Theoretical models for branch formation in plants

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Abstract
Various branch architectures are observed in living organisms including plants. Branch formation has traditionally been an area of interest in the field of developmental biology, and theoretical approaches are now commonly used to understand the complex mechanisms involved. In this review article, we provide an overview of theoretical approaches including mathematical models and computer simulations for studying plant branch formation. These approaches cover a wide range of topics. In particular, we focus on the importance of positional information in branch formation, which has been especially revealed by theoretical research in plants including computations of developmental processes.

Keywords Branch · Divarication · Mathematical model · Plant morphogenesis · Theoretical approach

Introduction
Branch architectures are observed in various plant organs including shoot meristems (Kuhlemeier 2007, 2017), inflorescence stems (Bommert and Whipple 2018), leaves (Efroni et al. 2010; Wang and Jiao 2018), roots (Hinsinger et al. 2005), prothallia (Momose 1967) and thalli (Parihar 1967). On a cellular level, the morphogenesis of some unicellular algae (Lacalli 1975a, b), leaf pavement cells (Higaki et al. 2017), and root hair cells (Payne and Grierson 2009) can be regarded as branching (Li et al. 2018). The branch formation repeatedly observed in plants is important from a morphological perspective.

Here, we review theoretical models for branch formation in the different hierarchies of plant architecture. These theoretical approaches have been used to understand the complex mechanisms involved. In particular, morphogenesis is a difficult process to image because it involves continuous deformation through localized growth. We can confirm the feasibility of a predicted condition by simulation, therefore simulations using adequate theoretical models have been important for solving the problems in morphogenesis involving branch formation. Theoretical research on animal branch development in recent years has been extensive whereas branch formation in plants has also been investigated traditionally (Cohen 1967; Honda 1971; Lindenmayer 1968, 1971; Meinhardt 1976, 1982). In the present article, we focus on the generation processes, complexity, environmental interactions, dimensionality, and mode selection for branching in plants.

Triggers for generation of branches
Growth inhomogeneity (i.e., differential growth rates) is the most important factor for generating complexity in plant morphogenesis, although programmed cell death also contributes to the formation of tubular structures, such as aerenchyma and tracheary elements (Jones and Dangle 1996). During organ formations, cell division and subsequent cell expansion show differences in their activities and deployment directions, and thus are reflected in the generation of growth inhomogeneity. Branches are initiated through growth inhomogeneity, and subsequently some branches elongate after their generation.

Mechanical stresses and their feedback via the cytoskeleton are considered to be one factor that controls the growth inhomogeneity in plants (Hamant et al. 2008). Mathematical models including feedback from a numerically predicted pressure distribution in an elastic medium
have been applied to shoot meristems (Bozorg et al. 2014) and sepal formation (Hervieux et al. 2016). In this framework, Hong et al. (2016) showed that organs lose their robustness to generate a regular size and shape without spatiotemporal averaging in their growth, i.e., inhomogeneities occur against regular boundaries, although the inhomogeneities are disorganized. Therefore, some mechanisms are needed to arrange the inhomogeneity.

The mechanical aspects of morphogenesis are important considerations for branch formation. For example, the jigsaw puzzle-like shapes of cotyledon pavement cells can be explained by a mechanical model in which excessive cell-wall growth promotes undulation and buckling of lateral cell walls (Higaki et al. 2017). In addition, activation feedback against the convex wall formations can arrange the shape of the jigsaw puzzle-like pattern (Sapala et al. 2018), although the buckling itself can generate furrows with a specific wavelength (Higaki et al. 2017; Takigawa-Imamura et al. 2015). When concave walls are connected by microtubules that prevent expansion, formation of convex wall shapes is activated. This effect subsequently prevents the connection of convex walls. For the initiation of the activation feedback, positional information such as distributions of Rho of plants (ROP) proteins may be related in.

