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BZM conceived the study, designed the research, performed experiments, and wrote the text; MS wrote the computer program and together with BZM discussed and interpreted the results

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INVITED ORIGINAL RESEARCH PAPER

The significance of γ-and λ-dislocations in transient states of phyllotaxis: how to get more from less – sometimes!

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Abstract

In some plants, developmental changes of phyllotaxis are so frequent that the whole spectrum of phyllotactic patterns becomes available for investigation and thus many unknown subtleties of phyllotaxis come to light. Among these, *Magnolia acuminata* is the most prominent. In a series of experiments performed in silico with application of a simple geometric model of phyllotaxis, we were able to confront the empirical data on phyllotactic transitions occurring in magnolia flowers with the results of computer simulations. They revealed that in addition to the ratio between the sizes of plant organs, the history of developing pattern was also important, especially for the direction of ontogenetic changes. The parameters of size tolerance and vertical tolerance in positioning a new element in the first available space, brought the effects of simulations closer to the real patterns. They helped especially to resolve the enigma of multiplication of parastichies (γ-dislocations) observed sometimes during determined growth of magnolia floral axes. We conclude that ontogenetic changes in phyllotaxis result mainly from changing sizes of organs in the course of development and that the changes do not always occur with mathematical accuracy.

Keywords

phyllotaxis; phyllotactic transitions; dislocations; magnolia; shoot apical meristem; virtual plants

Introduction

Regularity of phyllotaxis, distribution of lateral organs in a cylindrical plant shoot, is one of the keystone problems in structural biology. The phyllotactic pattern, following the basic principles of Euclidean geometry, represents an interesting example of a universal system, in which the elemental units of the pattern are packed on the surface of a cylinder. Their orderly arrangement allows the comparison of a plant shoot to a cylindrical crystal. This living crystal grows because new units are constantly being added to its upper end. A similar structure, but on hierarchically different levels of matter organization, have: cylindrical molecules – inorganic and organic, often chiral nanotubes [1–5], microtubules that are sometimes not only chiral but have changeable number of protofilaments [6], membrane nanotubes in cell-to-cell connections [7], stromules interconnecting plastids and other organelle extensions [8,9].

Packing units on the surface of a cylinder may have many solutions, thus it is easy to predict that the quality of phyllotactic pattern should vary. The empirical studies proved that indeed there are many phyllotactic patterns in nature. Some of them, being an intrinsic property of a plant, are in fact the species-specific traits of taxonomic significance. There have been numerous attempts to structure this phyllotactic diversity into a system of classification. The most robust is the division of the patterns

into two categories: achiral and chiral ones. In achiral patterns, the opposite (S – oriented to the left and Z – oriented to the right) lines connecting lateral organs in ontogenetic sequence are inclined to the longitudinal axis at the same angle, whereas in the chiral patterns the two angles are different. From the latter patterns, one seems to be best known and most frequently encountered, namely the main Fibonacci pattern present, among many other species, in a model plant *Arabidopsis thaliana*, both in its rosette and in the inflorescence. In our earlier work, we had attempted to explain the prevalence of this pattern in plants by its developmental stability [10].

It should be mentioned, however, that there are plants like *Torreya* or *Cephalotaxus* exhibiting main bijugy as a dominant chiral pattern [11–14]. Separating the two main types of patterns, as useful as it is in taxonomy, does not seem to be fully justified in light of numerous observations of developmental, ontogenetic changes of one pattern into another occurring in phylogenetically different genera of plants: in *Lycopodium* [15], *Juniperus* [16], *Thuja* [17], *Magnolia* [18–20], *Verbena* [21], *Anagallis* [22], and many others. Taking into account that all eudicots, which have at maturity chiral phyllotaxis, start their development from an achiral, whorled pattern of opposite cotyledons, and that their flower has again a whorled architecture, which has been beautifully demonstrated for *Arabidopsis* [23], these transformations must be treated as natural and very common.

The question is what causes this phyllotactic diversity and especially these ontogenetic transitions? It is plausible to assume that these phenomena are the results of unstable geometry of a developing shoot apical meristem (SAM) and variable sizes of lateral organ primordia. These parameters are genetically controlled as shown by the phenotypes of *wushel* and *clavata* mutants [24–28] or *abphyl* mutants [29–31]. Geometric changes are notably associated with seasonal changes in apex organogenic activity, especially with the sequential changes of organ identity. In the vegetative phase of development, in consecutive flushes of the shoot axis, the primordia of cataphylls follow the primordia of the leaves proper. This case is best illustrated by *Torreya*, where large primordia of winter bud scales are initiated in an achiral, decussate pattern of phyllotaxis, the subsequent needle primordia, evidently smaller, are arranged in a helical, bijugate manner [14]. With the transition to the generative phase, the primordia of the leaves proper change their identity to inflorescence bracts or flower parts. In *Epilobium* [32], *Verbena* [21], and in a model plant *Antirrhinum* [33,34] vegetative phyllotaxis is decussate but it changes into helical in the inflorescence. In the floral meristems, the primordia of sepals are followed by primordia of petals, stamens, and carpels. In the *Magnolia* flower, the initial phyllotaxis of the large perianth primordia is tricussate, whereas the arrangement of much smaller primordia of stamens and carpels is helical [18–20,35,36]. Sometimes, however, transitions are observed that are not associated with the change in organ identity – in *Magnolia* vegetative shoots the initial distichy changes into the spiral arrangement of leaves (Fig. 1) and in its flowers, within the domain of apocarpic carpels, one chiral pattern often transforms into another [18–20]. There are also situations when organ identity changes but phyllotaxis does not, as in *Arabidopsis*, where phyllotaxis of the leaves proper in a rosette is in principle the same as that of the bracts in the inflorescence.

The aim of the study was to explain some phenomena associated with ontogenetic changes of phyllotaxis, observed especially in magnolia, our model plant (Fig. 1), where floral phyllotaxis is diverse and phyllotactic transitions frequent. To do this, we performed the experiments in silico analyzing the effects of developmental changes in the sizes of lateral organ primordia. We used a previously developed, special computer program "Phyllotaxis" [21] with some new features added in the course of the study. In many variants of computer simulations, we were able to demonstrate that within the frame of general tendencies of increasing or diminishing the primordia size the fluctuations in the rate of the changes are necessary to obtain some observable effects in natural phyllotactic lattices. We were particularly interested in the conditions facilitating the appearance of dislocations – the peculiar defects of these lattices associated with pattern transformation. In material science, the edge dislocations are the linear crystallographic defects present locally in a crystalline material. They appear there, where a new plane of crystal units (atoms or molecules) is added to the regular crystal structure [37–39]. In the planar array of units, perpendicular to the extra plane, they appear as bifurcations of the imaginary lines connecting the

