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Modeling Flowers and Inflorescences

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ABSTRACT

Modeling approaches, using mathematical and computational tools for visualization and simulation, are gaining new interest in the field of developmental biology. These methods are providing new insights into molecular interactions, growth processes and morphological evolution. The distinctive reproductive structures of angiosperms, flowers and inflorescences, are of particular interest from both a developmental and evolutionary perspective. Here we review the diversity of studies which have used modeling approaches to investigate the structure and development of flowers and inflorescences. Models of architecture (branching and determinacy) and phyllotaxis (primordia arrangement) are described, focusing on different factors ranging from environmental pressures to physical constraints, chemical signaling, and genetic determination. Modeling has also been used to provide a description and framework for understanding growth at the level of single floral organs. In addition, we also consider models that explore the behaviour of gene regulatory networks involved in the development of plant reproductive structures. Models of flowers and inflorescences are still mostly disconnected, and integrating these will help explain the developmental processes underlying morphological diversity. Modeling is a useful tool for testing hypotheses and guiding empirical research and will undoubtedly become an increasingly important component of integrative studies of plant development and evolution.

Keywords: development, evolution, gene regulatory networks, phyllotaxis, plant architecture

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INTRODUCTION

Plant development is a continuous process with parts developing from meristematic regions where cells divide and differentiate. The shoot apical meristem (SAM) is the region at the tip of the stem consisting of a few hundred totipotent cells (that can differentiate into any type of cell) from which the aerial parts of the plant develop. At the flank of the SAM, determinate primordia producing leaves or flowers, and axillary meristems (e.g. producing inflorescences) are formed. Complex processes operate during primordia development at different scales: from molecular signals within a cell to cellular interactions, tissue patterning and organ formation. Integrating the multiple factors that underlie the resulting three-dimensional (3D) structures is one of the central challenges of plant developmental biology. The complexity of these interactions requires the use of formal methods of analysis. In particular, modeling approaches are becoming prevalent in this field.

Modeling typically involves the use of **mathematical** and/or **computational** tools to visualize and **simulate** the system under study (terms in bold are defined in the glossary). Although in the field of plant biology, the term modeling is frequently associated with *in silico* or virtual plants, it encompasses a diversity of approaches depending on the biological process under investigation. These include models of plant architecture (simulating how different components are assembled on a plant), models of cell-cell interactions, and models incorporating genetic regulatory networks (reviewed in Alvarez-Buylla *et al.* 2007; Godin 2000; Prusinkiewicz 2004; Prusinkiewicz and Rolland-Lagan 2006). Modeling is increasingly seen as important for understanding plant development (Gutiérrez *et al.* 2005; Hammer *et al.* 2004; Minorsky 2003; Yuan *et al.* 2008) by serving to: i) simulate biological processes and predict the effects of changes in selected factors, ii) visualize the interplay of processes acting on different levels (e.g. molecular and cellular), and iii) test hypotheses and guide empirical research.

Modeling methods have been used for decades to investigate biological and developmental mechanisms and dynamics (reviewed in Lewis 2008; Prusinkiewicz 1993; Tomlin and Axelrod 2007). Early modeling approaches were seminal in developing these tools in relation to cellular

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networks and pattern formation (e.g. Turing 1952) but were limited in their explicative power by the availability of experimental data (Tomlin and Axelrod 2007). However, over the past decade, modeling of development has found a new impetus through the combination of the rapid increase in genomic and proteomic data, novel techniques in image capture, greater computational power and both analytical and theoretical advances. These advances have spurred the collaboration of biologists, mathematicians and computer scientists, whose work is starting to reveal new insights into developmental mechanisms.

Here we review modeling approaches that have been used in relation to flowers and inflorescences. Flowers are one of the most intensely studied systems in plant developmental biology. The interest in these reproductive structures, the hallmark of angiosperms, arises from their biological significance, having played an important role in the evolutionary success of this group (Theissen and Mezler 2007; Crepet and Niklas 2009). Flowers are generally arranged in a stereotypical pattern with sterile organs (sepals, petals) surrounding the stamens and carpels. However, they vary greatly in the size, appearance and number of their constitutive parts. In addition, flowers can be solitary or grouped into inflorescences, which also vary in their organization.

Many simulation studies involving plant reproductive structures have been carried out in the context of agronomical experiments, where organ formation is predicted *in silico* under limiting resources (e.g. Faust and Heins 1994; Larsen and Persson 1999; Cole *et al.* 2005). However, these studies do not aim to explain the endogenous processes underlying form and development and will not be covered here. In the present review, we survey the variety of methods which have been used to model plant reproductive structures at different levels (**Fig. 1**) and the dynamic processes which generate them (from genetic and cellular interactions to physical constraints). Furthermore, we highlight the potential of these approaches for understanding the diversity and evolution of floral and inflorescence structures.

MODELING INFLORESCENCE ARCHITECTURE AND PHYLLOTAXIS

Inflorescences are modular structures, with their constitutive parts (flowers with or without pedicels, bracts, and internodes) regularly reiterated along the growth axis. Inflorescence growth can be determinate or indeterminate depending on the presence, or absence, of a terminal flower at the apex. Moreover, inflorescences vary in their level of complexity. They can be either simple, with growth along a single axis, or compound, where branching occurs and flowers are borne on secondary axes. Because of these defining features (modularity, regularity, varying levels of complexity), inflorescences have been highly suitable for modeling. In this section, we review modeling approaches which have been used to reproduce and to account for various inflorescence architectures and phyllotactic patterns.

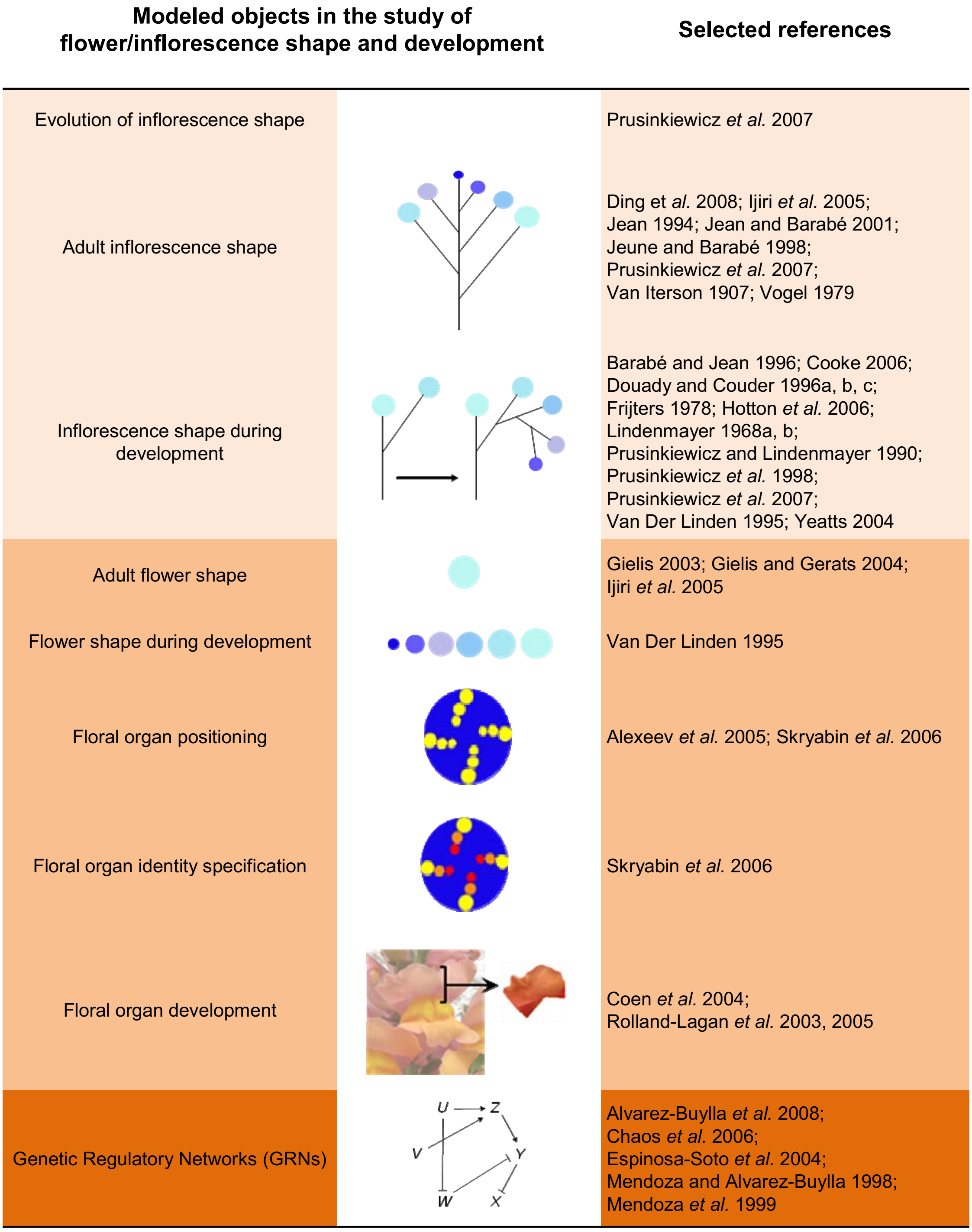
Modeling inflorescence architecture – simulation and evolutionary inferences

