

Magnolia flower - the living crystal

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The geometric principles of form development in nature are universal: they pertain both to living and non-living matter. The phenomenon of periodic pattern formation, expressed so well in crystals, is also observed in living organisms, especially plants, which in a composition of their body resemble crystals because of very regular arrangement of their lateral organs: leaves, flowers or flower parts. The reason for this regularity is that the plant organs are produced iteratively. Like crystal units in growing crystals, they are being added continuously to the developing body of the plant in a process of its undetermined growth. One of the most beautiful examples of the crystal-like nature of a plant is the magnolia flower.

The beauty of magnolia flower, as all lovers of this plant know, lies in its color, shape and unique delicate fragrance. All these features are variable, which is the reason many of us dream about having in our garden as many forms of magnolia as possible. Pink, yellow, orange, purple, pure white, creamy white, and blue-green flowers of these fragrant beauties decorate our life. However, not all magnolia lovers know that the hidden beauty of this exceptionally charming plant is an extremely diverse floral phyllotaxis.

Phyllotaxis is a distribution of lateral organs in plants. As already mentioned, it is very regular, although the circumferential spacing of organs may be diverse. The students of their diversity have classified the patterns of phyllotaxis into two categories: whorled and spiral (helical). In whorled patterns more than one pattern element is initiated at the same level of the shoot. In spiral pattern its elements are initiated consecutively, one after another, and may be connected in developmental sequence by the spiral or helical line ascending along the shoot. Magnolia flower demonstrates them all, having whorled perianth and spirally arranged generative parts.

Perianth structure – is it always whorled?

In the perianth the tepals are usually assembled in three whorls, each whorl consisting of three elements. Exceptions from this trimerous condition have been observed in *M. sprengeri*, *M. campbelli* and *M. grandiflora*, where tetramery sometimes occurs (Fig. 1). This type of meristic variation in floral patterns is not uncommon in angiosperms and in the past it must have played a key role in evolutionary transition from trimery, characteristic for some magnolids and monocots, to tetramery and pentamery of the dicots.



Fig. 1. *Magnolia grandiflora* – unusual tetramerous flower with three visible whorls of tepals; each whorl is composed of four elements. (photo by Richard Figlar)

Another modification of the perianth structure is when the tepals are initiated on the axis of the flower according to a spiral mode. In this case the seemingly trimerous condition represents, in fact, the false whorls. They appear often, although not exclusively, on the border between the perianth and the generative zone in so-called tepalodic flowers. The tepalody in magnolia, as a petalody in roses or peonies, occurs when the uppermost perianth elements differentiate from already formed and spirally arranged primordia of stamens (Figs. 2, 3). Flowers become more “showy” and fragrant and thus attractive to beetles and...gardeners. No wonder that in a course of evolution this strategy of flower development has been stabilized in some species. *Magnolia stellata* in particular (Fig. 4), but also *M. obovata* (Figs. 3, 6), have typically tepalodic flowers. Setting up the primordia of flower parts in a spiral mode, characteristic for stamens and pistils, and making the tepals from them proves that in flower morphogenesis the two genetic systems—the one responsible for organ identity and the second for the organ spacing—may act independently. This, of course, increases the diversity of flower forms.