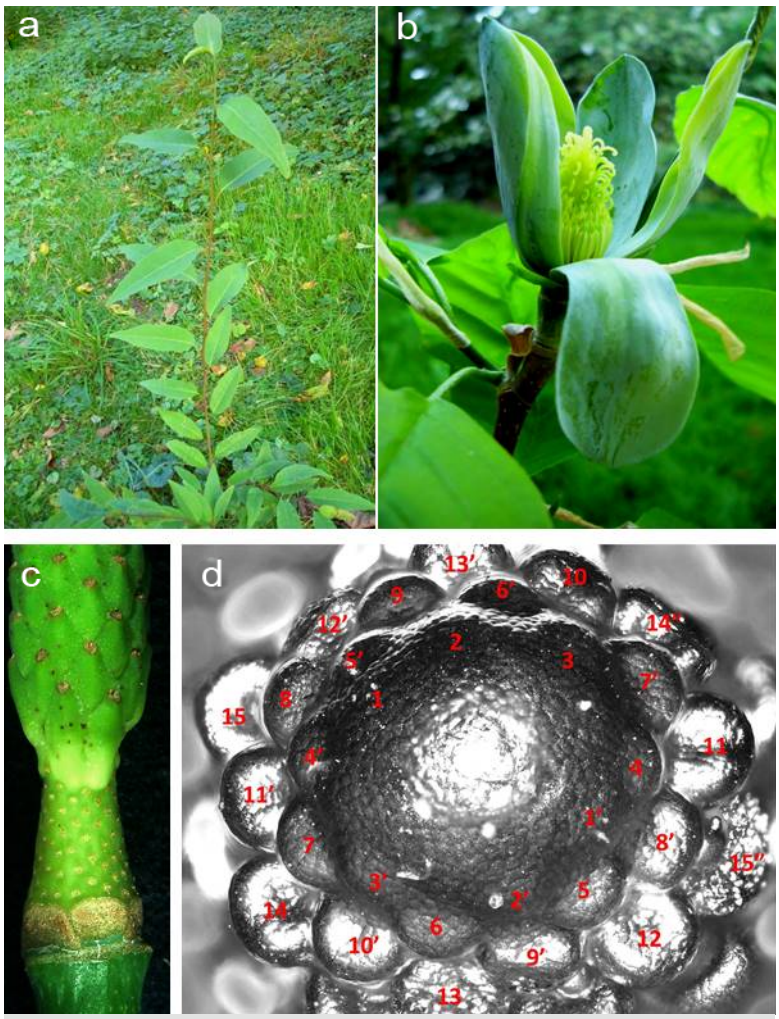

Fig. 1 Overview of *Magnolia* structures suitable for phyllotaxis research. **a** Young vegetative shoot of *M. salicifolia*: the initial distichy is followed by the main Fibonacci pattern. **b** Flower of *M. acuminata* with characteristically elongated floral axis enfolded in a trimerous perianth and covered by numerous, helically arranged, stamens and carpels. **c** Aborted floral shoot of the same magnolia after blooming. **d** Sputter coated epoxy replica of the floral apex of *M. acuminata* with the 6s:8z pattern of the Lucas bijugy, two z-oriented ontogenetic helices connect the carpel primordia numbered in each pair with and without an accent.

units. The analogous dislocations can be seen in a polar phyllotactic lattice when a new parastichy emerges between existing two, or, conversely, when two existing parastichies unite. The appearance of but one dislocation in the phyllotactic lattice means a total reconstruction of phyllotactic pattern [40,41].

Material and methods

Preparation of plant material

Floral buds of *Magnolia acuminata* trees were harvested in June, i.e., at the time when the embryonic flowers start forming primordia of stamens and carpels for the next blooming season. The buds were stored in the fridge before dissecting and making their permanent copies in the form of epoxy casts. The technique of microrelief replicas of the apex surface had been used according to the procedure described by Williams and Green [42]. The silicon dental impression compound Reprosil®, a product of Dentsply International Inc., was used for making nontoxic moulds. They were filled subsequently by Spurr's liquid epoxy resin; the polymerized casts, after hardening, were sputter coated.

After blooming season in the second half of July, the floral shoots that have not been pollinated are massively aborted from magnolia trees. They were collected from the ground. Their gynoecial part is sturdy enough at this stage to make modeling clay replica possible (Fig. 1c). Before that, phyllotaxis of each gynoecium was determined by counting opposite parastichies and recording their numbers in the *as*:*bz* formula (Adler's opposed parastichy pair [43] supplemented by the s and z indices of parastichy orientation). The most interesting cases were selected for copying. A piece of commercially available modeling clay was flattened and over its smoothened surface the cylindrical gynoecium was rolled by more than 360 degrees to make sure that the same pattern element – marker of the surface – was replicated twice on the opposite sides of the replica. The clay replicas were then photographed with a digital camera Olympus SP-565 UZ. The images show the surface of the gynoecium as seen from the inside of the shoot, thus the chirality of each phyllotactic pattern is opposite to the real one. To avoid confusion, we labeled them on the images as seen. The peculiar optical effect allows the perception of the copied negative image of the surface as a positive one. This illusion comes from a subjective decision where the light comes from.

Microscopy

Sputter coated resin casts of floral apices of magnolia were photographed in epi illumination using an Olympus BX50 Microscope, Olympus Camera DP71 and Cell B Software (Olympus Optical Co., Poland). Images were taken sequentially at different

