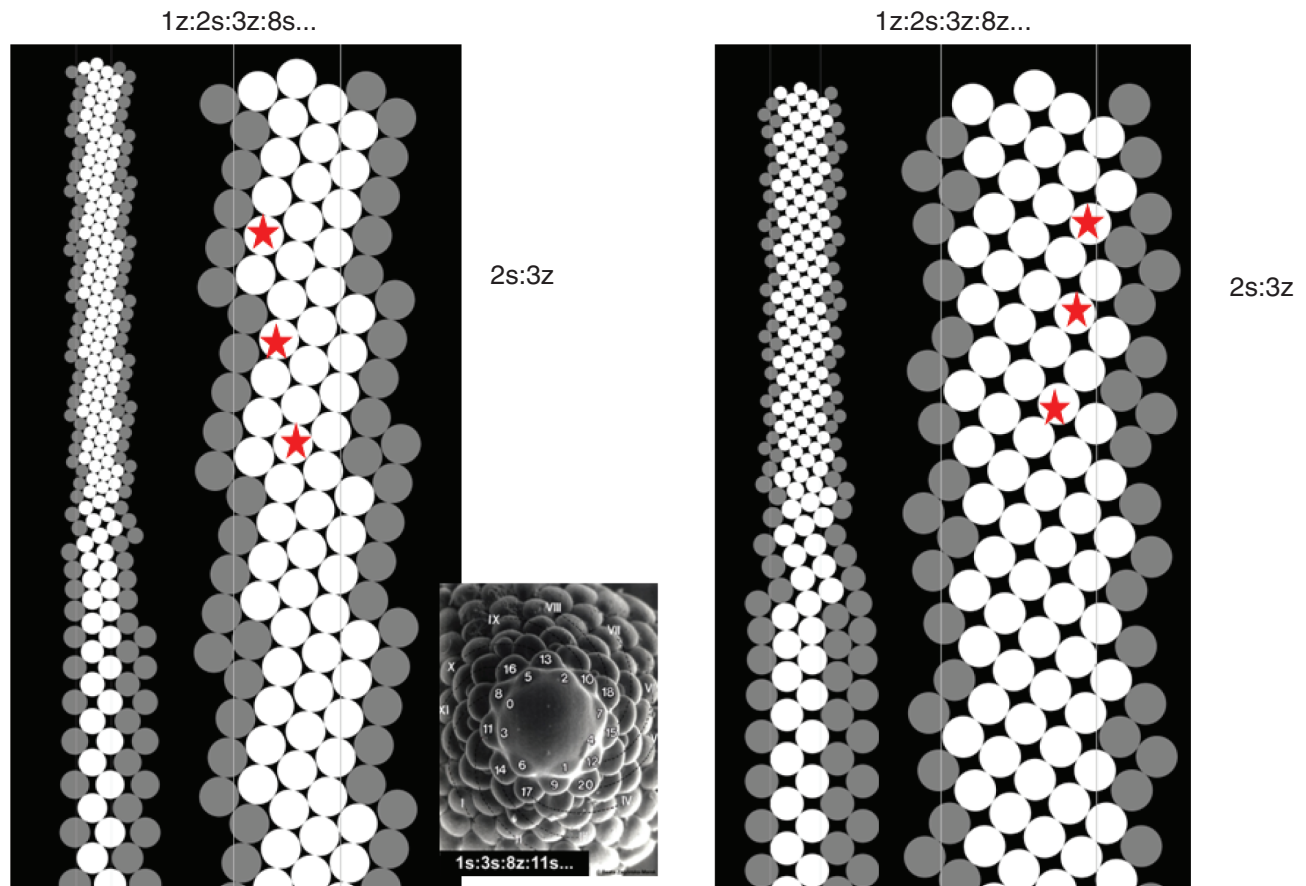


Fig. 5. The effect of initial PA (angle of parastichy intersection in the initial phyllotactic pattern) value on the type of ultimate phyllotactic pattern. In both simulations all parameters except PA have been the same. On the right the resulting pattern is the main Fibonacci in expression $2s : 3z$. Similarly expressed is the pattern on the left. This low expression covers up the fact that this pattern is different: its divergence is 129.76 not 137.5, the parastichy 8 (connecting every 8th pattern element – red asterisks) runs in the opposite (s) direction to parastichy 3 (z), whereas in the main Fibonacci pattern shown on the right orientation of parastichy 8 and 3 is the same (z). See the detailed description of both simulations in the text. The scanning electron microphotograph shows a floral apex of *Magnolia* with $8z : 11s$ pattern (from Zagórska-Marek 1994; with permission from the publisher). This is the same pattern as in the simulation on the left but its expression is higher.