Molecular-based positional information, especially existing as periodic patterns, is important for plant branch formation (Lacalli 1975b; Meinhardt 1982; Meinhardt and Gierer 1974). As suggested by Turing (1952), the mechanisms underlying the formation of such patterns can be explained by reaction–diffusion (RD) systems. The conditions required for RD pattern formation can be applied to arbitrary interactions of molecules such as WUSCHEL–CLAVATA in the shoot meristem (Fujita et al. 2011), and SPEEACHLESS–SCREAM and EPI-DERMAL PATTERNING FACTOR 2 in stomatal positioning (Horst et al. 2015). On the cellular level, ROP proteins are considered to be crucial factors that provide the positional information observed in root hairs (Jones et al. 2002; Molendijk et al. 2001), pavement cells (Fu et al. 2005), and tracheary elements (Nagashima et al. 2018). The ROP localization was explained within the framework of a RD model (Nagashima et al. 2018; Payne and Grier son 2009).

In addition, PIN-FORMED (PIN)-mediated polar auxin transport (PAT) is considered to provide various types of positional information in plants. Though many mathematical models have been proposed for the required traits of positional information, the self-organization properties of auxin and different directions of PIN and auxin patterns against auxin flux, that summarized by van Berkel et al. (2013), indicated inadequacies of the models.

Simple to complex branches

To generalize plant branch formation, here we consider situations where disk-like architectures gradually produce branches during their growth processes (Fig. 1a–d). When the apparent branching rules of the branches are different, differences become prominent as growth progresses as shown in Fig. 1. Complex architectures, such as nested branches (i.e., branches hierarchically composed of side branches; Fig. 1b–d, e–j) tend to overlap (Harrison and Kolář 1988; Holloway and Harrison 1999; Nakamasu et al. 2014), e.g., the disc developed in a limited space in Fig. 1b. The complexity of branching depends on the frequency of branch generation (i.e., branching times); therefore, to prevent tangled branches, branch generation or subsequent elongation needs to be restricted as Fig. 1a with no side branch. This restriction has effect to maintain the simplicity of branch shape. Leaf-and-flower generation occurs only in the shoot meristem; therefore, not only spatial restriction but also temporal continuums of shoot meristem identity create different branch architectures from simple to complex and more (Prusinkiewicz et al. 2007). Furthermore, formation of a fractal structure by the scale-down of repeating units enables efficient use of the limited space, thus avoiding branch overlap without interrupting the generation of complexity (Holloway and Harrison 1999) (Fig. 1c, d, h–j). Shortened branch lengths were also incorporated into tree-like architectures in Honda’s model (Honda 1971). As shown in Fig. 1e–j, different branching rules show equivalent results to the contraction of branch length in three-dimensional trees based on Honda’s model (Borchert and Honda 1984; Honda 1971). These localized and/or fractal-like branch architectures have many examples in plants as follows. Restriction of branch generation is observed in situations where the number of inflorescence branches is increased (Nakagawa et al. 2002) or leaves are dissected (Berger et al. 2009; Larue et al. 2009) by genetic manipulations. Self-similarities are observed as fractal structures in leaf veins, canopies (Mandelbrout 1983), fern leaves (Barnsley 1988), and Romanesco cauliflower.

The two-dimensional branch architectures termed divarications are often observed in leaves. Such diversified leaves are categorized as serrations, lobes, and leaflets mainly according to their degree of protrusion. Simple and compound leaves are sharply distinguished from one another, though the arrangement of lobes or leaflets in divarications often show commonalities (Nakamasu et al. 2017). A heterophyllous plant, Rorippa aquatica, has sequential peripheral complexity from an elliptically shaped simple leaf to a finely dissected leaf (Nakayama et al. 2012). This type of heterophyll can be
understood by the model that combines both strategies mentioned above (A. Nakamasu, N. J. Suematsu, and S. Kimura, unpublished data). In the model, spatial restrictions explain the formation of simpler shapes, as shown in leaves in *Arabidopsis thaliana* L. (Bilsborough et al. 2011). Also, the relative reductions of spatial scale permit the natural tapering of divarication units toward the distal ends and avoid overlaps, as reported in Holloway and Harrison (1999).