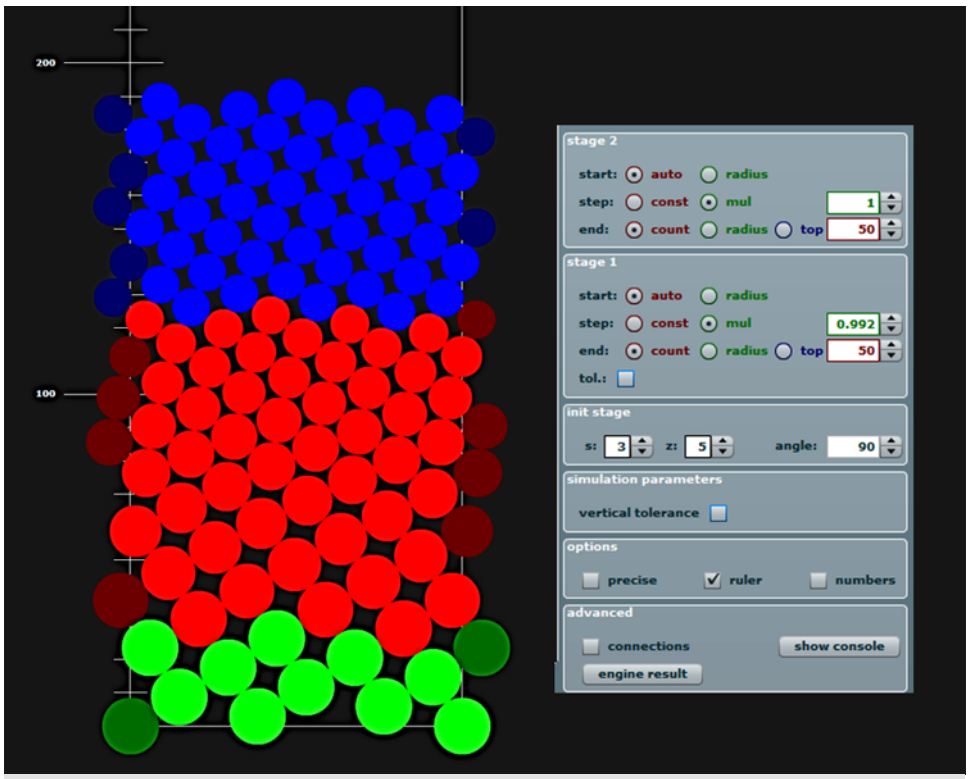

Fig. 2 Window of a computer program "Phyllotaxis". The parameters of simulation are given in a grey panel. They have always been recorded and stored together with the images presenting visual effects of simulations. This information for all the cases analyzed further is available in Fig. S1.

optical levels of each apex. Then, we used the focus stacking technique with the help of the Helicon Focus 6 program, a product of Helicon Soft Ltd (http://www.heliconsoft.com). The resulting images were comparable or sometimes even better to those obtained in a scanning electron microscope (SEM). This method is much faster and less expensive by far than using SEM. The phyllotaxis of each apex on the final compound image was determined by means of counting parallel parastichies in each set of the opposed parastichy pair. Subsequent primordia were numbered decreasingly in order of their initiation.

Computer program

For the experiments in silico, we used the upgraded version of the "Phyllotaxis"– a computer program written by the second author of this work. The phyllotaxis model, on which the program was based, was already described in our previous work [21]. The most important assumptions of this model are: (***i***) an infinite cylinder of a constant width as simulation space, (***ii***) primordia as circles of a changing radius, and (***iii***) primordia emerging in the first available space, in lowest possible position between the two neighboring, already existing primordia. In Fig. 2, we show the simulation window with a panel, which allows changing parameters of computer simulations. The images of the panels were always taken and stored together with the images of simulation visual effects. They are available in supplemental materials. The most important parameters are: (***i***) the initial pattern (green circles) set up arbitrarily by selecting parastichy numbers and the angle of their intersection, (***ii***) the rate of increase or decrease in primordia size in two consecutive stages of simulation (red and blue circles), in which this rate can be different, (***iii***) size and vertical tolerance available in stage one only. The latter two parameters are new. Size tolerance means that the size of primordia, changing systematically, may vary at random within a certain range of diameter values – each consecutive circle may be a little smaller or bigger than expected from ongoing continuous change in its size. Vertical tolerance in turn means that primordium is not always initiated in the lowest position in the first available

space. This obviously increases the number of possible initiation sites. The selection of a particular site affects further development of phyllotactic pattern in a different way than the selection of any other site.

The program is suitable for quantitative analysis – it records the position and the size of each successively emerging element in a simulation space.

Results

As already mentioned, the ratio between the size of initiated organ primordium and the size of organogenic surface of the shoot apical meristem is important for the quality of emerging phyllotactic pattern. Plant shoot development is a dynamic process involving changes in the ratio by modifying either one of the two parameters or both simultaneously. When the apex circumference is reduced, relative to the size of primordia, the expression (order) of the phyllotactic pattern decreases and so does the number of conspicuous parastichies in the opposed parastichy pair [43]. In the opposite situation, with a rising order of phyllotaxis, the number of contact parastichies is increased.

In our experiments, we applied the changes in primordia size only. The primordia, represented by the circular units, were positioned one after another in a constant simulation space, observing the principle of filling the first available space in the lowest possible position [44–46]. The model and its assumptions were the same as described in our previous works [10,21].

Phyllotactic transitions

When all new primordia were of the same size, the initial pattern set up at the beginning of simulation was propagated indefinitely unaltered (Fig. 3a–d). Only when the changes in primordia size were applied did pattern transformations become possible. When the changes were continuous, i.e., the size of each consecutive primordium was bigger or smaller by the same fraction of the size of the preceding primordium, the expression of the initial chiral pattern was changing but the pattern itself did not – the parastichy numbers still belonged to the same mathematical series. This situation can be seen in the upper portions of the virtual shoots with the primordia decreasing in size in Fig. 3e–g. The parastichies change there in the following sequence: 1s:2z → 2z:3s → 3s:5z → 5z:8s … for the main Fibonacci (Fig. 3e), 2z:4s → 4s:6z → 6z:10s … for the main bijugy (Fig. 3f), or 3z:6s → 6s:9z → 9z:15s … for the main trijugy (Fig. 3g). In a course of these transitions, the primordia packing switched between tight and loose. Both these states differ significantly in how effectively the organogenic space is being used, even though the pattern quality is practically the same, as in Fig. 3a–d. Stabilizing primordia size at any moment of growth would naturally promote only one of these conditions in further development.

However, we also noted that under some circumstances the same continuous changes in primordia size might lead to discontinuous, qualitative changes of phyllotaxis – to the transformation of an achiral pattern into a chiral (Fig. 3e–g,j – bottom parts) and vice versa (Fig. 3h,i) or even to the transformations between different chiral patterns (Fig. 3k,l). In some cases, the rearrangement of pattern elements proceeded smoothly (Fig. 3e–i), in others the moments were clear when, due to the continuous change in primordia size, the preceding pattern in its lowest expression entered the state of instability (Fig. 3j–l). This very interesting developmental situation and its causes have been described and discussed in our previous work [10].

The entirely new observation was that the same Lucas pattern changed into the main Fibonacci one with or without the reversal of ontogenetic helix depending upon the history of the virtual shoot (Fig. 3k,l). Two qualitative transformations shown in Fig. 3k result in the chirality of the final pattern different that in Fig. 3l, where transformation is only one. In both simulations, though the rate of change in primordia size is the same. In a vast majority of these particular transitions (Lucas – Fibonacci) recorded in nature, the reversal of ontogenetic helix was noted [18,47].