An important condition for virtual flowers and inflorescences to become the starting point of scientific studies is that they must be as faithful as possible to the natural structures represented. The method of Ijiri *et al.* (2005) and Ding *et al.* (2008)) takes into consideration the botanical characteristics of plant reproductive structures, such that their results are morphologically meaningful. Their method for modeling solid shapes is sketch-based, and consequently very user-friendly. In two successive steps, the user draws the shape of the inflorescence and that of a typical flower. The computer model then edits the organs according to the input parameters (e.g. the length of the internode (the segment of stem between two nodes), the length of the pedicel (subtending the flower), and flower size) deduced from the user-defined sketches and grafts the flowers onto the inflorescence backbone. It allows a representation of inflorescences and flowers that respects architecture, linkage points and relative position of organs, as drawn components and the relations among them are adjusted and corrected according to predefined mathematical and botanical rules. At present, this method only provides a tool for visualizing computer-generated flowers and inflorescences and, as it is based on a sketch and not on **computation** or **simulation**, it consequently does not have any predictive power. However, it could be a useful tool for obtaining 3D images of flowers and inflorescences and as such, could help interpret results of comparative studies focusing on, for instance, branching patterns or relative organ positions.

Models can thus be **descriptive**, aiming to reproduce a faithful image of natural shapes, or may also be explicative, when they enable the investigation of factors underlying the formation of a given structure. An example of the latter is given by Jeune and Barabé (1998), who explored with a mathematical approach the geometrical and biophysical rules that affect the spatial arrangement of inflorescence components. They compared the structure of the compact inflorescences of the Araceae with a theoretical structure where the average number of sides of floral primordia neighbouring an *n*-sided primordium is determined by physical laws. The discrepancy they observed between the measured shape and organization of inflorescences in Araceae and those predicted by theory was accounted for by the effect of physical constraint (the proximal environment of developing organs), the relative importance of which was quantified.

Architectural models of inflorescences aim to understand how branching patterns and complex architectures are generated. General branching patterns identified in the elaboration of many plant structures and entire plant architecture (reviewed in Barthélémy and Caraglio 2007) can be transposed to inflorescences. Lindenmayer (1968a, 1968b) was the first to propose a **mathematical** method (L-systems) to model the development of branched architectures. L-systems describe the elaboration of a structure using an algorithm that re-writes parts of an initial and simple object in order to build complex objects, this procedure being repeated each time a new level of complexity is added. This method has been very useful for reproducing branching systems such as those found in plants and breaking down the processes involved in growth. In plant biology, it has primarily been used in studies of tree architectural development and horticultural crop modeling (e.g. Wilson *et al.* 1999; Perttunen and Sievanen 2005). L-system is a tool that has also been integrated in the representation of the development of inflorescences with determinate and indeterminate growth (Frijters 1978; Prusinkiewicz and Lindenmayer 1990; Prusinkiewicz 1998) as well as entire plants (*Arabidopsis*: Mündermann *et al.* 2005; rice: Watanabe *et al.* 2005).

The genetic mechanisms underlying inflorescence architecture have been well documented in model organisms from both eudicot and monocot (primarily grass) clades, and often imply genes of large effect such as *LEAFY* (*LFY*), *APETALA1* (*AP1*) and *TERMINAL FLOWER1* (*TFL1*) (e.g. Bradley *et al.* 1996; Vollbrecht *et al.* 2005; Cassani *et al.* 2006; reviewed in Benlloch *et al.* 2007; Doust 2007; Wang and Li 2008). However, few studies have integrated genetic factors in developmental modeling. Recently, Prusinkiewicz *et al.* (2007) investigated the evolutionary constraints on inflorescence architecture by modeling the effects of transient genetic signals on development. They proposed a model combining architectural, genetic and fitness components that can account for the range of existing inflorescence architectures. Inflorescences are generally categorized into three main types (but see Prenner *et al.* 2009, who highlight the pitfalls associated with current inflorescence architecture terminology): i) cymes, with determinate growth where the principal axis is terminated by a flower and lateral axes form a branch repeating this pattern, ii) racemes, with indeterminate growth where flowers are borne in lateral posi-



Modeled objects in the study of flower/inflorescence shape and development	Selected references
Evolution of inflorescence shape	Prusinkiewicz *et al.* 2007
Adult inflorescence shape	Ding et *al.* 2008; Ijiri *et al.* 2005; Jean 1994; Jean and Barabé 2001; Jeune and Barabé 1998; Prusinkiewicz *et al.* 2007; Van Iterson 1907; Vogel 1979
Inflorescence shape during development	Barabé and Jean 1996; Cooke 2006; Douady and Couder 1996a, b, c; Frijters 1978; Hotton *et al.* 2006; Lindenmayer 1968a, b; Prusinkiewicz and Lindenmayer 1990; Prusinkiewicz *et al.* 1998; Prusinkiewicz *et al.* 2007; Van Der Linden 1995; Yeatts 2004
Adult flower shape	Gielis 2003; Gielis and Gerats 2004; Ijiri *et al.* 2005
Flower shape during development	Van Der Linden 1995
Floral organ positioning	Alexeev *et al.* 2005; Skryabin *et al.* 2006
Floral organ identity specification	Skryabin *et al.* 2006
Floral organ development	Coen *et al.* 2004; Rolland-Lagan *et al.* 2003, 2005
Genetic Regulatory Networks (GRNs)	Alvarez-Buylla *et al.* 2008; Chaos *et al.* 2006; Espinosa-Soto *et al.* 2004; Mendoza and Alvarez-Buylla 1998; Mendoza *et al.* 1999

Fig. 1 A summary of the objects investigated in modeling studies of flower and inflorescence shape and development. Selected references are associated with each type of modeled object.