**Open or closed branches**

In general, the branches of the aerial parts of plants, such as the body plan and leaf shape, have abundant variety and reproducible characteristics, and these branches are often used for taxonomic identification. Conversely, the underground branches of roots have less consistent features and tend to show phenotypic plasticity depending on their chemical and physical environments (reviewed in Hinsinger et al. 2005). The importance of environmental interactions in branching was recognized in early period on theoretical researches and its effects have been implemented into simulation of branch formation (Cohen 1967; Honda and Hatta 2004; Honda et al. 1997). Mech and Prusinkiewicz (1996) summarize the incorporation of such interactions into models such as L-system (Mech and Prusinkiewicz 1996). In this section, we focus on the boundaries between branches and the environment, and whether they are open or closed. With open boundaries, branches can interact via the external environment, but in the case of a closed boundary, branches can only recognize others (if possible) internally (Fig. 2).

Plant branches elongate in a space-filling manner, resulting in the generation of evenly distributed shapes. In cases of stochastic formation, the generated branches tend to disrupt the whole regularity. To avoid branch collision in this case, mutual interactions between the flexible environment and branch generation are needed, such as diffusion-limited aggregation (Witten and Sander 1981). A similar situation was also postulated in the phase field model used to express crystal growth (Kobayashi 1993). These branches are considered to need an open boundary to reduce branch overlap. As one such example in plants, leaf veins can be considered to be a branch architecture having an open boundary with the blade as an external environment (Fig. 2a, b). Although leaf veins also follow the same rule for prevention of overlaps,
loops (i.e., the collision of branches) are permissible in some exceptions. In mathematical models for leaf vein formation, the boundary between a blade and a premature vein is open, and molecules that determine the vein position can diffuse through the boundary whether flows are involved (Fujita and Mochizuki 2006; Mitchison 1980, 1981) or not (Meinhardt 1976). Such physical gradients spreading at the multicellular scale can react and have an effect within this range. This enables evenly distributed vein positioning with several cell intervals. Root formation can also be considered to have an open boundary. Both soil conditions and several types of feedback from the absorption of substrates by the root itself regulate rhizosphere geometries (Hinsinger et al. 2005; Walter et al. 2009). Historically, morphological analyses of roots architecture have been difficult, but recent technical advances should allow theoretical studies to progress (Band et al. 2012; Keyes et al. 2017).

By contrast, most types of branch formation in plants are considered to involve deformation with a closed boundary (Fig. 2c, d). It is well known that various types of intrinsic regulation of branch angle can produce the branch patterns observed in reality (Fisher and Honda 1977; Honda 1971) (Fig. 1e–j). It has been also proposed that appropriate rules for branch formation can reproduce the various traits of plants from a series of studies using L-systems (Prusinkiewicz and Lindenmayer 1990). Restriction of the mutual interactions between branches through the external environment is expected to results in branches lose their positioning control easily. However, spiral phyllotaxis tends to show divergence close to the golden angle, which is advantageous for avoiding overlaps when seen from above (Niklas 1988). So, how are such rules derived? It was pointed out that positional information with spatial periodicity is important for the positioning of the repetitive units (Meinhardt 1982). Positional information with a specific wavelength can be explained by molecular interactions within a boundary (Jonsson et al. 2006; Smith et al. 2006; Turing 1952).

Leaf primordia are formed in the “first available space” (Adler 1974; van Iterson 1907). From a geometrical perspective, it was suggested that equal spaces between primordia are essential to form the golden angle (Mitchison 1977; Richter and Schranner 1978). Phyllotaxis patterns including the golden angle arrangement can be reproduced by simulations of iterative insertion of a new primordium in the most distant place from the previous leaf primordia on a two-dimensional curved surface (Jonsson et al. 2006; Smith et al. 2006). Though some researchers suggested that temporal regulation or mechanical force are related to the patterning (Douady and Couder 1996a, b; Shipman and Newell 2004), these discussions and historical backgrounds are excellently summarized in Kuhlemeier 2007, 2017. Periodic growth of a boundary in a two-dimensional plane is another example of branch formation with a closed boundary. Various divarications can be generated by models using different traits with periodicity (Harrison and Kolár 1988; Holloway and Harrison 1999; Nakamasu et al. 2014). Contributions other than from the boundary are not considered for such branch positioning, and reproducible steady-state

|                         | Open boundary | Closed boundary |
|-------------------------|---------------|-----------------|
| **Growth activation**   | a             | c               |
| **Growth inhibition**   | b             | d               |