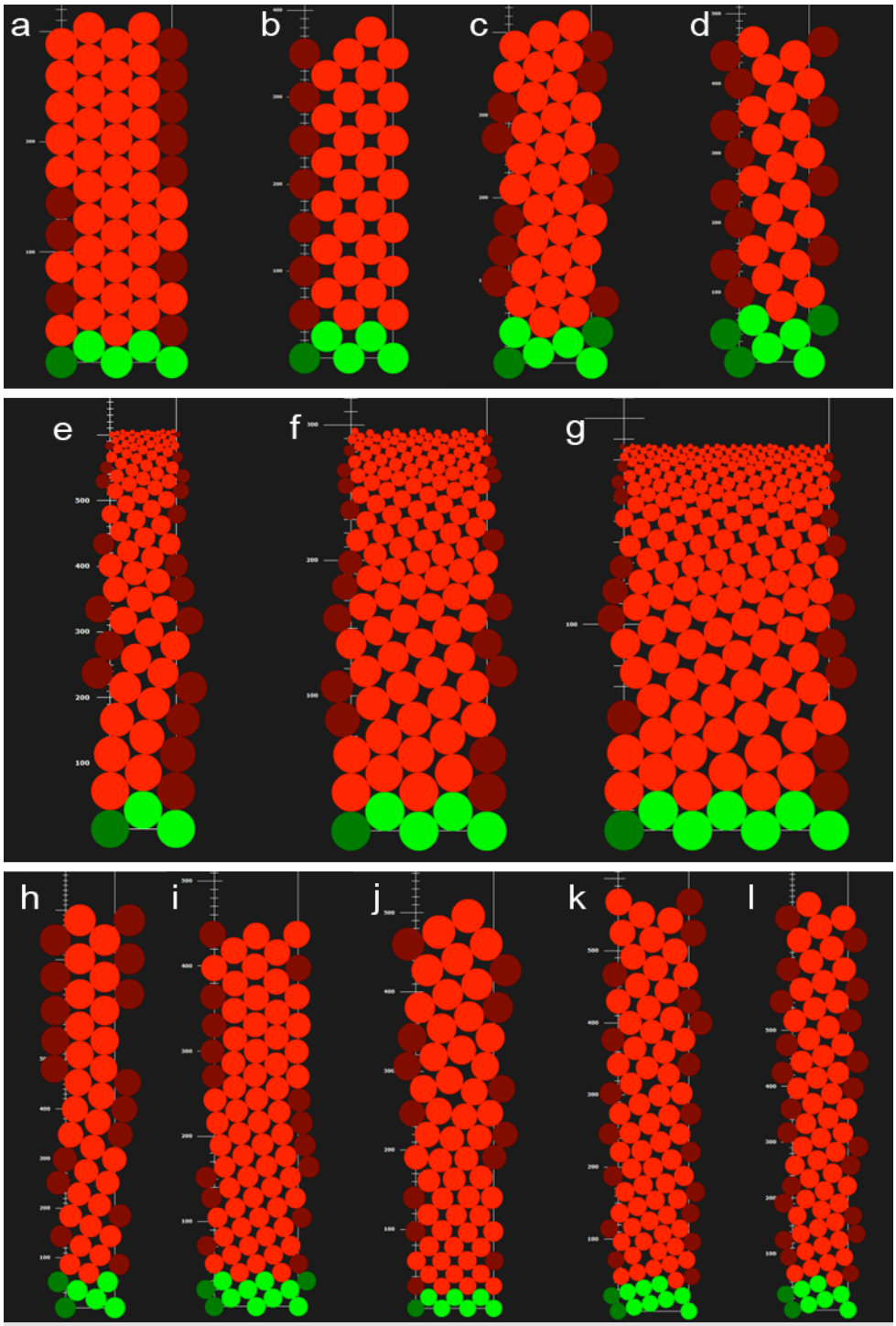

Fig. 3 Various phyllotactic lattices in computer simulations. **a–d** Different efficiency of packing elemental units (circles) on the split-open surface of a cylinder; tight and loose packing into 2s:2z achiral decussate pattern (**a,b**) and the same for the 1z:2s chiral, main Fibonacci pattern (**c,d**). **e–l** Pattern transformations resulting from the continuous decrease (**e–g**) or increase (**h–l**) of elemental unit size; achiral patterns change into chiral (**e–g,j**) and vice versa (**h,i**); 1s:1z distichy changes into 1s:2z main Fibonacci phyllotaxis (**e**), decussate 2z:2s pattern into 2z:4s bijugy (**f**), tricussate 3z:3s into 3z:6s trijugy (**g**), 1s:2z into distichy (**h**), bijugy into decussate (**i**), trijugy into 2s:3z Fibonacci (**j**), 1z:4s first into 1z:3s then into 1s:2z (**k**) and 1z:3s into 1z:2s (**l**); single parastichies disappear from the lattice in **j–l**. The developmental sequence of patterns is from the bottom up. Green color marks the initial pattern, red – the resulting pattern; the surface of a cylindrical virtual shoot is shown as a split open rectangular simulation space; the same pattern element on opposite margins of the space is marked with the same but bright and dull color. Here and on subsequent figures every centennial unit of the vertical scale is labeled: 100, 200, etc.

Notably, in some of these simulations, where the continuous change in primordia size was applied, clear dislocations could be seen. These were the same defects of phyllotactic lattice, as observed earlier in the reality of plant shoot development. What are the dislocations and what is their meaning for the phyllotaxis of the shoot?

Dislocations in vivo

In the natural discontinuous transitions of phyllotaxis in coniferous vegetative shoots or in magnolia flowers [14,38,39], when the pattern changes qualitatively – the parastichy numbers from the opposed parastichy pair before and after transition belong to the different series, e.g., 3:4 → 3:5. This is accomplished through dislocation – a peculiar event, which takes place usually in one set of parastichies only. Two parastichies unite in a phyllotactic lattice producing the effect further called λ-dislocation (Fig. 4a,b) or one of the parastichies bifurcates resulting in γ-dislocation (Fig. 4c,d). Both types of dislocations in phyllotactic patterns have been encountered in nature. The first to notice the phenomenon of missing or additive parastichies was Church [48]. In his classical work, there is a photograph of *Dipsacus* inflorescence, where these ephemeric parastichies are labeled with broken lines. Church did not analyze closely the meaning of these effects for the whole phyllotactic pattern. It was not until the number and orientation of parastichies before and after dislocation were recorded that we suddenly realized the significance of dislocations. It appeared that phyllotactic transitions occurring through dislocations put in question the real meaning of many descriptive concepts used traditionally in the theory of phyllotaxis such as divergence angle or ontogenetic helix. Only one λ-dislocation in a 4:8 tetrajugate pattern transforms it into a Lucas 4:7 pattern (Fig. 4a). The initial four ontogenetic helices are reduced to one. The same initial pattern may change into the 5:8 main Fibonacci phyllotaxis (Fig. 4d). In this transition, again only one γ-dislocation causes the reversal of ontogenetic helix course and an increase of the divergence angle from 34.4° (137.5°/4) to 137.5°. Similarly, the very rare 3:8 pattern with one ontogenetic helix and divergence of 132.7° changes either into trijugy (Fig. 4b) or tetrajugy (Fig. 4c), with three and four ontogenetic helices, respectively. All together, in the four floral shoots shown in Fig. 4a–d, six different patterns are present.