tions, and iii) panicles, which are branched structures whose growth along the main and lateral axes is terminated by a flower (**Fig. 2**). The model of Prusinkiewicz *et al.* (2007) suggests that a common mechanism with two variable elements, corresponding to the antagonistic transcription factors *LFY* and *TFL1*, is sufficient to produce the main inflorescence types. Moreover, the model accounts for wild type and single/double mutants of *LFY* and *TFL1* in the racemose inflorescence of *Arabidopsis thaliana*. Another original aspect of this study is that modeling was also used to investigate the ecological and life history context of inflorescence evolution. For instance, by considering the fitness of different architectures (calculated using mathematical and probabilistic methods) within the space of possible forms, the model predicted the effect of climate on the evolution of inflorescence type and their respective geographical distribution. Their results suggest that, in regions with unpredictable climates (i.e. temperate regions), inflorescences tend to bear fewer flowers but flower for longer. This corresponds to what is observed in nature, with cymes and racemes being predominant in temperate climates, and panicles in tropical ones. This study suggests that evolutionary transitions among the main types of inflorescences are not only constrained by developmental genetic mechanisms, but also by the effects of climate and plant longevity. It highlights the potential of modeling for providing a new perspective on the evolution of morphological diversity, in this case by testing the effects of changes in a common underlying factor. However, the prospects for modeling the mechanisms of the evolution of plant reproductive structures are dependent on improved knowledge of morphology and development, improved assessment of homology (derived from phylogeny), and consistent terminology (as noted by Prenner *et al.* 2009).

Position of new primordia on the inflorescence meristem: static and dynamic modeling of phyllotaxis

Phyllotaxis is the regular arrangement of lateral organs along a main axis, and is a feature of both vegetative and reproductive plant structures including inflorescences. In the latter, primordia are often more condensed than in the former, and in some cases can be extremely compact, as in the capitulum of Asteraceae where all flowers are inserted directly on a common receptacle (**Fig. 2**). The most prevalent phyllotactic patterns in vascular plants are distichous (alternate), decussate (where successive opposite leaf pairs are perpendicular), whorled, and in parastichies (i.e. spirals on a disk and helices on a cylinder). However, these common phyllotactic patterns represent only a small fraction of all possible patterns that can be created by repeating similar units in space. This was shown by Hotton *et al.* (2006) who compared observed and simulated phyllotactic patterns in two Asteraceae inflorescences using a **geometrical dynamic** model. The authors introduce a **mechanistic** representation of phyllotactic patterns which records both the position of florets and the developmental history of parastichies. This representation, called an ontogenic graph, does not impose large scale rules (e.g. a regular divergence angle between consecutive primordia) but rather local geometry rules. It offers a basis for comparing actual and possible patterns, simulated from an initial ring of florets based on the observed pattern.

Phyllotaxis is a botanical feature with a long history of modeling as it is regular and appears to follow certain mathematically defined patterns (e.g. the divergence angle between two successive primordia is often close to the golden angle ~137.5°, the number of parastichies in a spiral phyllotactic pattern is given by the Fibonacci series) (reviewed in Adler *et al.* 1997; Wilson 1995) (**Fig. 3**). A considerable number of theories and strategies have been proposed to recreate and explain phyllotaxis (reviewed in Korn 2008). Modeling has been used to investigate the role of physical constraints and chemical factors on primordia arrangement. Here we focus on studies modeling phyllotactic patterns in inflorescences.

Models of phyllotactic patterns in inflorescences have been developed since the early 1900's. Van Iterson (1907) addressed the issue of flower packing in an inflorescence by modeling circles on a cylinder. Packing of flowers in an inflorescence was also central to the study of Vogel (1979) who modeled a sunflower capitulum on a two-dimensional space. The study of van der Linden (1996) presented a **mathematical** and **geometrical** model of organ packing which integrated physical constraints. It consisted of two main processes: i) to create patterns where spheres of different sizes (mimicking spheres appearing successively, such that earlier spheres are larger) are positioned on a stem represented as an infinite cylinder, and ii) to translate the centre of the spheres and resize the spheres to simulate axial and radial growth of stem and organs. Van der Linden applied this method to both flowers and inflorescences, and focused on the phyllotactic transition from indeterminate (vegetative parts) to determinate growth (as in some reproductive parts). This method attempts to limit phyllotactic patterns to processes of primordia differentiation, compressibility and annular arrangement around the stem or on the meristem. However, the optimal packing hypothesis has been questioned; for instance Cooke *et al.* (2006) suggested that, based on results from **geometrical** modeling of inflorescences, phyllotactic patterns generally arise from local inhibitory interactions among the existing primordia already positioned.

Modeling to investigate phyllotactic patterns has also been used by physicists, who introduced concepts from their discipline such as energy, force and motion over space

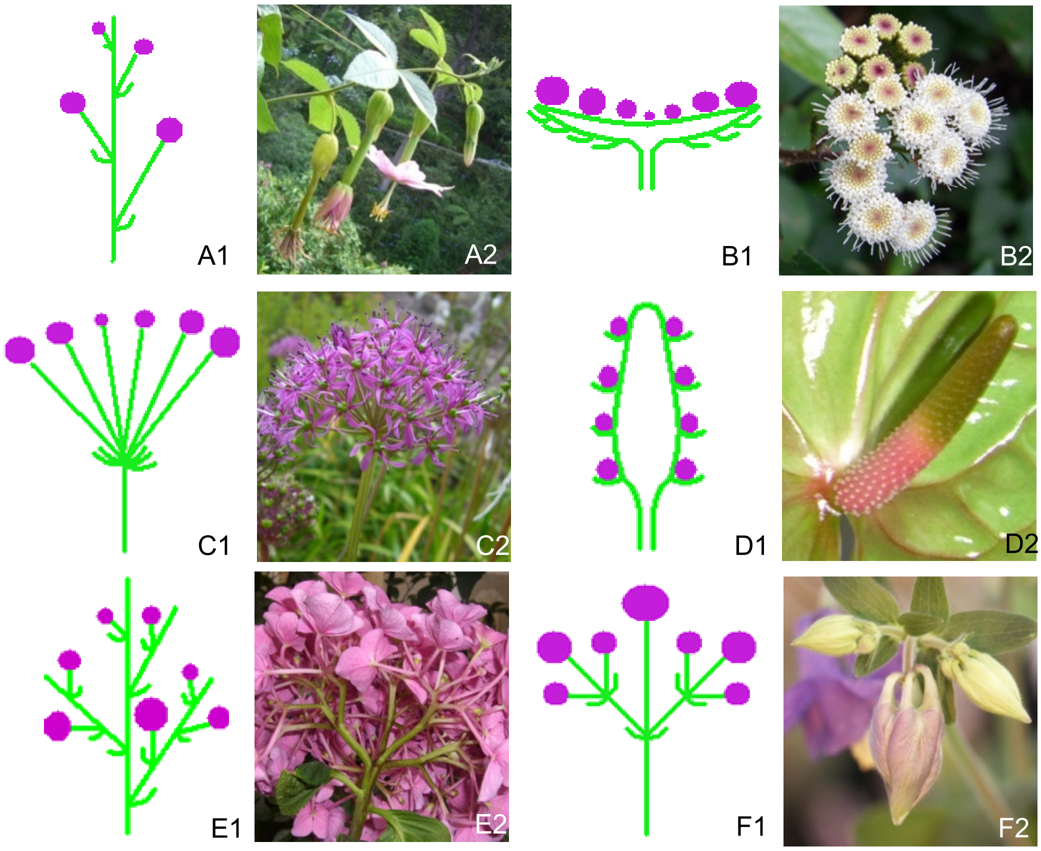
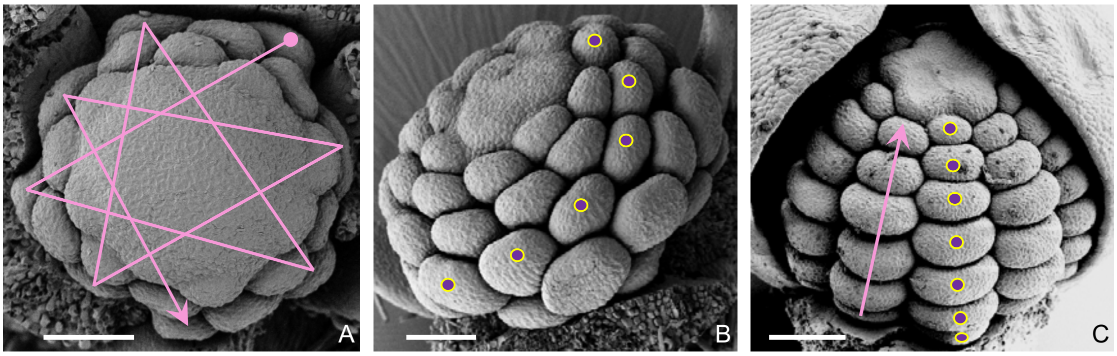