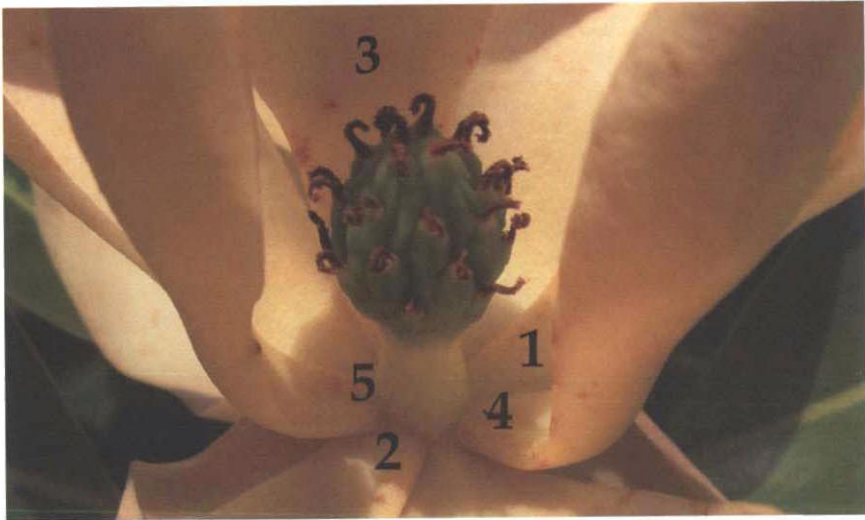


Fig. 2. *Magnolia virginiana* – close-up of the flower's inside shows that the upper "whorl" of tepals is not at all a whorl. The organ initiation in this flower entered a spiral mode (typical for the stamen's zone) in the uppermost part of the perianth. It is clear from the position of tepals 4, 2 and 5 that they are neither on the same level vertically nor spaced equally along the circumference. They have been numbered in ontogenetic sequence, from which it is clear that they had been initiated in spiral Fibonacci pattern. In this particular pattern three elements are initiated on one revolution of ontogenetic helix (spiral) at the angle 137.5° one from another. These five elements have developed tepal identity (the tepal genes delayed turn-off) even though they were positioned by the independent genetic system, which already spaced them according to the mode typical for stamens. (photo by Richard Figlar)



Fig. 3. *Magnolia obovata* – one of the first developing leafy stamens has not fully "decided" whether it is a tepal or a stamen. It is longer and wider than other stamens, but does have a red coloration at the base, as all others have.



Fig. 4. *Magnolia stellata* – the rich and attractive perianth of this "full" tepalodic flower (left) has the tepals arranged initially in whorls of three. The subsequent tepals are inserted along the spiral (right). This is not a deviation from the normal development, but the species-specific trait that has been evolutionarily stabilized. (Niagara Parks Botanical Gardens, School of Horticulture, Ontario, Canada)



Fig. 5. *Magnolia* "Yellow River" - the hybrid has morphologically undifferentiated perianth inherited from one of its parental species - *Magnolia denudata*. (Przeclawice Garden, Poland)

The identity of perianth elements is a matter of dispute. It is generally accepted that magnolia's perianth is undifferentiated, which means that it is not divided into calyx of sepals and corolla of petals. This is undoubtedly true for *Magnolia denudata* and its hybrids (Fig. 5) as well as for *M. campbellii* or *M. salicifolia*, even though some sources describe this situation as one in which the petals and sepals are

identical. However, some other species such as *Magnolia obovata* (Fig. 6), *M. acuminata* (Fig. 7) and *M. liliiflora* (Fig. 8), show that the morphology of their outermost whorl of tepals is clearly different, which result in its calyx-like appearance. In my laboratory at the University of Wroclaw, the study of magnolia DNA and of ABC gene expression pattern in the floral parts is presently underway. Magdalena Turczyn, my doctoral student, is working on this project in order to resolve the dilemma of true identity of morphologically diverse tepals.



Fig. 6. *Magnolia obovata* - the outer whorl of three perianth elements is very different than the inner whorls. Its parts are large, reddish and thinner than the tepals proper. Their delicate translucent beauty underlines the flower magnificence. Uppermost tepals are no longer set up in whorls. They develop at the expense of stamens (tepalody) and are getting narrower, sometimes even sharing some features with stamens as shown on Fig.3. (Przeclawice Garden, Poland)



Fig. 7. *Magnolia acuminata* – the first whorl of perianth elements is different than subsequent whorls and has calyx-like appearance: tepals are smaller and deep green, greener than the upper tepals, which are bluish- or yellowish-green. (Przeclawice Garden, Poland)