Fig. 2 Interactions with the external environment in branch formation. The formation of branch architecture in plants is considered to be produced by changes in growth intensity, which seem to include activation (a, c) and inhibition (b, d) of growth. Each case includes open boundaries (a, b) and closed boundaries (c, d). With open boundaries, branches can interact via the external environment (a, b). By contrast, with closed boundaries, the generated branches need to avoid overlaps (c, d). In some cases, even branches with closed boundaries can be modified by the local environment. e A crown shyness-like phenomenon observed in camphor trees, which is considered to be an example of the local interaction.
shapes can be obtained. A regular sequence of branch arrangements is observed when a ring is just grown depending on an equally spaced periodic pattern. Such programmed diversifications were modeled first with bifurcation and subsequently with lateral branching. (Harrison and Kolář 1988; Nakamasu et al. 2014) (Figs. 1b–d, 3b). In the case of lateral branching, the sequence of regular arrangements observed in the intact (i.e., not modified) branches was described using recurrence formulas (Nakamasu et al. 2014, 2017), and is coincidentally comparable to a specific parameter in (td)OL-systems with a delay (Prusinkiewicz and Lindenmayer 1990), though these models are completely different systems. The former utilizes the spatial scale to make form, whereas the latter model repeatedly adds a stable unit as measured in time to adjust the branch arrangement. This rule is appropriate to explain branch arrangements that include asymmetry observed in actual leaves (Nakamasu et al. 2014, 2017). Degree of branch asymmetry can be expressed as subtractions of sequential steps of the recurrence formula.

Continuous growth based on intrinsic periodicity can generate a certain branch pattern also in three dimensions, as exemplified by Holloway and Harrison (2008).

Two or three dimensions for branches

Branching does not occur in one dimension, it requires two or more dimensions. When we focus on a leaf indentation, a boundary can be captured as a one-dimensional curved line on a two-dimensional plane (Bilsborough et al. 2011; Nakamasu et al. 2014; Prusinkiewicz and Runions 2012) (Fig. 3). Though leaf primordia grow three-dimensionally as shown in Fig. 3a, almost all leaves can be considered to be two-dimensional planes with the adaxial and abaxial sides already specified (McConnell et al. 2011; Sawa et al. 1999; Siegfried et al. 1999). Therefore, the boundary is assumed to be equivalent to a rubber band (i.e., a one-dimensional circumference) in three-dimensional space (Fig. 3a). In many cases, deformations of the rubber band in three-dimensional space can be described similarly to that
on a two-dimensional plane (Fig. 3c). That is, the simulated divarication on two-dimensional plane can exist in three dimensions. The two-dimensional implementations are effective and efficient even if there are overlaps, because the three-dimensional space is practically useful to avoid the inevitable collision of divarication in two dimensions (Fig. 3a, b).

By contrast, because most plant organs develop from meristems (two-dimensional curved surfaces), branch positions need to be understood three-dimensionally (Honda 1971). In general, higher dimensions increase the degrees of freedom but are not simply applicable to the complexities of actual plant branches, such as when imaging young shoots of edible asparagus that retains a simple shape. A two-dimensional branch in three dimensions has more dynamic degrees of freedom than a three-dimensional branch in three dimensions. That is, the branch can escape in the vertical directions from leaf plane. Therefore, overlap on a two-dimensional plane is less critical. However, a three-dimensional branch cannot escape to four dimensions, so overlaps in three dimensions are unacceptable. Three-dimensional branches desperately need to avoid collision. Therefore, in plants that continue to form branch architectures throughout their lifetime, branching should be frequently confined to a limited region.