Fig. 2 Main types of inflorescences, with examples. Racemose: A1-2: simple raceme - *Passiflora mollissima*, Passifloraceae, B1-2: capitulum - *Ageratina* sp., Asteraceae, C1-2: umbel - *Allium* sp., Alliaceae, D1-2: spadix - *Anthurium* sp., Araceae, **Paniculate**: E1-2: panicle (compound raceme) - *Hydrangea macrophylla*, Hydrangeaceae. **Cymose**: F1-2: dichasial cyme - *Aquilegia alpina*, Ranunculaceae. In the diagrams, vegetative parts are in green: peduncles (subtending the whole inflorescence), pedicels (subtending single flowers) and bracts (leaf associated with flowers or inflorescences); flowers are in purple with flower size reflecting the order of initiation (larger flowers are initiated earlier).



Important features of phyllotaxis

- Spiral or whorled primordia initiation (producing parastichies or orthostichies)
- Plastochrone (time lapse between the initiation of two consecutive primordia)
- Size of meristem and organ primordia
- When phyllotaxis is spiral, i) number of parastichies is given by the Fibonacci series and ii) two consecutive primordia form an angle equivalent to golden angle (~137,5°) relatively to the centre of the meristem

Fig. 3 Features of spiral and whorled floral phyllotaxis. The order of primordia initiation on the floral meristem is shown by the pink arrows (A: spiral initiation, C: whorled initiation). Spiral phyllotaxis results in the formation of parastichies (curved lines, one parastichy is displayed in B). Whorled phyllotaxis results in the formation of orthostichies (columns of primordia, one orthostichy is displayed in C). Examples taken from Ranunculaceae floral buds (A and B: *Delphinium grandiflorum*, C: *Aquilegia alpina*). Scale bars: 100 µm. Important features of primordia arrangement that are often used as input parameters in models of phyllotaxis are listed.

and time. In a series of three papers, Douady and Couder (1996a, 1996b, 1996c) presented a **dynamic** model of phyllotaxis using notions of mechanics, where newly arising primordia are considered as interacting points, moving on the meristematic dome during its elongation. This model incorporates biologically relevant parameters such as plastochrones (the time lapse separating the initiation of two consecutive organs), primordia shape, velocity, and positioning, which are determinant factors for phyllotaxis first identified by Hofmeister (1868) and Snow and Snow (1952). Thei theoretical studies of Douady and Couder are illustrated by two botanical examples: the capitulum of Asteraceae and the tip of the stem of *Asparagus*.

Phyllotaxis has also been modeled under specific conditions in case studies of particular types of inflorescences: the capitulum of Asteraceae (Yeatts 2004) and the compact spadix of Araceae (Barabé and Jean 1996; Jean and Barabé 2001). The purpose of the first study was to mathematically model the growth and form of a capitulum from initiation of the florets to the cessation of growth. This descriptive work did not set out to explain the irregularities found in natural forms, unlike the studies of Barabé and Jean. Barabé and Jean (1996) studied the case of the inflorescence of *Symplocarpus* (Araceae) to model the influence of the overall shape of the inflorescence on local phyllotactic organization. By combining a **dynamic** model of phyllotaxis with a model of allometric growth (i.e. growth that changes the proportions of a structure), they showed that as the length-to-width ratio of the inflorescence increases, the number of parastichies decreases while plastochrones become longer. Jean and Barabé (2001) focused on the morphogenetic constraint applied to the relative position of flowers and used **mathematical** models (Jean 1994) to explain the apparent irregularities observed in the changes in phyllotactic patterns between young and mature spadices of Araceae. These models are based on ideas of branching and maximizing the stability and regularity of the inflorescence structure.

Studies of inflorescence phyllotaxis using modeling approaches have so far focused on pattern generation based on mathematical and physical rules. However, the control of phyllotactic patterns, characterized in the shoot apical meristem, is now known to involve a number of molecular signals (reviewed in Reinhardt 2005) which have yet to be included in models of inflorescence phyllotaxis. Independent studies of phyllotaxis at the shoot apical meristem have combined experimental data with modeling and computer simulations (Barbier de Reuille *et al.* 2006; Heisler and Jönsson 2006; Jönsson *et al.* 2006; Smith *et al.* 2006b) and provide a **mechanistic** explanation for patterning that is based upon active transport of the plant hormone auxin in zones where new primordia will be generated (reviewed in Kuhlemeier 2007). The question is whether the results from the shoot apical meristem can be transposed to other meristems, despite the differences in meristem size and speed of primordia initiation between vegetative and inflorescence meristems (Fleming 2006). Genetic and hormonal mechanisms operating in inflorescence meristems have been identified using classical molecular and genetic studies (Byrne 2003; reviewed in McSteen 2009). Therefore it should be possible to combine morphological models of inflorescence architecture with morphogenetic models in order to obtain a deeper understanding of the effects of intrinsic factors on inflorescence shape and development.

MODELING FLOWER SHAPE AND DEVELOPMENT

Although flowers are at the centre of plant genomic, developmental and morphological research, so far there have only been a few studies that have sought to model some of the processes involved in floral pattern formation and development. These studies have employed different strategies to investigate very different questions.

The overall shape of flowers, as with many other biological objects, displays geometric patterns which have inspired mathematical representations. Recently, a single equation, referred to as the Superformula, derived from the equation for a circle, has been proposed to generate many abstract and natural forms (e.g. starfish, shells and flowers) (Gielis 2003; Gielis and Gerats 2004). The formula integrates three biologically meaningful characteristics: size, shape and symmetry. The authors suggest that this mathematical approach for pattern generation is not only a useful visualization tool (which has been developed as programmes for 2- and 3D form generation), but may also provide insights into the evolutionary trends of biological shapes. They argue that their model encapsulates biophysical laws which play a crucial role in defining shape and structure, and illustrate this by using flowers and floral organs as an example, considering possible optimizations such as area use efficiency in floral buds, and perimeter shortening due to fusion. However, the significance of the Superformula in biology remains to be demonstrated, as it is not unique in its capacity to recreate shapes that resemble those found in nature (Whitfield 2003).