transition showed on Fig. 2. Their sequence revealed that the pattern 1, 2, 3, 8... is a transient condition between two successive expressions of the main Fibonacci pattern: 1 : 2 and 2 : 3 (Fig. 6). The divergence value 144, typical for the 1 : 2 expression (in orthogonal lattice) drops down slightly below 130 before rising again towards 138.46 for 2 : 3 and approaching finally 137.5 for higher expressions. In this area the primordia are tightly packed with very little space left between them. This results in the most efficient use of the organogenic surface. It became immediately clear that if the primordia acquired DM in this particular region, the pattern would become ‘petrified’ – it would transform no more in the simulation, but would be perpetuated as in the case shown in Fig. 5 on the left. When DM is reached in the higher up region – the main Fibonacci pattern is a result. The PA initial condition determines then where the ultimate value of R is going to be reached.

It remains to be seen whether the two options predicted by the model occur in nature. The good plant system for investigating it is an ancient woody magnoliid – *magnolia*. Its vegetative

phyllotaxis is known to transform readily from initial distichous to helical one. This research is currently under way.

In the unlimited continuous transitions with 1 : 1 IP, the 1, 2, 3, 8, 11... pattern rises from and transforms into the main Fibonacci pattern (Fig. 6). For now, it is unclear how to obtain, if possible at all, a progression from its low 2 : 3 expression towards the higher ones: 3 : 8 or 8 : 11, encountered in *magnolia* or *balsam fir*. These have also been found in *Annanas comosus* – a monocotyledonous plant with showy multiple fruit (Rutishauser and Peisl 2001; B. Zagórska-Marek, unpubl. data). In all these plants, the high expressions of the pattern discussed resulted from transitions involving patterns different that the main Fibonacci – tetrajugy (4 : 8) or Lucas (7 : 11). Further investigations are needed both of the nature of this pattern and of the conditions of its appearance in transitions.

It is evident from our study that the quality of phyllotactic pattern resulting from transition depends not only upon the relation of primordia sizes relative to the size of organogenic surface, but also upon how the emerging phyllotactic lattice is

rotated with respect to the axis of the system, and how efficiently the primordia are packed.

The parastichy orientation in a continuous transition puts in question the identity of phyllotactic pattern. In general, we believe that the problem of phyllotactic transitions will bring us soon to redefinition of some patterns and perhaps to their new classification.

Discontinuous change

Alternatively, the change of R in our simulations was abrupt. This is what usually happens when SAM enters a new phase of development and the primordia assume new identity: instead of being leaf primordia they become the primordia of inflorescence or flower elements. We have used two model cases to illustrate this type of transition and confront the simulation results with experimental data. The first case refers to the transition from vegetative to generative phase of development (case study *Verbena*), and the second to the multiple transitions between the primordia of floral parts (case study *Magnolia*).

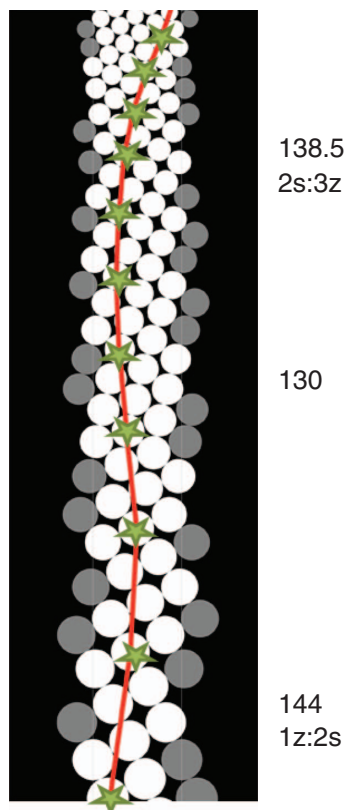


Fig. 6. Magnified fragment of the simulation of continuous change in R (radius of the circle representing organ primordium) from Fig. 2. A red line shows changing course of the line connecting every 8th element of the pattern (green asterisks). In the middle, between the lower and the upper region, each with the main Fibonacci phyllotaxis, the divergence between consecutive primordia averages 130° , 8-th parastichy is s -oriented and primordia are tightly packed. These are all symptoms of the emergence of transient 1, 2, 3, 8... phyllotaxis. Further description in the text. The expressions of Fibonacci pattern are given on the right side of the simulation together with the mean values of the divergence.

