Floral phyllotaxis of magnolia in computer simulations - towards understanding phyllotactic fingerprint

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Highlights: Magnolia's floral shoot, with its uniquely rich and diverse phyllotaxis, has been modeled with application of a special program based on geometric model of phyllotaxis. First survey of phyllotactic diversity obtained in the library of 1200 computer simulations proved that, besides the most common main Fibonacci, also other patterns, frequently encountered in nature, such as Lucas and bijugy, are readily formed. This is a part of extensive studies aimed to elucidate the mechanism of phyllotactic fingerprint – the species or genet specific pattern of phyllotactic diversity, first in magnolia flowers and then in other plant structures and taxa.

Keywords: phyllotaxis**,** *Magnolia*, floral parts, phyllotactic fingerprint, plant development, shoot apical meristem

INTRODUCTION

Double change in the identity of floral organ primordia, associated with the change in their sizes (Zagórska-Marek 1994, Xu 2006, Xu and Rudall 2006, Zagórska-Marek and Szpak 2008), creates the potential for extreme diversity of floral phyllotaxis in magnolia (Erbar and Leins 1982, Zagórska-Marek 1994). Yet different magnolia species or even genets execute this potential in different ways. Some have exceptionally rich, others rather limited spectrum of the diversity (Wiss and Zagórska-Marek 2012). The spectrum is so specific and persistent in consecutive blooming seasons that it can be treated as the individual tree's fingerprint (Zagórska-Marek 2011). Understanding this phenomenon seems to be a great challenge.

The aim of our work was to test, in computer simulations, how the changes in geometric parameters of primordia generated by apical meristem affect phyllotactic pattern formation in virtual magnolia flower. For that purpose we have used geometric model of phyllotaxis and special computer program Phyllotaxis ver. 0.3 (Zagórska-Marek and Szpak 2008).

RESULTS AND DISCUSSION

In the first step of testing we asked ourselves, is there a connection between evidently high and changing number of spirally arranged stamens and the number of patterns and phyllotactic transitions in magnolia gynoecium. We have noted in preliminary tests that the number indeed affects the quality of gynoecial phyllotaxis, defined (following Adler 1974) by modified contact parastichy pair formula $(a_s:b_z)$, in which s and z indices stand for parastichy orientation (Fig.1).
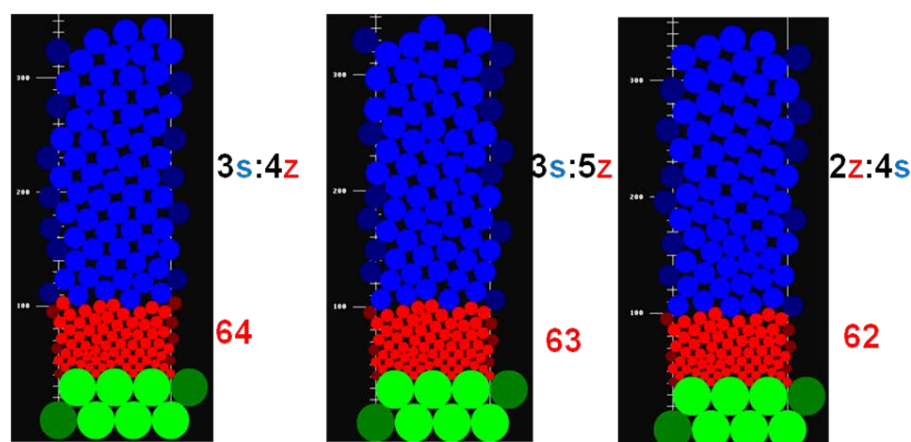

Fig. 1. Magnolia's virtual floral shoots. The parameters of all three simulations are the same except for the number of stamens (in red). Decreasing it by one in two consecutive steps, changes gynoecial phyllotaxis dramatically from Lucas (left), through main Fibonacci (middle) to bijugy (right); green, red and blue circles denote respectively the perianth elements, stamens and carpels. Gynoecial phyllotaxis is defined by contact parastichy pair formula.

Over 1200 pictures were created, divided into 3 groups. The only difference between them was the ratio between stable size of perianth elements and the size of the first stamen. The starting pattern of the perianth was always tricussate, with the 118° intersection angle between the 3s:3z connecting lines. In agreement with developmental changes observed in nature, we set the program to gradually increase the size of circles representing stamens and carpels. Speed of an increase was set to 1.001 for stamens and 1.004 for carpels, which means that every next stamen was bigger by 0.001 of the radius, and carpel was bigger by 0.004. To add a more realistic feel to the simulation we set a tolerance in radius change for 5%. The software allows setting a seed for the random number generator. The groups of simulations were created as follows: the small group (S), with the initial size of stamens set to 6.5 and of carpels to 8.0, the medium group (M) with the size of stamens set to 7 and of carpels to 8.5, and the large group (L) with the size of stamens set to 7.5 and of carpels to 9.0. We generated 400 pictures for each group, differing in a number of stamens from 60 to 100, having constant number of carpels set to 50, and differing in a seed for random factor from 1 to 10.