As with flowers on an inflorescence, floral organs are arranged on a floral meristem following regular phyllotactic patterns (spiral or whorled). Simulation studies of inhibitory fields surrounding primordia have proven to be important for testing hypotheses of pattern generation (Smith *et al.* 2006a). Inhibitory fields have long been invoked in the control of primordia positioning, and different mechanisms have been proposed, such as diffusion of a chemical inhibitor or depletion of a primordia-promoting factor (e.g. Reinhardt *et al.* 2003). In flowers, patterning of organ primordia on the floral meristem was investigated by mathematical modeling of inhibitory fields, using *A. thaliana* as a case study (Alexeev *et al.* 2005; Skryabin *et al.* 2006). According to their simulations, the expected number and position of floral organs in *A. thaliana* was recovered, provided two regions generating primordia are defined on the floral meristem: one at the base of the meristematic dome and one at the apex (Alexeev *et al.* 2005).

The determination of floral organ identity has been described at the molecular level by the ABC model (Coen and Meyerowitz 1991). The ABC model, first described in the model core eudicot species *A. thaliana* and *Antirrhinum majus* (Coen and Meyerowitz 1991) synthesizes how the formation of different flower organs is determined by the combinatorial interaction of a few homeotic gene functions: A class function specifies sepal identity, A + B petal identity, B + C stamen identity, and C carpel identity. The spatial arrangement of floral organs in four sequential whorls (from outermost sepals to innermost carpels) coincides with A, B and C expression patterns (reviewed in Krizek and Fletcher 2005). Refinements of the classical ABC model include the addition of D and E functions; D is required for ovule development (Colombo *et al.* 1995), whereas E, in addition to A, B, C and D, is crucial for floral organ development (Pelaz *et al.* 2000).

The inhibitory field model of Skryabin *et al.* was used to investigate the effects of the genes *APETALA2* (*AP2*, class A) and *AGAMOUS* (*AG*, class C) which control organ identity in different parts of the flower (Bowman *et al.* 1989, 1991). *Ap2* and *ag* mutants not only display changes in organ identity, but also changes in organ number and positioning (Bowman *et al.* 1989, 1991; Choob and Penin 2004). The patterns of organ formation observed in some mutant phenotypes were recovered under different conditions of the model. For instance, the proliferation of petals in the inner whorls of flowers of *ag* mutants was reproduced *in silico* under the assumption that the apical zone of reproductive organ (i.e. stamen and carpel) formation is absent (Alexeev *et al.* 2005; Skryabin *et al.* 2006). Although the model succeeds in reproducing observed patterns of floral organ arrangement, as described above, an assessment of whether all the predictions made by it (such as the presence of two zones of origin of organ primordia on the floral meristem) is still lacking. Nevertheless, it allows the exploration of poorly-understood factors such as local interactions between primordia on the spatial patterns of floral organ formation.

Understanding how complex organs develop from undifferentiated primordia, and relating the observed growth patterns to the underlying molecular activity, remains a difficult process. To bridge this gap, recent work has focused on the development of petals which, although conspicuous, are comparatively simple flat organs whose growth can be represented in 2D (Rolland-Lagan *et al.* 2005; Irish 2008). Initial steps have been taken for elucidating the mechanisms of petal growth in *A. majus*, and in these studies, modeling methods have played a central role (Rolland-Lagan *et al.* 2003; Coen *et al.* 2004; Rolland-Lagan *et al.* 2005). As internal developmental patterns cannot be observed directly, Rolland-Lagan *et al.* (2003; 2005) reconstructed *A. majus* dorsal petal growth by incorporating experimental data from clonal analysis (where dividing cells are genetically marked and their descendants identified visually in mature organs) into a dynamic growth map. This map divides the petal into a set of regions interconnected by “springs” giving the structure elasticity and allowing changes in shape to be accommodated. Different growth parameters (growth rate, main direction of growth, anisotropy – the degree with which growth occurs preferentially in one direction, and rotation) were estimated for each region from the shape of the clones induced at different points in time. Through a process of parameter estimation and corresponding grid adjustment, the developmental sequence of petal growth was retraced. The relative contribution of these parameters to final petal shape was determined by simulations under different parameter values, providing an explanation of morphological shape (Rolland-Lagan *et al.* 2003). For instance, it was found that asymmetry, an important characteristic of the dorsal petals of *A. majus*, was primarily determined by the main direction of growth rather than by unequal growth rates.

This type of growth modeling provides a framework for exploring the relationship between growth patterns and molecular signals. A preliminary model incorporating putative molecular signals and growth parameters has been proposed by Coen *et al.* (2004). This model simulates the combined effects of two classes of morphogens (polarizing – which determines the principal axis of growth, and regionalizing – which elaborates local differences) on growth rate, direction of growth and anisotropy in different regions of the dorsal petal of *A. majus*. The observed shape of mature petals was recovered under a given set of assumptions that can then be tested experimentally and compared to known phenotypes. To link this model to experimental data, the transcription factor *CYCLOIDEA* (*CYC*), a known determinant of petal asymmetry (Luo *et al.* 1999) and therefore a candidate morphogen for regional (dorso-ventral) differences, was used as an example. Under this model, simulation of ectopic expression of *CYC*, which removes the distinction between dorsal and lateral regions of the petal, corresponded to the mutant phenotype (Coen *et al.* 2004). It is clear that simulating the effect of genes on cellular assemblages, often considered a “black box” in developmental biology, will greatly help our understanding of the processes underlying floral development.

MODELING MOLECULAR PROCESSES INVOLVED IN PLANT REPRODUCTIVE DEVELOPMENT

Models that propose to explain the genetic control of primordia cell fate have changed our understanding of plant development and evolution. With the recent substantial increase in genomic data, it has become necessary to develop computational tools to synthesize this type of information. It is now common practice to represent gene interactions as gene regulatory networks (GRN). GRNs are composed of nodes, representing the network components which can be transcribed genes, non-coding RNAs, proteins, and signaling molecules, connected by edges indicating their interaction (usually activation or repression). Most of the regulatory networks proposed for different aspects of development of plant reproductive structures are qualitative architectural and **static** models. Accumulated genetic data have been summarized as GRNs for many aspects of plant development including early flower development (Wellmer *et al.* 2006), petal development (Irish 2008), and anther formation (Wijeratne *et al.* 2007).

Computational approaches designed not only to recover the architecture of the gene network but also infer its dynamic behavior have not yet been widely applied to plant developmental genetics (Alvarez-Buylla *et al.* 2007). However, a series of studies by Alvarez-Buylla *et al.* (reviewed in Alvarez-Buylla *et al.* 2010) have modeled the genetic interactions of well-characterized genes (ABC and non-ABC function) for flower and floral organ development.