Case study: *Verbena*

In *Verbena officinalis*, vegetative phyllotaxis is decussate (achiral), whereas on the inflorescence axis the bract distribution is helical (chiral). The transition from the decussate arrangement to the helical one, most commonly leads to the development of the main Fibonacci pattern. The frequent alternative is bijugy. The youngest (uppermost) primordia of leaves are larger, relative to the SAM circumference, than the primordia of bracts. Modelling this situation showed quickly the ambiguity of the first available space rule when the difference between the sizes of the primordia was sufficiently large. The DS parameter, a discontinuous percentage change in R , had to be smaller than 50%. In the simulations with $DS = 45\%$, after the change, all new primordia were small and all were the same size. The quality of the

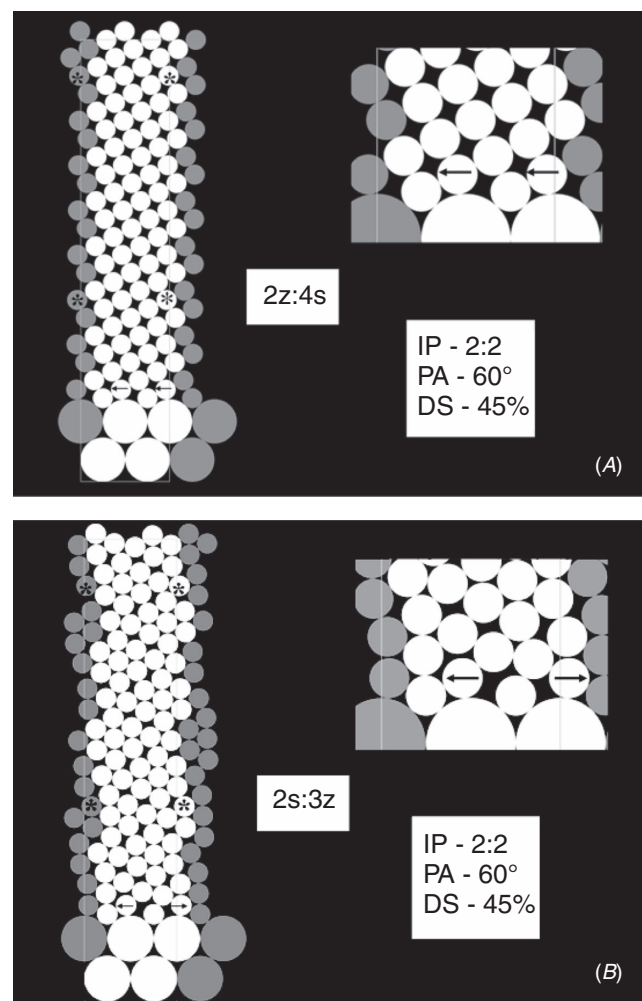


Fig. 7. Simulation of abrupt change in R (radius of the circle representing organ primordium). The primordia have been added according to the principle of first available space. The initial pattern is decussate, primordia decrease in size to 45% of the initial value of R . This creates quite large available space for two newly initiated, small primordia. In consequence only one of two equivalent positions: to the left or to the right (arrows) has to be selected by each of the two. (A) When the choice for both is the same, the developing pattern is bijugy; (B) when it is different, the main Fibonacci emerges.

emergent pattern depended upon how the small primordia were positioned in quite a large available space. When, in a case of two equivalent positions, the two small, 'generative' primordia had their initiation site selected identically – to the right or to the left – the developing pattern was bijugy, when the choice for both had been opposite – one to the left, the second to the right – the main Fibonacci pattern emerged (Fig. 7). The latter transition should be the most frequent among plants, quickly developing helical phyllotaxis from the initial pattern of opposite cotyledons or prophylls.

In a sense, this case resembles the one shown in Figs 1 and 2 except that there, with an initial pattern 1 : 1, ambiguity of the first available space rule resulted in two chiral configurations of the same pattern, but here, the number of possible patterns is greater (including their chiral variants). This increases phenotypic plasticity of the plant: it is definitely better to have two cotyledons than one.

