

Virtual phyllotaxis and real plant model cases

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Introduction

Phyllotaxis is the distribution of lateral organs in plants. The organ primordia are initiated reiteratively (Hofmeister 1868) on the organogenic surface of the shoot apical meristem (SAM). The regularity of phyllotactic patterns has always puzzled 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: of whorled - achiral patterns and of helical - chiral patterns. The **ontogenetic** aspect is that the pattern often changes together with the developmental phase of plant's growth. From the biological point of view it is 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 mechanism positioning the primordia of leaves, flowers or flower parts on the organogenic surface of SAM is unknown. 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 in the superficial cellular layer of SAM. Each primordium acts as a sink, competing for the hormone with others 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 neighboring primordia (Snow & Snow 1931, 1952). This space is created by the constant and continuous addition of new cells as a result 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). 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 (Banasiak, Zagórska-Marek 2006), play in this process.

This study was undertaken in hope of finding, in a computer simulation, the causes of phyllotactic transitions known from plant model cases. The principles affecting the direction of phyllotactic transition and thus the quality of the emerging pattern 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 represented by circles tightly packed on a cylindrical surface representing the organogenic, lateral surface of the growing SAM.

In order to understand the emergence of various patterns and their ontogenetic transitions, we have simulated SAM's growth using a special computer program. In our model we assumed:

- an infinite cylinder of a constant width as simulation space
- primordia as circles of a changing radius
- primordia emerging in the first available space

The “first available space” rule is ambiguous

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 applied were abrupt or continuous, quick or slow, with the radius decreasing or increasing. The results of the simulations showed, however, that the quality of the emerging pattern did not solely depend upon the way the primordia size was controlled. The position of a newly initiated primordium, appearing in the first available space between two, already initiated laterals, **sometimes had to be selected from two equivalent positions**. The choice, once made, affected the developing pattern of primordia spacing, even though all other parameters of the simulation were the same (Fig. 1). This shed a new light on the possible causes of transitions known to occur in plants.

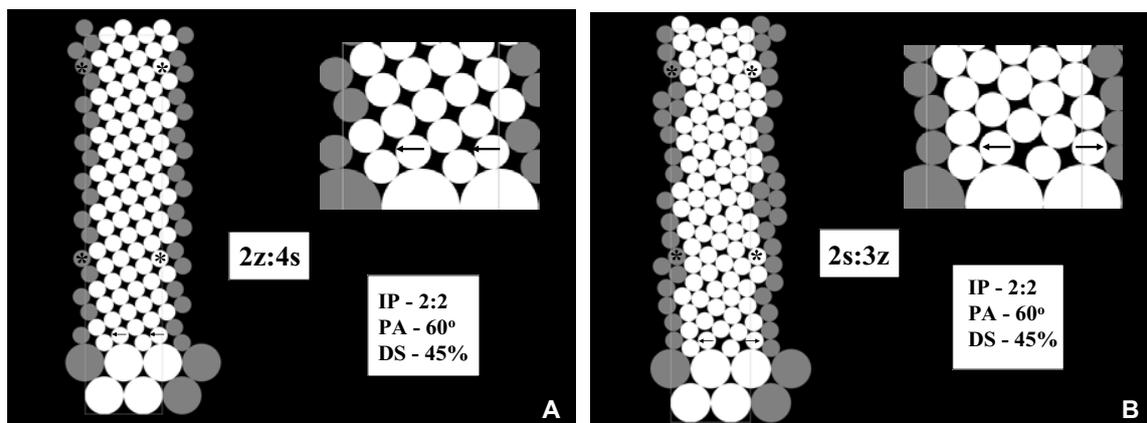


Fig. 1. The simulation of abrupt change in the size of circular primordia, added to the working space according to the principle of Snow & Snow. Only one of two equivalent positions: to the left or to the right (arrows) has to be selected by each of two newly initiated, small primordia. When the choice for both is the same – the developing pattern is bijugy (A), when it is different – the main Fibonacci emerges (B). The initial pattern (IP) is decussate. Primordia decrease in size (DS) by 45%. The same primordium is shown on the opposite sides of organogenic frame (as either grey or white), selected pairs are marked with asterisks. The numbers of the conspicuous parastichy pair identifying the emergent phyllotactic pattern are supplemented with S and Z indexes of parastichy orientation. They allow the recognition of pattern chirality.

The confrontation of simulation results with real cases showed that the quality of natural changes in phyllotaxis may indeed be affected:

- by the change in the size of a pattern element assuming new identity in the course of development (case study *Magnolia*)
- by the way the initiation site is selected from two equivalent positions in the first available space (case study *Verbena*)

Case study *Magnolia*

The outstanding diversity of phyllotactic patterns present in magnolia flowers (Zagórska-Marek 1994) is most probably an outcome of the double change in the size of floral primordia (Zagórska-Marek, Stoma 2005). The computer simulation of this case is very sensitive to even small changes in the values of parameters used. The initial pattern of the largest perianth primordia is tricussate (achiral), which explains the frequent appearance of trijugy in the later helical arrangement of the smaller stamen primordia and slightly larger carpel primordia. Together with the small size of generative elements in relation to the width of organogenic space, the double change can be held responsible for the rich spectrum of final phyllotactic solutions.

Still, some unexplained problems remain:

- qualitative changes in phyllotaxis sometimes occur within the zone of primordia of the same identity
- the spectrum of final patterns is species or genet specific (phyllotactic fingerprint) despite the general rule of a double change. More detailed quantitative studies are needed to resolve this dilemma.

Case study *Verbena*

The decussate (achiral) vegetative phyllotaxis of *Verbena* changes within inflorescence into the helical (chiral) pattern. It is mostly the main Fibonacci pattern. In the simulation it emerges from the decussate pattern when the two smaller, “generative”, primordia choose their initiation site oppositely in two equivalent positions (Fig. 2B). The above transition should be the most frequent among plants, which **quickly** develop helical phyllotaxis from the initial pattern of opposite cotyledones or prophylls. Sometimes the developing helical pattern is bijugy implying the situation already shown in Fig. 2A. The unresolved problem is that on the axis of inflorescence further sequential changes of phyllotaxis often take place even though the identity of primordia remains the same. The transitions involve helical patterns (Lucas, second accessory) as well as whorled (tricusate).

Conclusion

Simulation results quite well coincide with the real organographic changes in the systems of phyllotaxis exemplified by *Magnolia* and *Verbena* shoots. Similar coincidence has been observed by other authors for other plants (Couder 1998, Smith et al 2006b). 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.**

Our future specific goals in exploring the potentials of the model are to:

- systematically explain and predict all, including the less common patterns
- explain the direction of other pattern transitions i.e. why the pattern may be transformed in many different ways
- elucidate why the spectrum of patterns can be species or genet specific

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