They applied Boolean logic (where gene expression is coded as binary states (i.e. “on” or “off”) to which are applied AND, OR, NOR rules to a small GRN of flowering and floral identity genes (Mendoza and Alvarez-Buylla 1998; Mendoza *et al.* 1999; Espinosa-Soto *et al.* 2004; Chaos *et al.* 2006). In their more recent studies, simulation of the dynamics of a 15-gene network, grounded on experimental expression data in *A. thaliana*, recovered only a few steady states (where the activation state of genes in the network does not change over time) corresponding to the gene expression profiles experimentally observed in different types of cells such as those of sepals, petals, stamens and carpels (Espinosa-Soto *et al.* 2004; Chaos *et al.* 2006). These simulations incorporated a few novel predictions of gene interactions and highlighted a few discrepancies with experimental data, which could lead to further *in vivo* experiments. Modifications of the network provided clues regarding the evolution and conservation of the general flower plan in eudicots. The network was robust to point alterations in the logical rules (a proxy for small modifications in gene function), suggesting that overall network functionality may be conserved during evolution. In addition, simulation of the effect of gene duplication and functional divergence on the network, using *Petunia hybrida* as an example, reproduced known patterns of expression profiles in this species (Espinosa-Soto *et al.* 2004). The dynamics described in these studies are **deterministic**, but increasing evidence suggests that gene expression is a **stochastic** process (reviewed in Kaern *et al.* 2005; Raser and O’Shea 2005; Raj and van Oudenaarden 2008). The relative effect of stochastic perturbations on gene networks has recently been investigated for floral development (Alvarez-Buylla *et al.* 2008). The temporal sequence dynamics of the floral GRN of Chaos *et al.* (2006) was explored by introducing a variable error probability for each gene at each update of the system. Different modeling methods (**discrete**, with states updated synchronously, and **continuous**) resulted in similar patterns of temporal change which showed that stochastic modifications in gene expression were sufficient to induce shifts from one steady state (i.e. organ type) to another. The temporal sequence of these transitions (sepals, then petals, then carpels and stamens) was consistent with the order of expression over time of A, then B, then C function observed from experimental data (Schmid *et al.* 2003). Interestingly, unlike for floral organs, small perturbations were not generally sufficient to induce a shift from inflorescence to flower meristem, suggesting that other inducing signals are required.

CONCLUSION

Modeling flowers and inflorescences are two research areas which are largely disconnected at present. Models of flowers have not been the elementary pieces used to build models of inflorescences. The next step will be to design models where both flowers and inflorescences are simultaneously represented. Merging these two types of models will be key to understanding the diversity and evolution of plant reproductive structures in the context of development and to study i) the interactions of molecular signals acting on flowers and inflorescences, and ii) the constraints exerted by inflorescence architecture on floral development (for example, the potential effect of the position of a flower in the inflorescence on its symmetry (Endress 1999)).

It is noticeable that model-based studies are very rarely developed further in subsequent research. This may be due to the fact that certain models investigate very specific questions but also more generally, that models are not comprehensible to non-specialists owing to the lack of a common language between biologists and mathematicians/physicists. The former do not always understand the working of models and how these can be applied to their biological systems. The latter do not always understand the needs of biologists in term of conceptualization, simulation and integration. This problem could be resolved in part by strengthening communication and collaborations between scientists from different fields. Integrative studies have shown that they can produce original answers to problems that could not have been addressed without the combination of knowledge and ways of thinking of different scientific fields.

The efforts to model flowers and inflorescences have been patchy. Flowers in particular have not been the subject of many modeling studies. Only a small number of plant biologists are using this type of approach; nevertheless, over recent years there has been a growing interest in modeling plant developmental processes. Large scale projects have been initiated, which aim to model entire plants and the working of their components. These include The Computable Plant project (E. Mjolness, University of California, Irvine, and E. Meyerowitz, California Institute of Technology, USA), The Virtual Plant project (C. Godin, Institut National de Recherche en Informatique et en Automatique, Montpellier, France) and The Algorithmic Botany project (P. Prusinkiewicz, University of Calgary, Canada).

Modeling can be a very useful approach for understanding biological phenomena and their underlying mechanisms. It has the potential to incorporate vast amounts of data and can serve to test and generate hypotheses. In particular, modeling provides the power to predict biological processes (such as localised activity of a putative morphogen required for correct organ growth simulation, or changes in gene activity within a complex network under untested conditions) which cannot easily be uncovered experimentally. The significance of modeling in plant evolutionary biology will also increase as more data (developmental and genomic) become available for a greater number of species. It will undoubtedly become an increasingly important component of plant biology, and we expect it will become routinely associated to “classical” experimental investigations.

GLOSSARY OF MODELING TERMINOLOGY IN RELATION TO GROWTH AND DEVELOPMENT

Computational model: that uses computer resources to study the behaviour of a complex object

Continuous: where states are defined over the whole of a possible space (quantitative) and time is not interrupted (see ‘discrete’)

Descriptive: integrating measurements to reproduce form and function as given by these, also known as reconstructive

Deterministic: producing the same output for a given set of conditions with no randomness (see ‘stochastic’)

Discrete: that is not continuous; may refer to interrupted time points or to states where the number of values is finite (qualitative) (see ‘continuous’)

Dynamic: changing over a given time period; developmental (see ‘static’)

Geometrical model: explicit representation in a two-, three- or more dimensional space of the shape and structure of an object by means of geometrical tools

Mathematical model: representation of an object by numerical quantities (inputs, outputs and internal states variables), and a set of equations describing the interaction among these variables

Mechanistic: explains or reproduces form in terms of the underlying biological, chemical, or physical processes

Simulation model: a representation where, by changing variables, predictions can be made about the behaviour of the object

Static: at a fixed point in time (see ‘dynamic)

Stochastic: where a state can be modified by random variation; does not provide a single point estimate but a probability distribution of possible estimates (see ‘deterministic’).

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REFERENCES

Adler I, Barabé D, Jean RV (1997) A history of the study of phyllotaxis. *Annals of Botany* **80**, 231-244

Alexeev DV, Ezhova TA, Kozlov VN, Kudryavtsev VB, Nosov MV, Penin AA, Skryabin KG, Choob VV, Shulga OA, Shestakov SV (2005) Spatial pattern formation in the flower of *Arabidopsis thaliana*: mathematical modeling. *Doklady Biological Sciences* **401**, 133-135

Alvarez-Buylla ER, Benítez M, Balleza Dávila E, Chaos A, Espinosa-Soto C, Padilla-Longoria P (2007) Gene regulatory network models for plant development. *Current Opinion in Plant Biology* **10**, 83-91

Alvarez-Buylla ER, Chaos A, Aldana M, Benítez M, Cortes-Poza Y, Espinosa-Soto C, Hartasánchez DA, Lotto RB, Malkin D, Escalera Santos GJ, Padilla-Longoria P (2008) Floral morphogenesis: stochastic explorations of a gene network epigenetic landscape. *PloS ONE* **3**, 1-13

Alvarez-Buylla ER, Azpeitia E, Barrio R, Benítez M, Padilla-Longoria P (2010) From ABC genes to regulatory networks, epigenetic landscapes and flower morphogenesis: Making biological sense of theoretical approaches. *Seminars in Cell and Developmental Biology* **21**, 108-117

Barabé D, Jean RV (1996) The constraints of global form on phyllotactic organization: the case of *Symplocarpus* (Araceae). *Journal of Theoretical Biology* **178**, 393-397

Barbier de Reuille P, Bohn-Courseau I, Ljung K, Morin H, Carraro N, Godin C, Traas J (2006) Computer simulations reveal properties of the cell-cell signaling network at the shoot apex in *Arabidopsis*. *Proceedings of the National Academy of Sciences USA* **103**, 1627-1632

Barthélémy D, Caraglio Y (2007) Plant architecture: a dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny. *Annals of Botany* **99**, 375-407

Benlloch R, Berbel A, Serrano-Mislata A, Madueño F (2007) Floral initiation and inflorescence architecture: a comparative view. *Annals of Botany* **100**, 659-676

Bowman JL, Smyth DR, Meyerowitz EM (1989) Genes directing flower development in *Arabidopsis*. *The Plant Cell* **1**, 37-52