Case study: Magnolia

The outstanding diversity of phyllotactic patterns present in the terminal parts of magnolia flowers (Zagórska-Marek 1994; Zagórska-Marek and Wiss 2003) is most probably an outcome of the double change in the size of floral primordia generated on

SAM's organogenic lateral surface (Zagórska-Marek and Stoma 2005). The computer simulation of this case is very sensitive even to small changes in the values of the parameters used. The ambiguity of the first available space rule is also of importance here. The initial pattern of the largest perianth primordia is tricussate (achiral), which explains frequent appearance of trijugy in the later helical arrangement of the smaller stamen primordia and slightly larger carpel primordia (Fig. 8). In the simulation, very small primordia of stamens, again, have a choice of more than one position in the first available space, identically like in the case of *Verbena*. There are two variants of this situation: (1) asymmetric, when two small primordia are getting close one to another with the third one being far apart from the pair, or (2) symmetric, when all three are shifted in the same direction thus are equally spaced. This might be one of the reasons why helical phyllotaxis of generative elements in magnolia is extremely diverse, covering almost whole spectrum of patterns known to occur in nature. Frequent ontogenetic transitions through dislocations (bifurcations of parastichies) are observed in a carpel zone (Zagórska-Marek 1994). A tricussate start up pattern, together with rather small size of generative elements in relation to the width of organogenic space (ambiguity of available space rule), but above all, the double change in a size of pattern elements should be held responsible for the rich spectrum of final

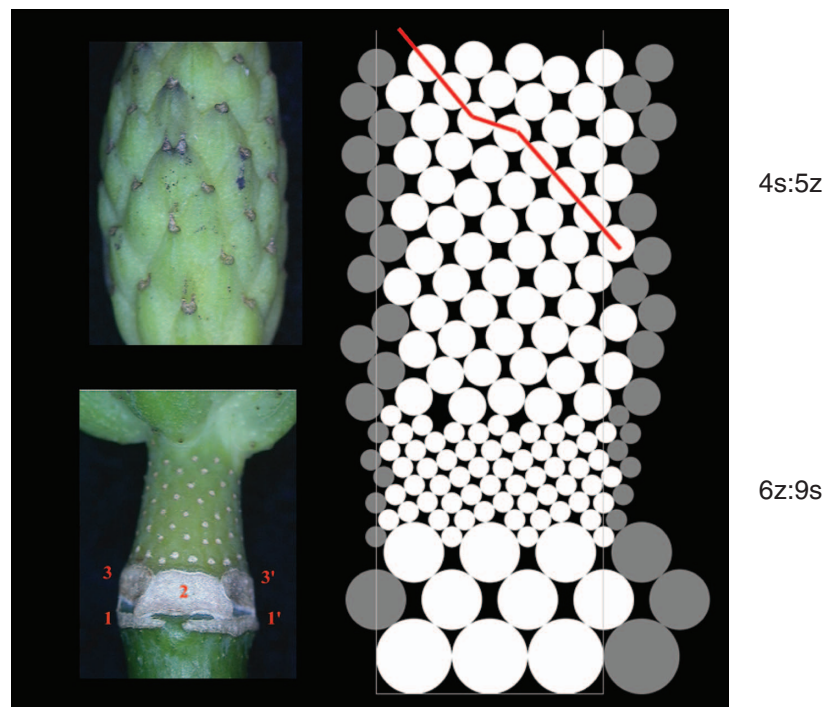


Fig. 8. Simulation of multiple phyllotactic transitions in magnolia generative shoot. Photographs show side view of three regions where flower parts have different identity: tricussate perianth, spiral androecium and also spiral gynoecium. In a simulation changes in R (radius of the circle representing organ primordium) are abrupt between perianth elements and stamens and also between stamens and carpels. The resulting patterns are trijugy in androecium and 1, 4, 5, 9... pattern in gynoecium. Both these phyllotactic systems are frequently encountered in magnolia flowers. The course of parastichies in one set is disturbed (red line). Note that between androecium and gynoecium phyllotaxis changes not only qualitatively, but also quantitatively. If it were not a case, the expression of phyllotaxis in gynoecium would be 5z:9s instead of 4s:5z as it is.

