

## Plant Morphogenesis 123: a renaissance in modern botany?

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Received October 5, 2018; accepted October 25, 2018; published online February 21, 2019

Plants are a group of multicellular organisms crucial for the biosphere on the Earth. In the 17th century, the founding fathers of modern botany viewed the bud as the basic unit undergoing the plant life cycle. However, for many understandable reasons, the dominant conceptual framework evolved away from the “bud-centered” viewpoint to a “plant-centered” viewpoint that treated the whole plant, consisting of numerous buds, as a unit and considered the entire plant to be the functional equivalent of an animal individual. While this “plant-centered” viewpoint is convenient and great progress has been made using this conceptual framework, some fundamental problems remain logically unsolvable. Previously, I have proposed a new conceptual framework for interpretation of plant morphogenesis, called Plant Morphogenesis 123, which revives a “bud-centered” viewpoint. The perspective of Plant Morphogenesis 123 allows us to address new questions regarding to the mechanisms of plant morphogenesis that are important, and technically accessible, but previously neglected under the “plant-centered” conceptual framework. In addition to describing these questions, I address a more fundamental question for further discussion: why do people study plants?

**Plant Morphogenesis 123, bud-centered viewpoint, developmental unit, life cycle, renaissance**

**Citation:** Bai, S.N. (2019). Plant Morphogenesis 123: a renaissance in modern botany? *Sci China Life Sci* 62, 453–466. <https://doi.org/10.1007/s11427-018-9457-1>

### Introduction: Are we in the midst of a “renaissance” in plant biology?

The term “renaissance” was recently used to describe two aspects of plant biology: once in a subtitle in the book *Deep Morphology*, edited by Stuessy, Mayer, and Horandl (2003), and the other in a News Feature in *Nature* by Ledford (2018). The former cheered the revival of morphological analysis in plant systematics using the then-popular “evo-devo” studies, which relate DNA sequences to floral structures. The latter welcomed the introduction of genomics and imaging technologies to the field of morphological investigation.

While the term “renaissance” simply refers to “a revival of or renewed interest in something”, it has traditionally been used to refer to an era of Western civilization during the 14th to 17th centuries, and it is often used in reference to a topic generally considered to have profound significance. Are the

above-mentioned events in plant biology significant enough to be called a renaissance?

Humans distinguish objects based on their shapes; therefore, plant taxonomy has traditionally been heavily based on plant morphological analyses. Over the past few decades, however, DNA sequencing has dominated the field of plant systematics, and the analysis of plant morphology has been marginalized. The return of morphological analysis to this field through the study of the genes that determine morphological traits can indeed be considered to represent a renaissance to taxonomy.

By contrast, it is doubtful whether the second event, the introduction of genomics and imaging technologies to morphological investigations, should be considered a renaissance. The continual improvements in technology make it difficult to specify what is being revived in the application of new techniques to these morphological investigations.

The use of morphological traits and their associated DNA sequences in plant systematics studies simply revives the

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emphasis on morphological traits, but what is behind these traits? According to Gifford and Foster (1989), “plant morphology attempts to explore and to compare those *hidden aspects* of form, structure, and reproduction that constitute the bases for the interpretation of similarities and differences among plants”. What are these “hidden aspects”? Are they the morphological traits themselves, or something else?

## What is to be revived? The “bud-centered” viewpoint of the founding fathers of modern botany

### *A brief history of modern botany*

In her classic book, *The Natural Philosophy of Plant Form*, Agnes Arber (1950) concisely summarizes the history of modern botany. In ancient Greece, Theophrastus classified plant organs into two categories: the *main parts*, such as the root, stem, bough, and twig, and the *annual parts*, such as the flower, leaf, fruit, and new shoots. Modern botany was founded in the 17th century by Nehemiah Grew and Marcello Malpighi with the publications of their pioneering works, *The Anatomy of Vegetables Begun* (1672) and *Anatomy Plantarum* (1675), respectively. In their views, each bud essentially represents an individual plant. For convenience, I would call it as “bud-centered” viewpoint. Grew further demonstrated the anatomical similarity of floral organs (sepal and petal/corolla) and leaves. However, their idea that a bud represents a plant is not embraced by contemporary plant biologists. The mainstream viewpoint, which can be traced back to Augustin-Pyramus De Candolle’s effort to use unifying botanical terminology based on Latin words in the early 19th century, is to view a plant as an individual consisting of a root, stem, leaf, flower, fruit, and seed. Buds are simply parts of a plant. This viewpoint is called “plant-centered” to contrast to the “bud-centered” one.