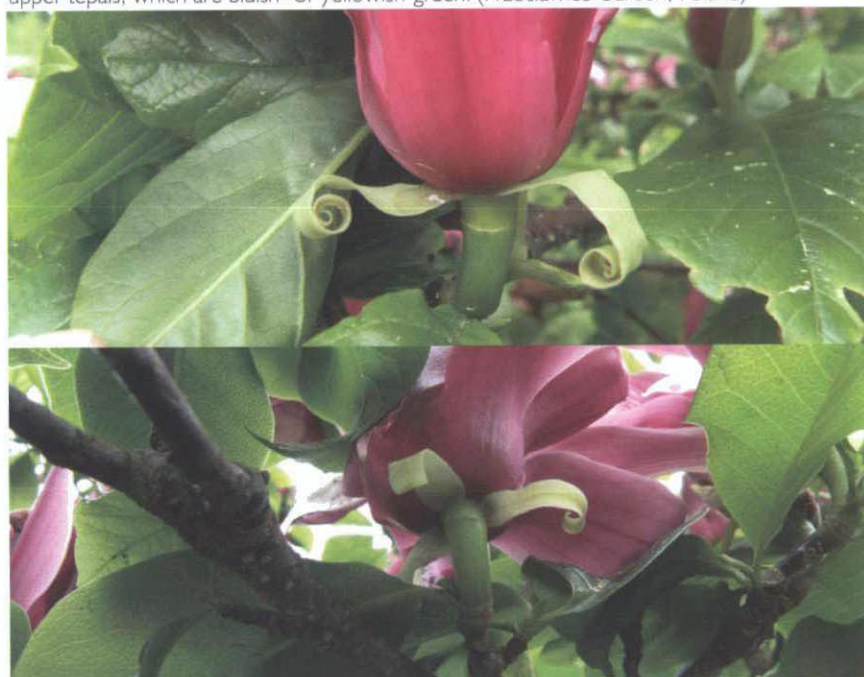


Fig. 8. *Magnolia liliiflora* – the tepals proper are large, intensely colored with purplish red, whereas the "tepals" of the first whorl are completely different - they are elongated light green ribbons curling at the end. (Kórnik Arboretum, Poland)

Generative zone – the universe of spirals

In developing their flowers, magnolias quickly pass from mostly whorled phyllotaxis of the perianth to the spiral phyllotaxis of generative parts. Spiral phyllotaxis is fascinating. The consecutive elements of phyllotactic pattern - the leaves or flower parts - can be connected with a spiral (helical) line winding up along the axis. This primary line, called ontogenetic spiral or ontogenetic helix, may be right-handed or left-handed; thus, every spiral pattern is represented by its two forms, each being a mirror image of the other. There are many spiral patterns differing in the constant value of angular distance (divergence angle) between consecutive pattern elements, which is routinely measured along the ontogenetic spiral. The most common angle in the most common main Fibonacci pattern equals 137.5 degrees, but there are many others, like 99.5, 151.1 or 77.9. The consequence of these angular differences is the varying number of secondary connecting lines, so-called parastichies. They become conspicuous when the phyllotactic pattern is composed of many elements tightly packed, as the scales are in the cones of conifers, the seeds in sunflower heads or... stamens and carpels on magnolia's elongated floral axis. In these very compact structures the ontogenetic spiral is simply not visible. By counting the secondary spirals, one may, however, easily identify the pattern present in a particular shoot. In this procedure the number of parallel parastichies inclined to the left (in one set) and the number of parastichies inclined to the right (in the second set) should be determined. The pair of their numbers ($m:n$) identifies the pattern unequivocally. In our studies we use the opposed parastichy pair formula with addition of S and Z indices of parastichy orientation. This enables identification of chiral configuration of the pattern because it tells which one of two possible mirror images, $m_s:n_z$ or $m_z:n_s$ it represents. Bare $m:n$ formula does not provide this extra information.

For a long time the diversity of spiral phyllotaxis has been underestimated. Patterns other than the main Fibonacci with its divergence angle 137.5 and the numbers of secondary spirals: 3:5, 5:8, 8:13..., have been encountered sporadically and in different plant structures. About three decades ago it was discovered that in magnolia flowers the diversity of spiral phyllotaxis is extremely high. Almost all theoretically predicted patterns have been found there. Thus, the magnolia flower, regarded mostly for its beauty, suddenly became the perfect object for studying phyllotactic diversity. A new model plant system for phyllotaxis research had been established.

Soon it appeared that not all *Magnolia* species share the feature to the same extent. The diversity may be expressed among the species with lower and higher intensity. The record holder is *M. acuminata*. Its phyllotactic spectrum, recorded for a population of flowers produced by an individual tree, is always extremely rich (Figs. 9, 10).



Fig. 9. *Magnolia acuminata* – a gallery of cones - aborted floral shoots - collected from four individual trees after blooming period. Their morphology – the color, size and shape - varies significantly among the trees, but is similar in each set of three cones representing the same tree. Despite this superficial similarity, the phyllotactic pattern in each of the three shoots is most certainly different.