Bowman JL, Smyth DR, Meyerowitz EM (1991) Genetic interaction among floral homeotic genes of *Arabidopsis*. *Development* **112**, 1-20

Bradley D, Carpenter R, Copsey L, Vincent C, Rothstein S, Coen E (1996) Control of inflorescence architecture in *Antirrhinum*. *Nature* **379**, 791-797

Byrne ME, Groover AT, Fontana JR, Martienssen RA (2003) Phyllotactic pattern and stem cell fate are determined by the *Arabidopsis* homeobox gene *BELLRINGER*. *Development* **130**, 3941-3950

Cassani E, Landoni M, Pilu R (2006) Characterization of the *Ra1* maize gene involved in inflorescence architecture. *Sex Plant Reproduction* **19**, 145-150

Chaos A, Aldana M, Espinosa-Soto C, García Ponce de León B, Garay Arroyo, Alvarez-Buylla ER (2006) From genes to flower patterns and evolution: dynamic models of gene regulatory networks. *Journal of Plant Growth and Regulation* **25**, 278-289

Choob VV, Penin AA (2004) Structure of flower in *Arabidopsis thaliana*: spatial pattern formation. *Russian Journal of Developmental Biology* **35**, 224-227

Coen ES, Meyerowitz EM (1991) The war of the whorls: genetic interactions controlling flower development. *Nature* **353**, 31-37

Coen E, Rolland-Lagan A-G, Matthews M, Bangham JA, Prusinkiewicz P (2004) The genetics of geometry. *Proceedings of the National Academy of Sciences USA* **101**, 4728-4735

Cole DJ, Morggan BJT, Ridout MS (2005) Models for strawberry inflorescence data. *Journal of Agricultural, Biological, and Environmental Statistics* **10**, 411-423

Colombo L, Franken J, Koetje E, Vanwent J, Dons HJM, Angenent GC, Vantunen AJ (1995) The *Petunia* MADS box gene *FBP11* determines ovule identity. *Plant Cell* **7**, 1859-1868

Cooke TJ (2006) Do Fibonacci numbers reveal the involvement of geometrical imperatives or biological interactions in phyllotaxis? *Botanical Journal of the Linnean Society* **150**, 3-24

Crepet WL, Niklas KJ (2009) Darwin's second 'abominable mystery': Why are there so many angiosperm species? *American Journal of Botany* **96**, 366-381

Ding Z, Xu S-C, Ye X-Z, Zhang Y, Zhang S-Y (2008) Flower modeling based on sketches. *Journal of Zhejiang University Science A* **9**, 481-488

Douady S, Couder Y (1996a) Phyllotaxis as a dynamical self organizing process Part I: the spiral modes resulting from time-periodic iterations. *Journal of Theoretical Biology* **178**, 255-274

Douady S, Couder Y (1996b) Phyllotaxis as a dynamical self organizing process Part II: the spontaneous formation of a periodicity and the coexistence of spiral and whorled patterns. *Journal of Theoretical Biology* **178**, 275-294

Douady S, Couder Y (1996c) Phyllotaxis as a dynamical self organizing process Part III: the simulation of the transient regimes of ontogeny. *Journal of Theoretical Biology* **178**, 295-312

Doust A (2007) Architectural evolution and its implication for domestication in grasses. *Annals of Botany* **100**, 941-950

Endress PK (1999) Symmetry in flowers: diversity and evolution. *International Journal of Plant Science* **160**, S3-S23

Espinosa-Soto C, Padilla-Longoria P, Alvarez-Buylla ER (2004) A gene regulatory network model for cell-fate determination during *Arabidopsis thaliana* flower development that is robust and recovers experimental gene expression profiles. *The Plant Cell* **16**, 2923-2939

Faust JE, Heins RD (1994) Modeling inflorescence development of the African violet (*Saintpaulia ionantha* Wendl.). *Journal of the American Society for Horticultural Science* **119**, 727-734

Fleming AJ (2006) Producing patterns in plants. *New Phytologist* **170**, 639-641

Frijters D (1978) Principles of simulation of inflorescence development. *Annals of Botany* **42**, 549-560

Gielis J (2003) A generic geometric transformation that unifies a wide range of natural and abstract shapes. *American Journal of Botany* **90**, 333-338

Gielis J, Gerats T (2004) A botanical perspective on modeling plants and plant shapes in computer graphics. *Proclamations International Conference on Computing, Communications and Control Technology* **VI**, 265-272

Godin C (2000) Representing and encoding plant architecture: a review. *Annals of Forest Science* **57**, 413-438

Gutiérrez RA, Shasha DE, Coruzzi GM (2005) Systems biology for the virtual plant. *Plant Physiology* **138**, 550-554

Hammer GL, Sinclair TR, Chapman SC, van Oosterom E (2004) On systems thinking, systems biology, and the in silico plant. *Plant Physiology* **134**, 909-911

Heisler MG, Jönsson H (2006) Modeling auxin transport and plant development. *Journal of Plant Growth Regulation* **25**, 302-312

Hofmeister W (1868) Allgemeine morphologie der gewächse. *Handbuch der Physiologischen Botanik* **1**, 405-664

Hotton S, Johnson V, Wilbarger J, Zwieniecki K, Atela P, Golé C, Dumais J (2006) The possible and the actual in phyllotaxis: bridging the gap between empirical observations and iterative models. *Journal of Plant Growth Regulation* **25**, 313-323

Ijiri T, Owada S, Okabe M, Igarashi T (2005) Floral diagrams and inflorescences: interactive flower modeling using botanical structural constraints. *ACM Transactions on Graphics* **24**, 720-726

Irish VF (2008) The *Arabidopsis* petal: a model for plant organogenesis. *Trends in Plant Science* **13**, 430-436

Jean RV (1994) *Phyllotaxis: A Systemic Study in Plant Morphogenesis*, Cambridge University Press, Cambridge and New York, 386 pp

Jean RV, Barabé D (2001) Application of two mathematical models to the Araceae, a family of plants with enigmatic phyllotaxis. *Annals of Botany* **88**, 173-186

Jeune B, Barabé D (1998) Interactions between physical and biological constraints in the structure of the inflorescences of the Araceae. *Annals of Botany* **82**, 577-586

Jönsson H, Heisler MG, Shapiro BE, Meyerowitz EM, Mjolsness E (2006) An auxin-derived polarized transport model for phyllotaxis. *Proceedings of the National Academy of Sciences USA* **103**, 1633-1638

Kaern M, Elston TC, Blake WJ, Collins JJ (2005) Stochasticity in gene expression: from theories to phenotypes. *Nature Reviews Genetics* **6**, 451-64

Korn RW (2008) Phyllotaxis: theories and evaluation. *International Journal of Plant Developmental Biology* **2**, 1-12

Krizek BA, Fletcher JC (2005) Molecular mechanisms of flower development: and armchair guide. *Nature Reviews Genetics* **6**, 688-698

Kuhlemeier C (2007) Phyllotaxis. *Trends in Plant Science* **12**, 143-150

Larsen RU, Persson L (1999) Modelling flower development in greenhouse *Chrysanthemum*. *Scientia Horticulturae* **63**, 225-239

Lewis J (2008) From signals to patterns: space, time, and mathematics in developmental biology. *Science* **322**, 399-403

Lindenmayer A (1968a) Mathematical models for cellular interactions in development I. Filaments with 1-sided inputs. *Journal of Theoretical Biology* **18**, 280-299