Interestingly, while the mainstream viewpoint continues to dominate, some scholars still persist with the “bud-centered” viewpoint. In the mid-18th century, Loeffling and Dehlberg compared a tree to a coral. Erasmus Darwin, the grandfather of Charles Darwin, also believed that “every bud of a tree is an individual vegetable being” (White, 1979). C.H. Waddington (1966) wrote in his book, *Principles of Development and Differentiation*, that the “branch meristem gives rise to a whole new cycle of growth and development”.

Beyond the fact that each bud does indeed undergo a complete life cycle, some empirical evidence from genetics and molecular biology supports this “bud-centered” viewpoint. Wang et al. (2009) reported that the differential regulation of *PERPETUAL FLOWERING1 (PEP1)* expression in different shoot apical meristems (SAMs) resulted in perennial flowering in *Arabidopsis*, in contrast to its famous homolog *FLOWERING LOCUS C (FLC)*, which causes annual flowering in *Arabidopsis*. Li et al. (1996) and Huang et al.

(1999) demonstrated that the application of growth regulators to particular buds specifically and locally affected their growth and differentiation into floral buds. These findings suggest that the regulation of flowering is a SAM-based, not whole plant-based, process.

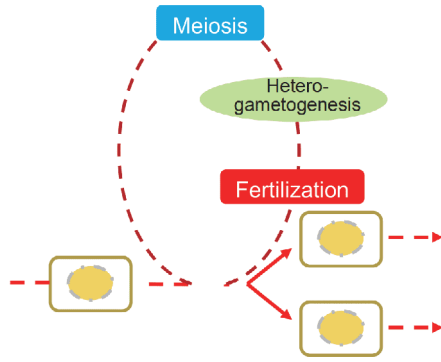
It is bewildering that the idea that the bud rather than the whole plant is the unit required to complete the plant life cycle was ignored for such a long time. More bewildering is the concept that a plant has an indeterminate development program (Goldberg, 1988): if a developmental program is indeterminate, when does the next generation begin?

### *The meaning of the term “life cycle”*

All eukaryotes, from unicellular to multicellular organisms, have a life cycle that starts with a zygote and ends at the gametes that committed to fusing (by fertilization) into the zygotes of the next generation. However, “life cycle” has arguably been used more as a descriptive term than one that reflects the underlying genetic and developmental changes. One definition is “the generation-to-generation sequence of stages in the reproduction history of an organism” (Campbell and Reece, 2005). The Oxford English Dictionary defines the life cycle as “the series of changes in the life of an organism including reproduction”. Based on such multicellular organism-based, reproduction orientated descriptions, it is difficult to compare the life cycles of animals and plants, as their morphogenetic and reproductive strategies are quite different. Under many circumstances, clones are thought to undergo “asexual reproduction”, which makes the situation even more complicated.

### *Discovery of the sexual reproduction cycle and Plant Morphogenesis 123*

After we became convinced that the development of unisexual flowers in cucumber is not an issue of sex differentiation (Bai and Xu, 2012), my colleagues and I began to look for the meaning of sex differentiation in plants. We developed the concept of a unique process called the “sexual reproduction cycle (SRC)”, which originally evolved in unicellular eukaryotes and has been maintained as a core process in all multicellular eukaryotes (Bai, 2015; Bai and Xu, 2013). The SRC is a specialized “cell cycle” integrating meiosis, heterogametogenesis, and fertilization (Figure 1). The net outcome is that one diploid cell becomes two, which is equivalent to a mitotic cell cycle in terms of cell number change. The difference is that the two resulting diploid cells contain heritable variations in response to the constantly changing environment. While the SRC is essentially a stress-response mechanism, it first defined functionally a “generation” at the unicellular level because the two daughter cells have different genetic settings from the starting cell.