Dislocations in silico

In modeling shoot apex development and its organogenetic activity, we have been able to reproduce both of the above defects in a phyllotactic lattice associated with ontogenetic transformations of phyllotaxis. As expected, a continuous increase in primordia size resulted in a decrease in the number of parastichy – via λ-dislocation (Fig. 4e), whereas a continuous decrease in primordia size caused the appearance of γ-dislocation (Fig. 4f).

However, through the continuous increase in primordia size it was not possible to obtain in silico the situation, observed sometimes in these real lattices of magnolia, in which γ-dislocations occurred in a carpel domain (Fig. 4c,d). These were rather puzzling effects in light of the fact that the floral apex with its determinate growth, at the final developmental stage of producing carpel primordia, should not allow for the multiplication of parastichies. The determinate growth means cessation of proliferative divisions in the population of the stem cells and this leads to unavoidable decrease in the ratio between the size of the organogenic surface and the size of primordia. One should expect only λ-dislocations in this case. Then we have noticed that in virtual magnolia flowers, the pattern of the terminal part of the floral axis (carpel domain) depended upon a very small change in a number of virtual stamens even when all other parameters of the simulations were the same (Fig. 5a,b). It immediately became clear that the profile of the interface between the domains of stamens and carpels was decisive for the ultimate pattern of floral phyllotaxis present in a carpel domain.

Inspired by this observation, concordant with the described above impact of phyllotactic system's history on the quality of a pattern emerging from transition (Fig. 3k,l), we introduced to our simulations the tolerance parameters.

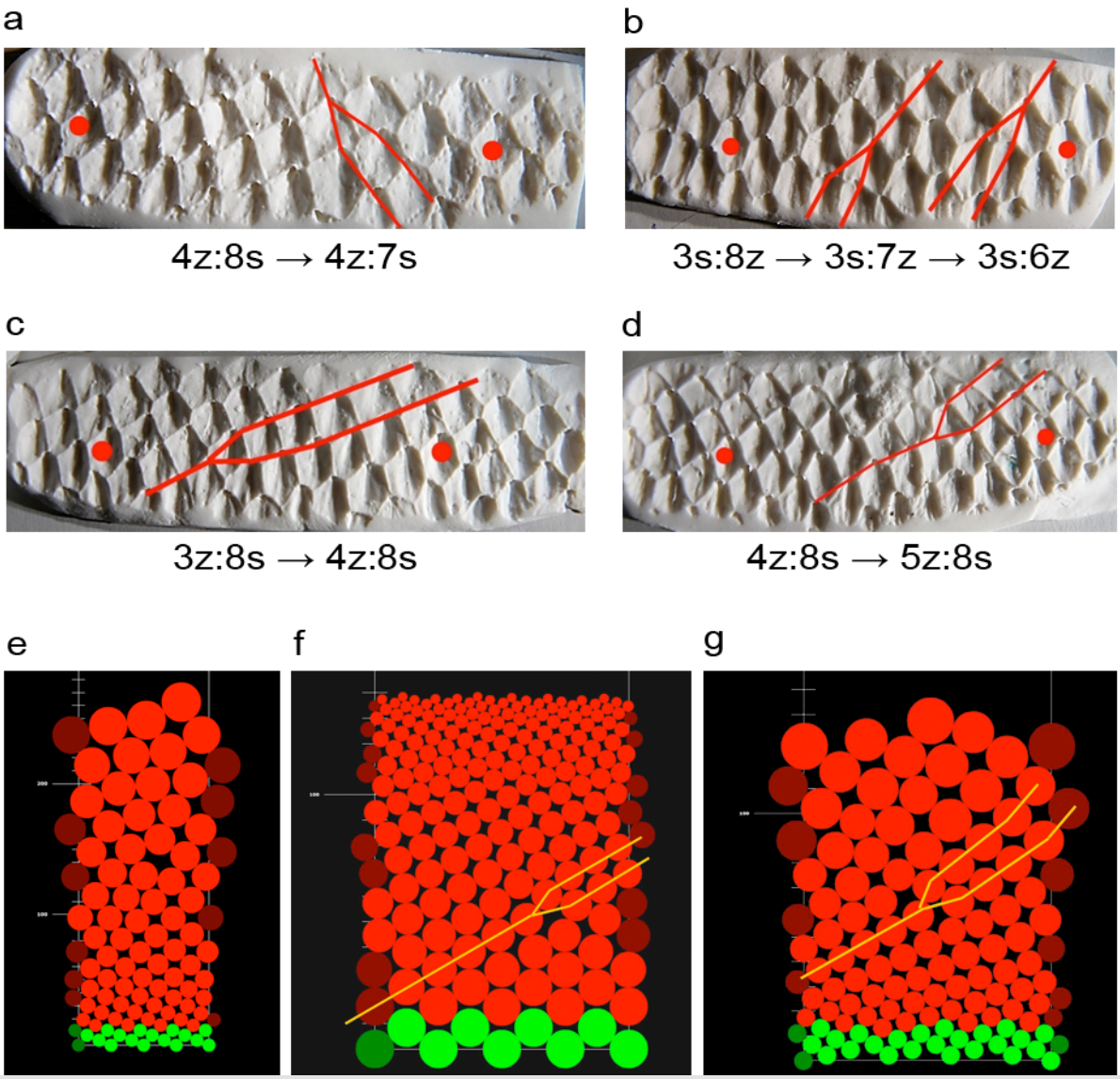

Fig. 4 Properties of the real and virtual lattices with phyllotactic transitions. **a–d** Modeling clay replicas of *Magnolia acuminata* floral shoots with phyllotactic transitions accomplished through λ-dislocations (**a,b**) and γ-dislocation (**c,d**); **e–g** The same dislocations in virtual lattices as the results of developmental increase (**e,g**) or decrease (**f**) in primordia size; in **e,f** the change in size is continuous, in **g** it fluctuates due to applied size tolerance, which causes the appearance of γ-dislocation; single dislocation changes 4:8 tetrajugy into 4:7 Lucas (**e**), achiral tetracussate into 4:5 chiral pattern (**f**) and tetrajugy into main Fibonacci pattern (**g**); if the rate of the decrease in **f** were different, this pattern would transform smoothly into tetrajugy, similarly as the patterns shown in Fig. 2**e–g**; the virtual transition in **g** is the same as the real one in **d**.

The significance of tolerance parameters

Two tolerance parameters added to our computer program as options and used in further computer simulations were (***i***) size tolerance and (***ii***) vertical tolerance. Introducing size tolerance, we have assumed that in nature the consecutive units of emerging phyllotactic pattern are neither exactly of the same size nor do they change their size by exactly the same fraction of the former size, which is practiced in many mathematical geometric models. It is also clear that the initiation of any new pattern element may not always take place in the lowest possible position, as required by the Snow and Snow and Hofmeister rules [44–46]. We have earlier pointed out that the first available space may sometimes be big enough to accommodate the emerging pattern element in two equivalent positions [21]. Hence, a parameter of vertical tolerance, together with the parameter of size tolerance, by virtue of increasing the number of equivocally determined initiation sites in the first available space, should be considered as very important factors affecting the frequency and the course of phyllotactic transitions.