In Fig. 4, virtual broccoli inflorescences with different branch rules were generated and then longitudinally sectioned. The rules used for each row of imagings in Fig. 4 correspond to those in Fig. 1h–j. Compared with Fig. 3b, two-dimensionally formed divarications are not simple longitudinal-sections of three-dimensional branches (Fig. 4c, f, i). Therefore, different discussion frameworks should be applied to two- and three-dimensional branches.

**Different modes of branches**

Branches often show two different structural modes, which are classified as bifurcation and lateral branching, as exemplified in Figs. 1, 4, and 5. The mode differences are observed in both two- or three-dimensional branches in leaves (Miyoshi et al. 2019) or body plans (Harrison 2017) (Fig. 5). However, three-dimensional branches are more diverse within a certain branch mode (Fig. 5b, c, e, f). The different modes can coexist even in the same organ of a single plant. For example, a liverwort gametophyte shows different modes of branching (Inoue et al. 2008). That is, a system that can select coexisting or independent modes...
is important for the formation of such branches. In leaves, the two different modes can be observed in closely related fern species (Miyoshi et al. 2019) (Fig. 5a, d). In addition, the formation of bifurcated leaves can be observed in pin mutants of *A. thaliana* (Reinhardt et al. 2003). Mutations of *slm1* (a PIN homolog) result in phyllotaxis and leaves showing the bifurcation mode in *Medicago polymorpha* L. (Zhou et al. 2011). It is known that the both modes can be described by patterning—growth coupling (Harrison and Kolář 1988; Holloway and Harrison 2008; Nakamasu et al. 2014). Then, the difference between the branch modes is considered to be explained by the difference in frequency-doubling of pattern, which can be treated as problems of pattern transition on a growing surface (Fujita et al. 2011; Holloway and Harrison 2008). PIN-mediated polar auxin transport is known to be a mechanism that can generate periodic positional information (Bilsborough et al. 2011; Jonsson et al. 2006; Smith et al. 2006; van Berkel et al. 2013). It is interesting that a different branch mode (bifurcation) becomes apparent with the loss of PIN function (Harrison 2017).

**Conclusion**

In this review, we first considered the mechanical aspects of branch formation and pattern-formation mechanisms by plant molecules. Second, we reviewed the effectiveness of spatiotemporal restriction of branch generation and the scale-down of added units to avoid the overlap that accompanies increasing branch complexity. We then discussed interactions with the external environment during branch formation. In addition, we presented examples of the differences between two- and three-dimensional branches, and the variation in branching modes deployed in these dimensions.

Recently, understanding of divarication based on equally spaced periodicity has progressed. The mechanism (i.e., patterning—growth coupling) ensures the generation of reproducible and regular divarication arrangements not only in bifurcation but also in monopodial branching. It is considered to be a two-dimensional version of programmed branching observed in the development of murine lungs by Metzger et al. (2008). Divarication is characteristic of plant leaves, therefore this finding is an achievement of plant derivation. However, actual leaves frequently show branch patterns different from the sequence of regular arrangements. Therefore, we need to consider such differences from the perspective of modification of the deterministic rule. Three-dimensional branching based on periodic positional information remains unexplored, though some reproducible branch arrangements have been predicted from the golden angle of divergence in phyllotaxis and the branch pattern of early lung formation in mice (Metzger et al. 2008). Frameworks to deal with deformation in three-dimensional space are needed for such studies, and related equipment has been developed (Matsuda et al. 2017; Okuda et al. 2018) and partially investigated. Plants with closed boundaries in which the intrinsic branching patterns tend to be maintained may be advantageous for this kind of investigation. Because almost all branched organ formations in animals are considered to include interactions with the surrounding environment (Iber and Menshykau 2015; Miura 2015), the resulting branches might be somewhat different from the intact arrangements. The differences in branching modes that are commonly observed in plants and animals are parallel problems, and have been treated theoretically in limb, lung and kidney formation in animals (Hirashima et al. 2009; Menshykau et al. 2012; Miura et al. 2006; Xu et al. 2017). Then the factors which determined the mechanism of transition were mathematically analyzed (Crampin et al. 2002). To address this problem, an understanding of positional information at the molecular level is required. Subsequently, the plant-specific pattern-formation mechanism of the PAT system, which is described by many models, should be integrated. On these points, references from case studies of animal may be relevant for future perspectives.