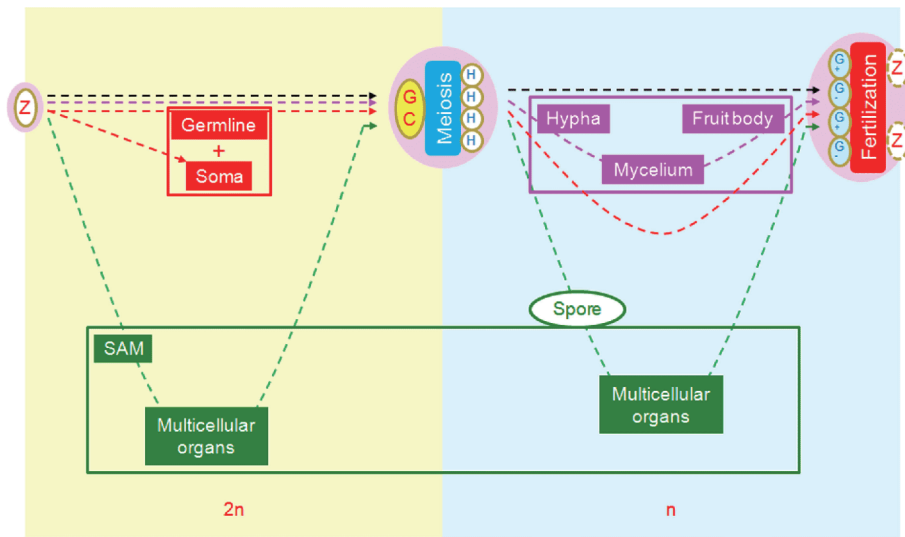


**Figure 1** A diagram of the modified cell cycle called “sexual reproduction cycle (SRC)”. The three rounded rectangles containing yellow ovals represent diploid cells. The red dashed line and arrows represent one diploid cell become two (a cell cycle). Dark red dashed curve represents a process, in which three biologic events, i.e., meiosis, fertilization and heterogametogenesis, integrated, and inserted into the cell cycle represented by two rounded rectangles (blue and red, respectively) and an oval (light green). Through the SRC, a diploid eukaryote can autonomously increase genetic variations and increase adaptability to the unpredictably changed environment. Reprinted from Bai, 2016 by permission of Science Press.

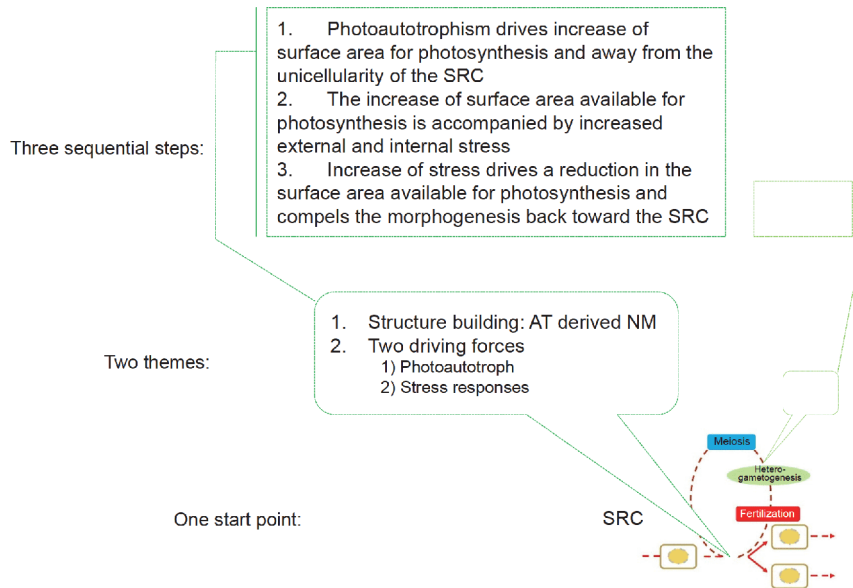
The key events in the SRC, such as meiosis and heterogametogenesis in unicellular eukaryotes, are stress induced (for a detailed review, see Bai, 2015). Under non-stress conditions, it is possible for zygotes and/or meiotically produced cells to undergo mitosis and produce multiple cells in either or both intervals of the SRC: between the zygote and the meiotic cell, and/or between the meiotically produced cells and the gametogenic cells. It is therefore reasonable to propose that the organization of the multiple cells produced in these intervals leads to the emergence of multicellular organisms. **Figure 2** depicts a scenario in which animals are