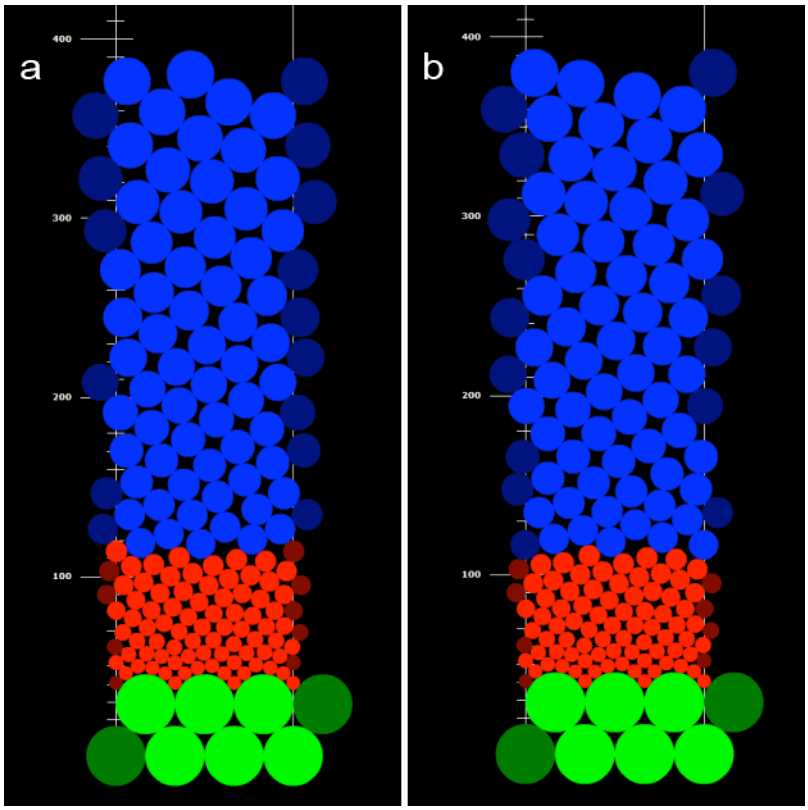

Fig. 5 Two virtual floral shoots of magnolia differing in a profile of the interface between the domains of stamens and carpels. The large perianth primordia are arranged in two trimerous whorls (green), they are followed by numerous small stamen primordia (red) and slightly bigger carpel primordia (blue); all parameters of both simulations are the same with one exception – the number of stamens in **b** is lower by one from that in **a** (red dot on the left), this small change makes a substantial difference: the final pattern in gynoecium zone (blue) in **a** is 2s:3z main Fibonacci whereas in **b** it is 1s:3z Lucas; the chirality of ontogenetic helix (order of initiation) in both final patterns is different.

Application of size tolerance resulted in the appearance of γ-dislocation under circumstances of the systematically decreasing ratio between the size of the organogenic surface and the size of a phyllotactic pattern element (Fig. 4g). This decrease is expected for the shoots with determined growth. In our simulations it was obtained by increasing the primordia size. The most important conclusion from this experiment is that the appearance of γ-dislocation in a real plant system does not reliably reflect the direction of developmental changes in the shoot apical meristem's geometry. They may appear in these shoots where the ratio was increasing as well as in those where the decrease of this parameter was taking place.

Using tolerance parameters we have also succeeded in transforming in silico a peculiar 3:8 pattern into the pattern different than the main Fibonacci (Fig. 6c). This extremely rare pattern emerges sometimes in magnolia flowers, in the lower part of gynoecium (Fig. 4b,c and Fig. 6d) probably as a result of rapid, discontinuous change in the size of primordia switching from the stamen to carpel identity. In silico, in a continuous transition, when the size of primordia constantly increases, this pattern changes without exception into the main Fibonacci pattern, regardless of the rate of the increase (Fig. 6b). The opposite tendency increases this pattern's expression only (Fig. 6a). Size tolerance together with vertical tolerance caused the 3:8 pattern's qualitative transformation into the 4:7 Lucas pattern (Fig. 6c). Interestingly, it was identical with the real one, which is relatively frequent in magnolia flowers (Fig. 6d). In both cases, γ-dislocation and λ-dislocation appear in the same area of the lattice and 11 parastichies continue their course unchanged from one pattern to another (Fig. 6c,d).

It is likely that the tolerance is responsible for the qualitative changes of the main Fibonacci pattern, that have been documented in the natural plant systems [18,47]. In computer simulations, the pattern appears to be the most stable pattern of all, under circumstances of perfectly continuous change in primordia size [10,21].

Discussion

Ongoing quest for the mechanisms of robustness in phyllotaxis in experimental plant biology [49,50] is heavily affected by the fact of relative stability of the main Fibonacci in a model plant *Arabidopsis thaliana*. The major challenge then is to find out the level of noise that guarantees maintenance of the pattern. Too much noise, caused for instance by mutations affecting "happy balance" of metabolic pathways, results in alterations of phyllotaxis such as reversal of ontogenetic helix, switch to distichy, etc., as mentioned by Mirabet et al. [49]. However, in light of the omnipresence of developmental phyllotactic transitions in plants, there is more discussion needed on what robustness of phyllotaxis really means. For instance, what does it mean