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**Compliance with ethical standards**

**Conflict of interest** The authors declare that they have no conflict of interest.

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**References**

Adler I (1974) A model of contact pressure in phyllotaxis. J Theor Biol 45:1–79
Band LR, Fozard JA, Godin C, Jensen OE, Pridmore T, Bennett MJ, King JR (2012) Multiscale systems analysis of root growth and development: modeling beyond the network and cellular scales. Plant Cell 24:3892–3960

Barnsley MF (1988) Fractals everywhere. Academic, San Diego

Berger Y, Harpaz-Saad S, Brand A, Melnik H, Sirding N, Alvarez JP, Zinder M, Samach A, Eshed Y, Ori N (2009) The NAC-domain transcription factor GOBLET specifies leaflet boundaries in compound tomato leaves. Development 136:823–832

Bilsborough GD, Runions A, Barkoulas M, Jenkins HW, Hasson A, Galinh C, Laufs P, Hay A, Prusinkiewicz P, Tsiantis M (2011) Model for the regulation of Arabidopsis thaliana leaf margin development. Proc Natl Acad Sci USA 108:3424–3429

Bommert P, Whipple C (2018) Grass inflorescence architecture and meristem determinacy. Semin Cell Dev Biol 79:37–47

Borchert R, Honda H (1984) Control of development in the bifurcation system of Tabaebia Rosea: a computer simulation. Bot Gaz 145:184–195

Bozorg B, Krupinski P, Jonsson H (2014) Stress and strain provide positional and directional cues in development. PLoS Comput Biol 10:e1003410

Cohen D (1967) Computer simulation of biological pattern generation processes. Nature 216:246–248

Couturie E, du Pont SC, Douady S (2011) The filling law: a general principle: phyllotaxis and effect of gravity. J Theor Biol 289:47–64

Crampin EJ, Gaffney EA, Maini PK (2002) Stability analysis of non-autonomous reaction-diffusion systems: the effects of growing domains. J Math Biol 44:107–128

Douday S, Couder Y (1996a) Phyllotaxis as a dynamical self organizing process part I: the spiral modes resulting from time-periodic iterations. J Theor Biol 178:255–274

Douday 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. J Theor Biol 178:275–294

Efroni I, Eshed Y, Lifschitz E (2010) Morphogenesis of simple and compound leaves: a critical review. Plant Cell 22:1019–1032

Fisher JB, Honda H (1977) Computer simulation of branching pattern and geometry in Terminalia (Combretaceae), a tropical tree. Bot Gaz 138:377–384

Fu Y, Yu Y, Zheng Z, Wasteneys G, Yang Z (2005) Arabidopsis interdigitating cell growth requires two antagonist pathways with opposing action on cell morphogenesis. Cell 120:687–700

Fujita H, Mochizuki A (2006) Pattern formation of leaf veins by the positive feedback regulation between auxin flow and auxin efflux carrier. J Theor Biol 241:541–551

Fujita H, Toyokura K, Okada K, Kawaguchi M (2011) Reaction-diffusion pattern in shoot apical meristem of plants. PLoS One 6:e18243

Hamant O, Heisler MG, Jönsson H, Krupinski P, Uyttewaal M, Bokov P, Corson F, Sahlin P, Boudaoud A, Meyerowitz EM, Couder Y, Traas J (2008) Developmental patterning by mechanical signals in Arabidopsis. Science 322:1650–1655

Harrison CJ (2017) Auxin transport in the evolution of branching forms. New Phytol 215:545–551

Harrison LG, Kolář M (1988) Coupling between reaction-diffusion prepattern and expressed morphogenesis, applied to desmids and dasyyclads. J Theor Biol 130:493–515