This finding has been confirmed for trees growing in campuses and parks of both the United States and Poland; thus, the extreme phyllotactic diversity of this species is certainly a species-specific trait. It is difficult to comprehend why this very good natural species is so variable in this trait, whereas the famous hybrid *M. ×soulangiana* exhibits rather uniform floral phyllotaxis with preference of the main Fibonacci pattern. My survey of available plant material (unpublished data) showed that variable phyllotaxis, similar to that



Fig. 10. *Magnolia acuminata* - population of aborted floral shoots collected from under the tree after blooming. Phyllotactic pattern is recorded routinely in every one of the shoots by counting its secondary spirals. Then the phyllotactic spectrum of the patterns frequencies (phyllotactic fingerprint) is made for the tree.

in *M. acuminata*, may also be present in *Magnolia figo* and, to some extent, in *M. salicifolia* growing in Japan in its natural stands in the Kurama area near Kyoto. The profile of phyllotactic diversity in the *Magnolia* genus and its distribution among the species deserves special attention. It may shed some additional light on phylogenetic relationships. This would obviously require starting an extensive research program engaging magnolia specialists from all around the world having access to more restricted areas, from which the appropriate plant material could be obtained.

Magnolia

Studying more closely the available trees of *M. acuminata* in Poland, we have been able to demonstrate that each individual tree has its own characteristic spectrum of patterns, which is a kind of phyllotactic fingerprint. The selected trees in the Botanical Garden of Wrocław University, monitored for over 10 years, showed that the same spectrum is repeatedly produced every consecutive blooming season. One tree favors, for instance, the 6:9 pattern, whereas at the same time the other, neighboring, tree every year makes preferably 5:8, 4:7 and 4:6 patterns in its flowers (Fig. 11).

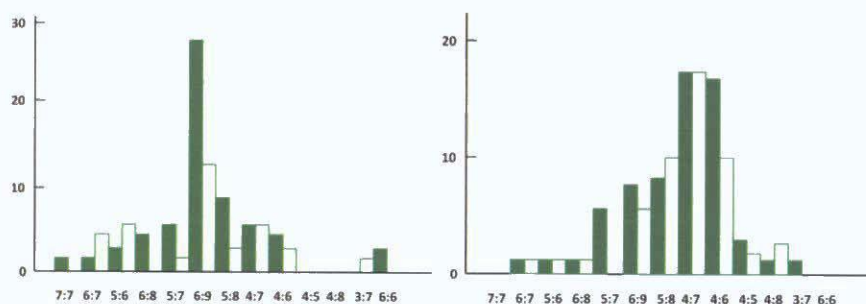


Fig. 11. *Magnolia acuminata* – two diagrams of phyllotactic pattern frequency (“phyllotactic fingerprints”) made for two different trees growing in the Botanical Garden of the University of Wrocław, Poland.

To understand better the meaning of these spectra and of the preferences the particular trees have, we would like to initiate, with possible help from MSI volunteers, an expanded research project involving the survey and monitoring of some selected individual trees of *M. acuminata*, which grow in their natural stands within the range of the species in North America. I had a taste of this projected adventure, visiting last year with my respected colleagues from MSI the oldest *Magnolia acuminata* tree growing in Ontario since pre-settlement time (Fig. 12). She deserves, in my opinion, to have her own name for surviving so many years in dignity and beauty. Let it be Old Lady. Having in mind their phyllotactic individual character, I usually name old trees that I visit and monitor every year here in Poland.



Fig. 12. *Magnolia acuminata* - the oldest tree in Ontario and its admirers from Magnolia Society International during our visit in May of 2010.

A sample of floral buds collected from the Old Lady showed the presence following phyllotactic patterns in a carpel zone:

4z:6s (3) 5z:7s 6s:7z (3) 5z:6s 5z:8s (3) 6s:9z 5s:9z 7z:9s 4z:7s

The sample was obviously too small to show the real "fingerprint" of the Old Lady. Will this ever be determined? Will the same patterns show up next year?