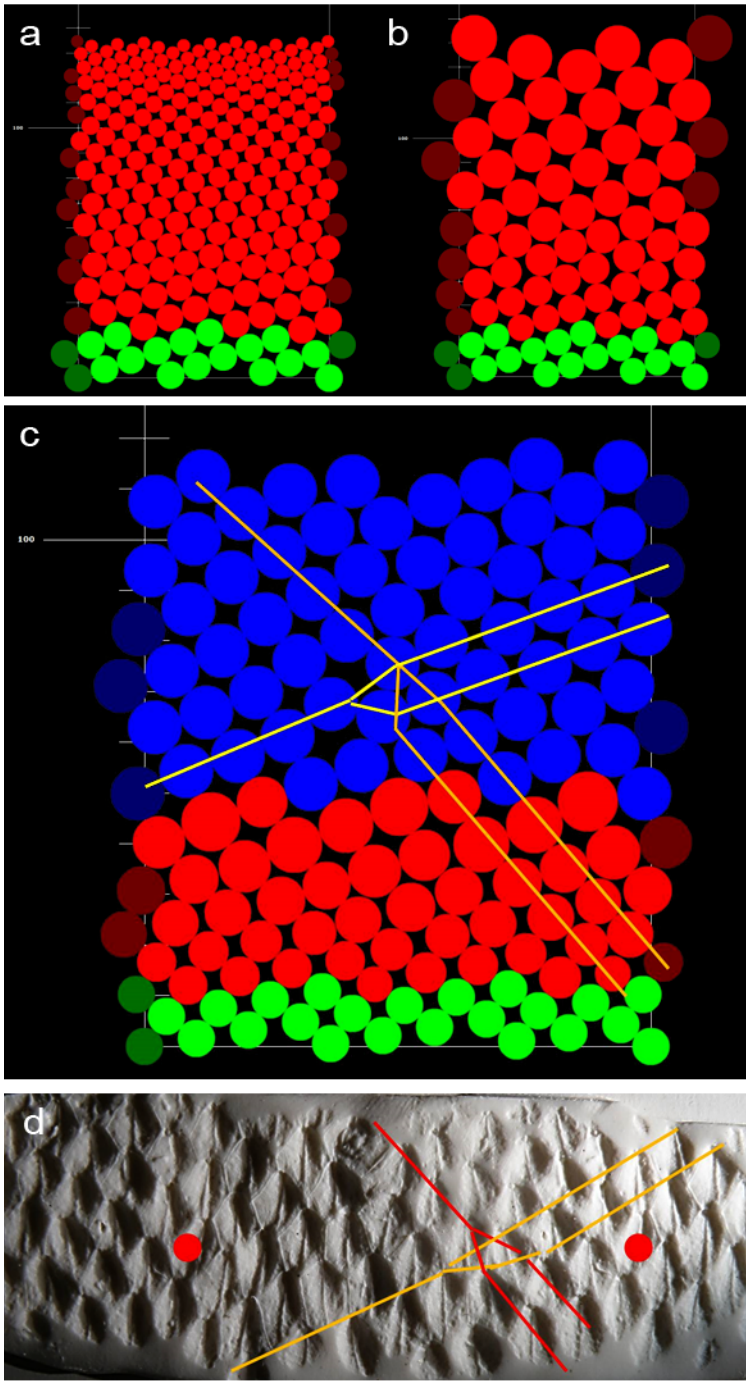

Fig. 6 Transformations of 3:8 chiral pattern in silico and in vivo. The effects of continuous decrease (**a**) or increase (**b**) of primordia size in computer simulation: in **a** the expression of the initial pattern is rising upward: 3:8 – 8:11 – 11:19 …, in **b** – a quick change into 3z:5s Fibonacci takes place; application of tolerance parameters in **c** causes transformation of the 3z:8s pattern into the 4z:7s Lucas phyllotaxis; virtual transformation in **c** is identical with the real one recorded in modeling clay replica shown in **d**, it was obtained with application of tolerance parameters in a red zone, blue pattern elements are all of the same size; dislocations emerge in a blue zone as late effects of the former irregularities in a process of pattern formation.

"the maintenance of the pattern" – maintenance of its order (expression) or quality? The consequent, continuous change in size of organ primordia, proceeding without or with a very small noise, changes order of phyllotaxis but may also bring its qualitative change as demonstrated by our transition from Fibonacci to distichy shown in Fig. 3h, the same as the one noted by Mirabet et al. [49] Yet, there are phyllotactic transitions that cannot be explained without introducing sufficient noise called in our paper tolerance. They are available for analysis in *Magnolia* floral axis, where phyllotaxis is extremely variable.

The field theory, widely accepted today, proposes that the regular spacing of primordia, initiated at the shoot apical meristem, is due to existence of inhibition fields [51,52]. The biochemical factor required for their formation is auxin concentration changing in the space of the shoot apical meristem's surface [53,54]. The size of the field is defined in physiological terms as the size of an area surrounding each primordium where the auxin concentration is below the threshold required for the initiation of a new primordium. In our model, the sizes of the fields are visualized by the geometric sizes of primordia packed on the shoot apical meristem's surface. This simple representation already used by other authors [55] allowed us to analyze the long-range effects of the changes in the field size for phyllotaxis. We have obtained a whole palette of possible transformations of phyllotaxis including those associated in many plant species with the developmental phase shift. We succeeded in transforming in silico the achiral into chiral patterns and vice versa. Developmental coexistence of these patterns has been earlier predicted by Douady and Couder [56] and further analyzed by Smith et al. [57]. Here, we would like to point out how concordant our results are with the analyses of the sizes of apical meristems in maize plants with ABPHYL syndrome [29–31] or in *dec* mutants in rice [58]. Larger apical meristem in these plants have helical or decussate phyllotaxis instead of distichous, which is typical not only for the WT rice and maize plants but also for the majority of monocots – grasses and orchids. Here, in Fig. 1 it can be seen that distichy is also present in the vegetative shoots of magnolia [59]. Among many other primeval traits it is likely evidence of the common ancestry of this early divergent lineage of flowering plants and monocots [19,60]. What is important, in our simulations the ratio between the size of simulation space and the size of primordia in the case of distichy was the smallest (Fig. 3e,h). Apart from rather common changes in phyllotaxis, less known esoteric transitions occurring between various chiral patterns,

which often involve dislocations, have also been successfully reproduced in silico (Fig. 3k,l, Fig. 4e,g, and Fig. 6c).

Despite the intuitively correct prediction that the rapid changes in primordia size associated with developmental changes in organ identity should be the main factors affecting phyllotaxis, we have demonstrated that a continuous small change in primordia size may also lead to symmetry breaking in developing pattern and qualitative change in phyllotaxis (Fig. 3). The observation that phyllotactic transition is affected by the past history of developing phyllotactic system (Fig. 3k,l) and that the qualitative change of the pattern may be delayed to the moments when the geometric changes stabilize (Fig. 6c), is particularly important. This peculiar "butterfly effect" [61] may explain why phyllotaxis sometimes changes for no obvious reasons. The significant role of history in the development of phyllotactic patterns has been earlier shown through experiments performed in vivo [62] and in silico [57]. Last but not least outcome of this research is that in development the plants are not that mathematically accurate in "calculating" the geometry of their organs. Only this explains the phenomenon of γ-dislocations in determined floral shoots (Fig. 4g) or observable in vivo transformations of the rare 3:8 phyllotaxis (Fig. 6c). The tolerance means that the shoot apical meristem sequestring iteratively a poll of stem cells for the lateral organ primordium, takes sometimes a little more, sometimes a little less of them from the whole population. Or rather – using the terminology of the field theory – the inhibition field surrounding the primordium is once a little bigger and then a little smaller. This simply may be caused by the inherent noise of chemical reactions [63] that can be more or less efficiently filtered in biological systems [64]. Our analysis brings some interesting implications for the field theory – to explain the real developmental changes in phyllotaxis, especially those interesting ones in magnolia, we must accept that the sizes of the fields are not constant but modulated – capable of dynamic changes. Changing organ identity for these is not required, as we have shown in our simulations of the continuous changes.