Hervieux N, Dumond M, Sapala A, Routier-Kierzkwowsa A, Kierzkowski D, Roeder AHK, Smith RS, Boudaoud A, Hamant O (2016) A mechanical feedback restricts sepal growth and shape in Arabidopsis. Curr Biol 26:1019–1028

Higaki T, Takigawa-Imamura H, Akita K, Kutsuna N, Kobayashi R, Hasezawa S, Miura T (2017) Exogenous cellulase switches cell interdigation to cell elongation in an RIC1-dependent manner in Arabidopsis thaliana cotyledon pavement cells. Plant Cell Physiol 58:106–119

Hinsinger P, Gobran GR, Gregory PJ, Wenzel WW (2005) Rhizosphere geometry and heterogeneity arising from root-mediated physical and chemical processes. New Phytol 168:293–303

Hirashima T, Iwasa Y, Morishita Y (2009) Dynamic modeling of branching morphogenesis of ureteric bud in early kidney development. J Theor Biol 259:58–66

Holloway DM, Harrison LG (1999) Algal morphogenesis: modelling interspecific variation in Microsterias with reaction-diffusion patterned catalysis of cell surface growth. Philos Trans R Soc Lond B 354:417–433

Holloway DM, Harrison LG (2008) Pattern selection in plants: coupling chemical dynamics to surface growth in three dimensions. Ann Bot 101:361–374

Honda H (1971) Description of the form of trees by the parameters of the tree-like body: effects of the branching angle and the branch length on the sample of the tree-like body. J Theor Biol 31:331–338

Honda H, Hatta H (2004) Branching models consisting of two principles: phyllotaxis and effect of gravity. Forma 19:183–196

Honda H, Hatta H, Fisher JB (1997) Branch geometry in Cornus kousa (Cornaceae): computer simulations. Am J Bot 84:745–755

Hong L, Dumond M, Tsugawa S, Sapala A, Routier-Kierzkwowsa A, Zhou Y, Chen C, Kiss A, Zhi M, Hamant O, Smith RS, Komatsuzaki T, Li C, Boudaoud A, Roeder AHK (2016) Variable cell growth yields reproducible organ development through spatiotemporal averaging. Dev Cell 38:15–32

Horst RJ, Fujita H, Lee JS, Rychel AL, Garrick JM, Kagwachi M, Peterson KM, Trii KU (2015) Molecular framework of a regulatory circuit initiating two-dimensional spatial patterning of stomatal lineage. PLoS Genet 11:e1005374

Iber D, Menshukau D (2015) The control of branching morphogenesis. Open Biol 3:130088

Inoue A, Furuki T, Imaichi R (2008) Developmental morphology of irregularly-shaped gametophytes of the liverwort Mizutania riccardoidea (Mizutaniaceae). Acta Phytotax Geobot 59:239–247

Jones AM, Shen J-J, Li C, Boudaoud A, Meyerowitz EM, Couder Y, Harpaz-Saad S, Brand A, Melnik H, Sirding N, Alvarez JP, Kierzkowsa A, Kierzkowski D, Roeder AHK, Smith RS, Boudaoud A, Hamant O, Chang Y, Gu Y, Liu Y, Li Z, Zhang J, Li Z, Zou J, Zha M, Li C, Boudaoud A, Roeder AHK (2016) Variable cell growth yields reproducible organ development through spatiotemporal averaging. Dev Cell 38:15–32

King JR (2012) Multiscale systems analysis of root growth and development. J Theor Biol 290:47–64

Kuhlemeier C (2007) Phyllotaxis. Trends Plant Sci 12:1360–1385

Kuhlemeier C (2017) Phyllotaxis. Curr Biol 27:853–909

Lacalli TC (1975a) Morphogenesis in Micrasterias I. Tip growth. J Embryol Exp Morphol 33:95–115

Lacalli TC (1975b) Morphogenesis in Micrasterias II. Pattern of morphogenesis. J Embryol Exp Morphol 33:117–126