In every case, the initial phylotactic pattern, in the 3rd row, starting from the end of androecium zone, and the ultimate one, in the 3rd row down from the end of gynoecium, i.e. from the top of virtual floral shoot, have been determined. This way, apart from the initial gynoecial pattern we also acquired information on pattern rearrangements in given subgroups. Patterns were identified by counting contact parastichies and recorded in a form of contact parastichy pair formula ($a_s:b_z$). To process all these data we developed a small program (Counter ver. 0.1).

Qualities and frequencies of patterns have been summarized for all analyzed cases (Table 1), because there was no significant difference in these parameters among three groups. The most common was the main Fibonacci pattern. The Lucas pattern was the second and bijugy the third most frequent among the patterns. We have noted extreme asymmetry of pattern chiral configurations, which in nature occur in more similar frequencies. This effect of simulations is not yet fully understood.

Table 1. Quality and frequency of ultimate gynoecial patterns; F – main Fibonacci, L – Lucas, Bi – bijugy, T –tetrajugy, Tr- trijugy, P- pentajugy, irr.- irregular pattern

pattern expression	3s:5z	4s:5z	4s:6z	4s:4z	3s:4z	5s:5z	5s:6z	4s:7z	3s:3z	2s:4z	2s:5z	irr.
Nº of cases	356	128	225	131	301	3	2	4	8	6	1	35
pattern type	F		F(Bi)	F(T)	L	F (P)		L	F(Tr)	F(Bi)		

In the next step, we analyzed the pattern rearrangements (phyllotactic transitions) in all 3 groups: S, M, L. The data for each group had been divided into 5 subgroups, according to the range of changes in the number of stamens: first one with 60 to 68 stamens, second with 69 to 76, third with 77 to 84, fourth with 85 to 92 and fifth with 93 to 100. The highest rate of phyllotactic transitions was recorded for each range in S group (Table 2).

Table 2. Number of rearrangements associated with changing number of stamens in 3 groups: S, M and L

range	60-68	69-76	77-84	85-92	93-100	Sum
S	58	40	47	39	40	224
M	26	14	17	22	29	108
L	31	24	13	13	7	88

From the same set of data it was possible to extract the information, which pattern is developmentally the most stable. Among the 5 most common patterns, surprisingly, the most stable was the Lucas pattern (Table 3).

Table 3. Gynoecial pattern stability. Most stable are those where an initial pattern frequency and the frequency of cases, in which the same pattern was stable, are similar. Their ratio is given at the bottom of the table.

Pattern	3s:5z	4s:5z	4s:6z	4s:4z	3s:4z
initial	493	119	255	58	104
ultimate	356	128	225	131	301
stable	342	60	190	33	103
%	69,37%	50,04%	74,50%	56,89%	99,00%

Finally we plotted the data about rearrangements in to a graph (Fig.2). To have a right scale we divided the number of rearrangements in each subgroup by the number of rearrangements in the whole group (S, M, L).
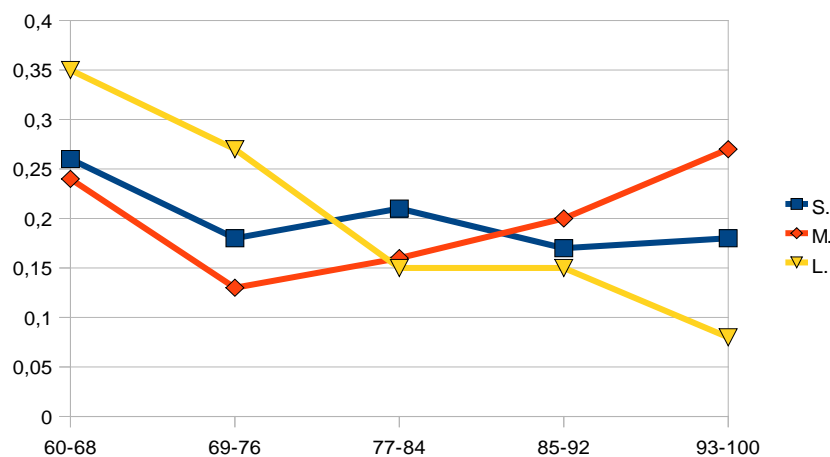

Fig. 2. Frequency of rearrangements depending upon the number of stamens in 3 groups: S, M and L. In the range between 77 and 92 stamens the pattern, regardless its quality, is the most stable.

It has been shown already, in similar simulations, that some phyllotactic patterns in their lowest expressions are more developmentally stable than others (Szpak and Zagórska-Marek 2011). In magnolia, however, pattern expressions in gynoecium are high. Shown here clear disproportion between the number of rearrangements in S and L group of magnolia virtual floral shoots as well as pattern stability, which depends upon the number of organs generated by floral meristem, are in fact the first hints of why some magnolias may have gynoecial phyllotaxis more diverse than others. More accurate empirical data should be collected, to create a collation with the data obtained from simulations. We also feel that developing a program for analyzing the quality of phyllotactic pattern should be considered to eliminate the human error in diagnosing the effects of simulations. More research is also needed to understand fully the phenomenon of phyllotactic fingerprint – our working hypothesis that changing number of stamens may favor selection of the specific patterns has been neither falsified nor verified, yet!

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