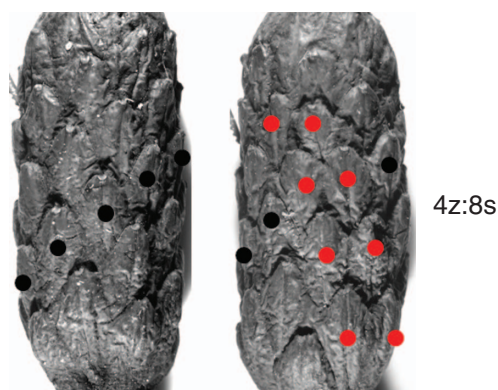


Fig. 9. Mature gynoecium of magnolia flower with tetrajugate phyllotaxis, viewed from two opposite sides. Four parastichies curving locally out of helical course can be seen on one side (right photograph). This is the same effect as that shown in Fig. 8. Moreover, the defect (pointed out by the pairs of red dots) is propagated upward in opposite direction (to the left) to the direction of ascending helices – exactly as in the simulation in Fig. 8.

phyllotactic solutions. In our simulations, we have sometimes observed the development of totally chaotic arrangements of pattern elements. Screening large populations of magnolia generative shoots shows that this situation is also present in nature (Zagórska-Marek 1994). Frequent appearance of parastichies with a somewhat irregular course *in silico* and *in vivo* (Figs 8 and 9) explains why, in some cases, phyllotaxis of magnolia gynoecium is undeterminable, with only one set of parastichies clearly helical (B. Zagórska-Marek, unpubl. data). Similar effects have been observed *in silico* in tiling patterns of phyllotaxis by Atela and Gole (2007) and earlier, both *in silico* and *in vivo*, by Couder (1998) for *Helianthus* giving, according to the latter author's opinion, some substance to the Plantefol's claim on existence of 'foliar helices' (Plantefol 1948).

Conclusion and future goals

Our simulation results coincide well with the real organographic changes in the systems of phyllotaxis exemplified by *Magnolia* and *Verbena* shoots. Other authors observed similar concordance using different plant model systems (Couder 1998; Hotton *et al.* 2006; Smith *et al.* 2006b; Hellwig *et al.* 2008). The new development in our model application is that, sometimes, there is more than one initiation site available for an emerging primordium. Its selection, together with other factors such as the varying extent and rate of change in primordia size, affects the quality of the resulting pattern and ontogenetic transition. We note that, in some plants such as *Dipsacus* or *Torreya*, the pattern subsequent to decussate is always bijugy, suggesting that there is yet another factor, besides the primordia's competition for auxin, which selects arbitrarily the initiation site for new primordium. This observation may put in question the absolute autonomy of SAM in its organogenic activity (Banasiak and Zagórska-Marek 2006).

Still, some unexplained problems remain. Firstly, qualitative changes in phyllotaxis sometimes occur within the zone of primordia of the same identity. In *Verbena*, on the axis of inflorescence, further sequential changes of phyllotaxis often

take place even though the identity of bract primordia remains the same. The transitions we have modelled (data not shown here since this research is still in progress) involve helical patterns (Lucas, second accessory) and whorled (tricussate); similarly, in *Magnolia* flowers, dislocations, frequently observed in a carpel zone, rearrange the primordia, which maintain their identity. Of the same type are the transitions in *A. balsamea* vegetative shoots, that occur within one annual increment of the axis (Zagórska-Marek 1985). Secondly, the spectrum of final patterns in *Magnolia* is species or genet specific, despite the general rule of a double change in primordia size of flower elements. Different *Magnolia* species, or even the trees within one species, may have specific distribution of various phyllotactic patterns. This 'phyllotactic fingerprint' can be maintained throughout the period of many years (Zagórska-Marek 1994, 1999). Truly challenging are the species having exclusively main Fibonacci pattern in the carpel arrangement (e.g. *Magnolia hypoleuca*, *Magnolia virginiana*). Evidently the unknown species or genet specific factor controls the direction of transitions in magnolia's floral phyllotaxis.

Our future specific goals in exploring the potentials of the presented model in more detailed, quantitative studies, are to explain systematically and predict all (including the less common) patterns, explain the direction of other pattern transitions, i.e. why a given pattern may be transformed in many different ways, and, finally, elucidate why the spectrum of patterns can be species or genet specific.

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