Among the methods which would allow documenting the patterns present in cylindrical cones of magnolia, the modeling clay replicas appeared to be the most satisfactory. Unrolled surfaces of cylindrical shoots replicated in clay presented the regularity of patterns and their striking resemblance of crystal lattices (Fig. 13). In some of them the bifurcations of connecting lines have been noted. They were analogous to imperfections of crystal lattices known to crystallographers as dislocations. In phyllotactic lattices they have been interpreted as the markers of phyllotactic transitions. Phyllotaxis was evidently capable of changing in the same shoot from one pattern of organ distribution to another, completely different pattern. The change was usually accomplished by simple addition or subtraction of only one of the connecting lines. To date, we have described many variants of phyllotactic transitions. Some of them minimized the change in phyllotactic lattice, but dramatically affected the divergence angle or even altered the configuration of ontogenetic spiral. To understand it, let us consider the following transition: from 3s : 5z to 3s : 4z. Only one of Z parastichies disappears here, but the divergence angle changes from 137.5 to 99.5 and, what is even more dramatic, the ontogenetic helix alters its course from S to Z.

Playing with replicas is very entertaining. This experience conveys us back to childhood. Please pay attention to quite unusual properties of the replica photograph shown in Fig. 13. The sculptured surface of gynoecium composed of elevated carpels rolled over the clay produces the complementary hollow pattern. Yet, looking at the photograph of the replica, we experience the illusion of seeing the pattern elements as rising, elevated structures. This illusion depends upon where we locate the source of light. Try hard to see the light coming from the right side (turning head upside down helps) and you will see the hollow pattern as it is in reality. Another interesting property of the replica is that it alters orientation of connecting lines – those oriented on the shoot surface to the right in the replica run in opposite direction – to the left. We see them as if looking at the surface of the shoot from its inside.

Magnolia

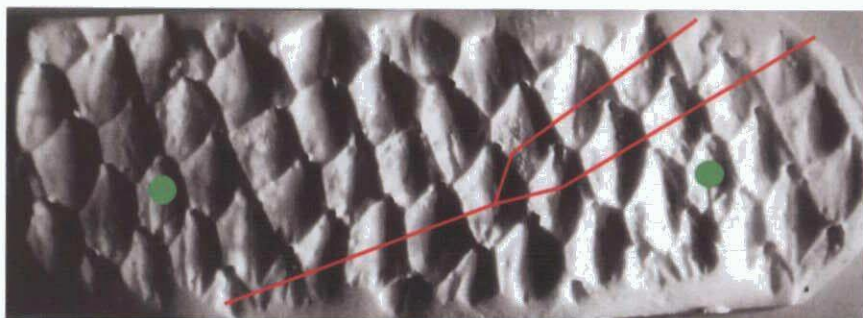
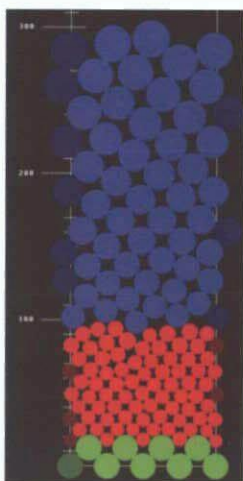


Fig. 13. *Magnolia acuminata* – modeling clay replica of the upper (gynoecial) part of cylindrical "cone" obtained by rolling it over the clay. The unrolled surface shows the very regular arrangement of carpels and resembles closely the crystal lattice. The similarity is enhanced by the presence of dislocation (red line) – the imperfection frequently encountered in crystals. In phyllotactic lattice the dislocation means that the pattern of lateral organ spacing changes – here the initial pattern of three connecting lines inclined to the right and eight inclined to the left (3:8) transformed into the 4:8 pattern. Green circles on the opposite sides of the replica point out the same carpel, which has been replicated twice after the shoot had been rolled over 360 degrees.



To summarize, not only the presence of various patterns in a population of flowers, but also the ability of changing the pattern in ontogeny of a particular flower paints ultimately the whole picture of magnolia's rich phyllotactic diversity. This green living crystal, suddenly revealing its hidden beauty, is now becoming a real treasure for developmental plant biology.

Now, after describing the phenomenon, it is about time to study its mechanisms and understand where the diversity comes from. In my research group we employ computer modeling in creating and studying virtual magnolia flowers with diverse floral phyllotaxis. They might not be as beautiful

Fig. 14. The virtual magnolia in computer simulation. The circles tightly packed in a simulation rectangular space represent the floral parts initiated in the ontogenetic sequence along the floral axis: green for trimerous perianth elements; red for spiral stamens and blue for spiral carpels.

as the real ones, but they are very informative (Fig. 14). We have learned, among other things, that one of the factors causing phyllotactic transitions might be a double change in organ identity and size during development of the embryonic floral shoot. This research, supported by the grant from Polish Ministry of High Education, is currently under way.

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