Lindenmayer A (1968b) Mathematical models for cellular interactions in development II. Simple and branching filaments with 2-sided inputs. *Journal of Theoretical Biology* **18**, 300-315

Luo D, Carpenter R, Copsey L, Vincent C, Clark J, Coen E (1999) Control of organ asymmetry in flowers of *Antirrhinum*. *Cell* **99**, 367-376

McSteen P (2009) Hormonal regulation of branching in grasses. *Plant Physiology* **149**, 46-55

Mendoza L, Alvarez-Buylla ER (1998) Dynamics of the genetic regulatory network for *Arabidopsis thaliana* flower morphogenesis. *Journal of Theoretical Biology* **193**, 307-319

Mendoza L, Thieffry D, Alvarez-Buylla ER (1999) Genetic control of flower morphogenesis in *Arabidopsis thaliana*: a logical analysis. *Bioinformatics* **15**, 593-606

Minorsky PV (2003) Achieving the in silico plant. Systems biology and the future of plant biological research. *Plant Physiology* **132**, 404-409

Mündermann L, Erasmus Y, Lane B, Coen E, Prusinkiewicz P (2005) Quantitative modeling of *Arabidopsis* development. *Plant Physiology* **139**, 960-968

Pelaz S, Ditta GS, Baumann E, Wisman E, Yanofsky MF (2000) B and C floral organ identity functions require *SEPALLATA* MADS-box genes. *Nature* **405**, 200-203

Perttunen J, Sievanen R (2005) Incorporating Lindenmayer systems for architectural development in a functional-structural tree model. *Ecological Modelling* **181**, 479-491

Prenner G, Vergara-Silva F, Rudall PJ (2009) The key role of morphology in modelling inflorescence architecture. *Trends in Plant Science* **14**, 302-309

Prusinkiewicz P (1993) Modeling and visualization of biological structures. *Proceedings of Graphics Interface '93*, pp 128-137

Prusinkiewicz P (1998) Modeling of spatial structure and development of plants: a review. *Scientia Horticulturae* **74**, 113-149

Prusinkiewicz P (2004) Modeling plant growth and development. *Current Opinion in Plant Biology* **7**, 79-83

Prusinkiewicz P, Lindenmayer A (1990) *The Algorithmic Beauty of Plants*, Springer, New York, 228 pp

Prusinkiewicz P, Rolland-Lagan A-G (2006) Modeling plant morphogenesis. *Current Opinion in Plant Biology* **9**, 83-88

Prusinkiewicz P, Erasmus Y, Lane B, Harder LD, Coen E (2007) Evolution and development of inflorescence architectures *Science* **316**, 1452-1456

Raj A, van Oudenaarden A (2008) Nature, nurture, or chance: stochastic gene expression and its consequences. *Cell* **135**, 216-226

Raser JM, O'Shea EK (2005) Noise in gene expression: origins, consequences, and control. *Science* **309**, 2010-2013

Reinhardt D (2005) Regulation of phyllotaxis. *International Journal of Developmental Biology* **49**, 539-546

Reinhardt D, Pesce E-R, Stieger P, Mandel T, Baltensperger K, Bennett M, Traas J, Friml J, Kuhlemeier C (2003) Regulation of phyllotaxis by polar auxin transport. *Nature* **426**, 255-260

Rolland-Lagan A-G, Bangham JA, Coen E (2003) Growth dynamics underlying petal shape and asymmetry. *Nature* **422**, 161-163

Rolland-Lagan A-G, Coen E, Impey SJ, Bangham JA (2005) A computational method for inferring growth parameters and shape changes during development based on clonal analysis. *Journal of Theoretical Biology* **232**, 157-177

Schmid M, Uhlenhaut NH, Godard F, Demar M, Bressan R, Weigel D, Lohmann JU (2003) Dissection of floral induction pathways using global expression analysis. *Development* **130**, 6001-6012

Skryabin KG, Alekseev DV, Ezhova TA, Kozlov VN, Kudryavtsev VB, Nosov MV, Penin AA, Choob VV, Shestakov SV, Shul'ga OA (2006) Type specification and spatial pattern formation of floral organs: a dynamic development model. *Theoretical Biology* **33**, 523-535

Smith RS, Kuhlemeier C, Prusinkiewicz P (2006a) Inhibition fields for phyllotactic pattern formation: a simulation study. *Canadian Journal of Botany* **84**, 1635-1649

Smith RS, Guyomarc'h S, Mandel T, Reinhardt D, Kuhlemeier C, Prusinkiewicz P (2006b) A plausible model of phyllotaxis. *Proceedings of the National Academy of Sciences USA* **103**, 1301-1306

Snow M, Snow R (1952) Minimum area and leaf determination. *Proceedings of the Royal Society London B* **139**, 545-566

Theissen G, Mezler R (2007) Molecular mechanisms underlying origin and diversification of the angiosperm flower. *Annals of Botany* **100**, 603-619

Tomlin CJ, Axelrod JD (2007) Biology by numbers: mathematical modelling in developmental biology. *Nature Reviews Genetics* **8**, 331-340

Turing AM (1952) The chemical basis of morphogenesis. *Philosophical Transactions of the Royal Society of London, B* **237**, 37-72

Van Der Linden FMJ (1996) Creating phyllotaxis: the stag-and-drag model. *Mathematical Biosciences* **133**, 21-50

Van Iterson G (1907) *Mathematische und Mikroskopisch-Anatomische Studien Über Blattstellungen*, Gustav Fisher, Jena, 331 pp

Vogel H (1979) A better way to construct the sunflower head. *Mathematical Biosciences* **44**, 179-189

Vollbrecht E, Springer PS, Goh L, Buckler ES, Martienssen RA (2005) Architecture of floral branch systems in maize and related grasses. *Nature* **436**, 1119-1126

Wang Y, Li J (2008) Molecular basis of plant architecture. *Annual Review of Plant Biology* **59**, 253-279

Watanabe T, Hana JS, Room PM, Hasegawa T, Nakagawa H, Takahashi W (2005) Rice morphogenesis and plant architecture: measurement, specification and the reconstruction of structural development by 3D architectural modelling. *Annals of Botany* **95**, 1131-1143

Wellmer F, Alves-Ferreira M, Dubois A, Riechmann JL, Meyerowitz EM (2006) Genome-wide analysis of gene expression during early *Arabidopsis* flower development. *PloS Genetics* **2**, 1012-1024

Whitfield J (2003) Maths gets into shapes. *Nature Science Update*, March 31 2003, http://www.nature.com/nsu/030331/030331-3.html

Wijeratne AJ, Zhang W, Sun Y, Liu W, Albert R, Zheng Z, Oppenheimer DG, Zhao D, Ma H (2007) Differential gene expression in *Arabidopsis* wild-type and mutant anthers: insight into anther cell differentiation and regulatory networks. *The Plant Journal* **52**, 14-29

Wilson PI (1995) The geometry of golden section phyllotaxis. *Journal of Theoretical Biology* **177**, 315-323

Wilson PA, Hanan JS, Room PM, Chakraborty S, Doley D (1999) Using Lindenmayer systems to model morphogenesis in a tropical pasture legume *Stylosanthes scabra*. *Canadian Journal of Botany* **77**, 394-403

Yeatts FR (2004) A growth-controlled model of the shape of a sunflower head. *Mathematical Biosciences* **187**, 205-221

Yuan JS, Galbraith DW, Dai SY, Griffin P, Stewart Jr. CN (2008) Plant systems biology comes of age. *Trends in Plant Science* **13**, 165-171