What may change the size of the field, then? One plausible factor is the efficiency of the auxin drainage by the developing primordium. The significant role of veins differentiating beneath the primordium in scavenging and absorbing auxin from the surface and later canalizing its flow downward has been very recently demonstrated [65]. The effectiveness of this process must affect the size of the inhibition field.

The other possible factor is the rate of auxin transport and biosynthesis, which may also modulate auxin concentrations outside the fields. The consequence of the auxin model [53,54] is that the new primordium at the shoot apex is initiated where the auxin concentration is sufficiently high. The possibility of modulating auxin concentrations by cytokinins and controlled expression of the genes such as *PLETHORA* or *INDETERMINATE DOMAIN* involved in auxin biosynthesis, transport and degradation is now being intensely studied [50,66–69]. The area between adjacent inhibitory fields corresponds to Snow and Snow's first available space. We have shown earlier in our experiments in silico that this space may sometimes be big enough to accommodate more equivalent initiation sites than one [21]. Which one is chosen? Is this selection random? Or there is another modulatory mechanism involved? According to Steeves and Sussex [52], well before Larson [70], this possibility was considered and the vascular system was proposed to be a source of regulatory signals. It was Larson, however, who was first to provide solid evidence that the changes in the vascular architecture are preceding the corresponding changes in the order of phyllotaxis taking place at the shoot apical meristem. Now, there is growing evidence that the signals moving acropetally from the developing strands of the primary vascular system may affect phyllotaxis by controlling initiation sites at the shoot apex and it cannot be excluded that this is through the auxin signaling. One may speculate that basipetal transport of auxin from the primordium acting as a sink, confined to procambial strands and later to the cambium of primary vascular bundles makes the hormone available for lateral diffusion to the adjacent, already differentiated protoxylem and xylem. Once it has entered these conducting elements, auxin would have to move back – up to the apical meristem. To date, auxin presence in xylem sap is yet to be demonstrated. That the signals coming from the vascular strands may indeed affect phyllotaxis, as postulated by Larson [70], has been revealed first in conifers [14] and then in the *pin* mutants of *Arabidopsis* [71]. In *Torreya*, phyllotaxis of the small needle

primordia is bijugate. When the large primordia of winter bud scales start emerging the phyllotaxis slowly changes into decussate. At the same time, the distance between the differentiated vascular strands and the initiation sites significantly increases. In other conifers, where the distance is maintained, such as *Picea* or *Abies*, phyllotaxis of the needles and bud scales is principally the same, it continues from year to year what may be called an example of axial homodromy. In *Torreya*, every consecutive year the chirality of bijugy is established de novo, at random, which is yet another proof of the shoot apical meristem being temporarily released from the influence of the vascular system. During further stages of needle primordia formation, the distance of the vascular system from initiation sites is small. Even more interesting facts are provided by the analysis of organogenesis in *Arabidopsis* mutants with the defective polar auxin transport. Banasiak [71] was the first to become intrigued by the fact that *pin* mutants are capable of producing healthy, well-developed leaves in the vegetative rosette, where the internodes are very short. She has shown that in bolting inflorescence the organogenesis is completely blocked in effect of growing vertical distances between the youngest protoxylem elements and the potential initiation sites of the apical meristem. Thus, it is possible that to the list of factors changing the size of the fields – cytokinins and genes regulating auxin biosynthesis and degradation, the acropetal vascular signaling will soon be added.

The whole scenario of the genetic regulation of phyllotaxis is very complex and is yet to be understood. Only one single mutation of the *PERIANTHIA* gene in *Arabidopsis* changes its canonic tetramerous architecture into pentamery [72], also a single gene mutation of the *ABPHYL* gene in maize alters its phyllotaxis via enlarging the shoot apical meristem. Double *cycloidea* and *dichotoma* mutants in *Antirrhinum* do not only have peloric flowers, but except for the pistil they have six floral parts in each whorl instead of the five typical for WT plants [73].

The genetic regulation is behind the changes in organ identity, which are often, but do not have to be, associated with the qualitative changes in phyllotaxis. The new size of the inhibition field surrounding the new identity primordium is crucial. When the change in the size is abrupt – phyllotaxis transformation is expected. Sometimes, however, the changes must be small and then the same phyllotactic pattern continues from one phase of shoot development to another as in the sunflower or in conifers with axial homodromy.

In fact, there are many examples suggesting the independence of two genetic mechanisms which act within plant shoot meristem. One of them is the quite well known mechanism specifying the identity of lateral organs, the other, more enigmatic, is responsible for their spacing. In *Magnolia stellata*, the primordia already set up in a spiral manner, typical for the stamens, i.e., generative parts, develop subsequently into petals even though in the perianth petals are usually whorled in the genus [74]. The leaf-like organs in triple ABC mutant in *Arabidopsis* maintain floral whorled phyllotaxis, even though the leaves and bracts in this plant are spirally initiated. This situation much resembles the earlier reported case of *Impatiens balsamina* where in the reverted floral meristem the whorled floral distribution of now vegetative organs remains unaltered [75]. Similarly to *Arabidopsis*, the vegetative phyllotaxis in this plant is spiral.

We believe that in this work we have offered a new insight into all these individual cases. The results of computer simulations of the shoot growth allow us to see in a simplified way how changing sizes of inhibition fields, visualized as geometric sizes of the lateral organ primordia, may affect phyllotaxis, triggering (or not) phyllotactic transitions. The experiments in silico may become a powerful tool in our attempts to understand better the nature of changing phyllotaxis.

Conclusions

The experiments in silico confirm that the quality of phyllotactic pattern is determined by the ratio between the primordia size and the circumference of the shoot apical meristem, but also by the history of the developing phyllotactic system. Even continuous changes in this ratio may bring qualitative changes in phyllotaxis involving transitions

between chiral and achiral patterns. The changes in the ratio and in phyllotaxis usually are but do not have to be associated with the change in the identity of plant organ primordia. Tolerance in positioning of primordia in the first available space explains the direction of some special phyllotactic transitions encountered in nature. Developmental addition of parastichies (γ-dislocation) is possible even when the surface of the shoot apical meristem decreases. The *Magnolia* flower is recommended as a model plant for phyllotaxis research because of its richness in phyllotactic spectrum. It gives us an insight into the subtleties of phyllotaxis not available in other plants.

The potential for ontogenetic changes in phyllotaxis of a growing plant shoot is great. In light of our findings, even though they explain why phyllotaxis changes and why it may be so diverse, it is still amazing how precise and strict the control of organogenesis must be in all these prevailing situations when the perpetuated phyllotactic pattern remains unaltered.

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Supplementary material

The following supplementary material for this article is available at http://pbsociety.org.pl/journals/index.php/asbp/rt/suppFiles/asbp.3532/0:

Fig. S1 Panels with parameteres of simulations shown in subsequent figures of the main text.

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