Larue CT, Wen J, Walker JC (2009) A microRNA-transcription factor module regulate organ size and patterning in Arabidopsis. Plant Physiol 150:450–463

Li J, Kim T, Szymanski DB (2018) Multi-scale regulation of cell branching: modeling morphogenesis. Dev Biol. https://doi.org/10.1016/j.ydbio.2018.12.004
Okuda S, Miura T, Unoue Y, Adachi T, Eirak M (2018) Combining Turing and 3D vertex models reproduces autonomous multicellular morphogenesis with undulation, tubulation, and branching. Sci Rep 8:2386

Parikh NS (1967) Bryophyta. Indian Universities Press, Allahabad

Payne RJH, Grierson CS (2009) A theoretical model forROP localisation by auxin in Arabidopsis root hair cells. PLoS One 4(12):e8337

Prusinkiewicz P, Lindenmayer A (1990) The algorithmic beauty of plants. Springer, New York

Prusinkiewicz P, Runions A (2012) Computational models of plant development and form. New Phytol 193:549–569

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

Reinhardt D, Pesce ER, Stieger P, Mandal T, Baltensperger K, Bennett M, Trass J, Friml J, Kuhlmeier C (2003) Regulation of phyllotaxis by polar auxin transport. Nature 426:255–260

Richter PH, Schranner R (1978) Leaf arrangement. Geometry, morphogenesis, and classification. Naturwissenschaften 65:319–327

Sapala A, Runions A, Routier-Kierzowska A, Das Gupta M, Hong L, Hofhuis H, Verger S, Mosca G, Li C, Hay A, Hamant O, Roeder AHK, Tatsiantis M, Prusinkiewicz P, Smith RS (2018) Why plants make puzzle cells, and how their shape emerges. eLife 7:e52794

Sawa S, Watanabe K, Goto K, Kanaya E, Morita EH, Okada K (1999) FILAMENTOUS FLOWER, a meristem and organ identity gene of Arabidopsis, encodes a protein with a zinc finger and HMG-related domains. Genes Dev 13:1079–1088

Shipman PD, Newell AC (2004) Phyllotactic patterns on plants. Phys Rev Lett 92:168102

Siegrfried KR, Eshed Y, Baum SF, Otsuga D, Drews GN, Bowman JL (1999) Members of the YABBY gene family specify abaxial cell fate in Arabidopsis. Development 126:4117–4128

Smith RS, Guyomarc’h S, Mandal T, Reinhardt D, Kuhlmeier C, Prusinkiewicz P (2006) A plausible model of phyllotaxis. Proc Natl Acad Sci USA 103:1301–1306

Takigawa-Imamura H, Morita R, Iwaki T, Tsuji T, Yoshikawa K (2015) Tooth germ invagination from cell–cell interaction: working hypothesis on mechanical instability. J Thor Biol 382:284–291

Turing AM (1952) The chemical basis of morphogenesis. Philos Trans R Soc Lond B 237:37–72

van Berkel K, de Boer RJ, Scheres B, ten Tusscher K (2013) Polar auxin transport: models and mechanisms. Development 140:2253–2268

van Dersch G (1907) Mathematische und mikroskopisch-anatomische Studien über Blattställungen. Fischer, Jena

Walter A, Silk WK, Schurr U (2009) Environmental effects on spatial and temporal patterns of leaf and root growth. Annu Rev Plant Biol 60:279–304

Wang Y, Jiao Y (2018) Auxillary meristem initiation—a way to branch out. Curr Opin Plant Biol 41:61–66

Witten TA, Sander LM (1981) Diffusion-limited aggregation, a kinetic critical phenomenon. Phys Rev Lett 47:1400–1403

Xu H, Sun M, Zhao X (2017) Turing mechanism underlying a branching model for lung morphogenesis. PLoS One 12:e0174946

Zhou C, Han L, Hou C, Mysore KS, Wang Z (2011) Developmental analysis of a Medicago truncatula smooth leaf margin1 mutant reveals context-dependent effects on compound leaf development. Plant Cell 23:2106–2124

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