derived from the interpolation of multicellular structures into the first (diploid) intervals, fungi are derived from the interpolation into the second (haploid) intervals, and plants are derived from the interpolation into both intervals.

The above-mentioned SRC-derived origin of multicellular organisms does not explain how the morphogenetic process takes place, however. Based on experimental evidence that germ cell initiation is triggered by an altered redox status (Kelliher and Walbot, 2012; Chen et al., 2015), we proposed a new conceptual framework called “Plant Morphogenesis 123 (PM123)” to explain how multicellular plants complete their life cycle (Bai, 2017; **Figure 3**). The “1” refers to the presence of one starting point, the SRC. The “2” refers to two themes: (i) the method for building multicellular structures, likely via the molecular mechanisms underlaid by the L-system (Prusinkiewicz and Lindenmayer, 1990; Prusinkiewicz and Runions, 2012), and (ii) the regulation of the changes in morphological structure, as represented by the morphology of lateral organs initiating from growth tips, which are ultimately driven by the balance of photoautotrophy and stress responses. The “3” refers to the three sequential steps in morphogenesis during the completion of the plant life cycle. The first step is photoautotrophism, which drives the growth of photosynthetic surface area and moves away from the unicellularity of the SRC. The second step is the increase in external and internal stress that accompanies this increase in surface area. In the third step, this mounting stress drives a reduction in photosynthetic surface area, directing morphogenesis back toward the unicellularity of the SRC. Through PM123, the life cycle is completed, a plant developmental unit (PDU) derived from a bud or Waddington’s branch is formed, and numerous PDUs are



**Figure 2** Comparison of morphogenetic strategies of animals, fungi, and plants within the framework of the SRC. Yellow background indicates the diploid phase and blue background indicates the haploid phase. In the intervals between zygote and diploid germ cells, the interpolation of multicellular structures occurs in animals (red) and plants (green), whereas none are present in fungi (pink). In the intervals between meiotically produced cells and gametogenic cells, the interpolation of multicellular structures occurs in fungi and plants but not in animals. Reprinted from Bai, 2015.



**Figure 3** A diagram of the PM123 theory. Two multicellular structures are interpolated into the two intervals (green framed for the diploid and light green framed for haploid) during the SRC (the “1” of the PM123). Represented in diploid phase, two themes (the “2” of the PM123) underlie the morphogenesis of the multicellular structures: structure building, the “axial tree” (AT) derived neo-modularization (NM), and two driving forces for sequential changes of organ types, including photoautotroph and stress response. Three sequential steps (the “3” of the PM123) are elaborated in the upper frame. Reprinted from Bai, 2019.

integrated into the colony that we refer to as a plant.

### ***A renaissance in modern botany: PM123 revives the “bud-centered” viewpoint of the founding fathers***

While the concept of the SRC is new, the conceptual framework known as PM123 is not completely novel. In the early 20th century, Bower proposed that reproduction is a default state and that vegetative growth is interpolated into development to postpone the process of reproduction (Bower, 1935). If we replace Bower’s “reproductive state” with the more definitive concept of the “SRC” and “vegetative growth” with multicellular structures, the PM123 conceptual framework is quite similar to Bower’s interpolation theory. One crucial difference is that in PM123, we clearly claim that a plant is a colony consisting of numerous PDUs, the buds. From this point of view, PM123 represents a renaissance in modern botany, as it revives the concept, proposed by the founding fathers of modern botany, that each bud is essentially an individual. [Figure 4](#) briefly summarizes the evolution of the conceptual frameworks of plant morphogenesis.

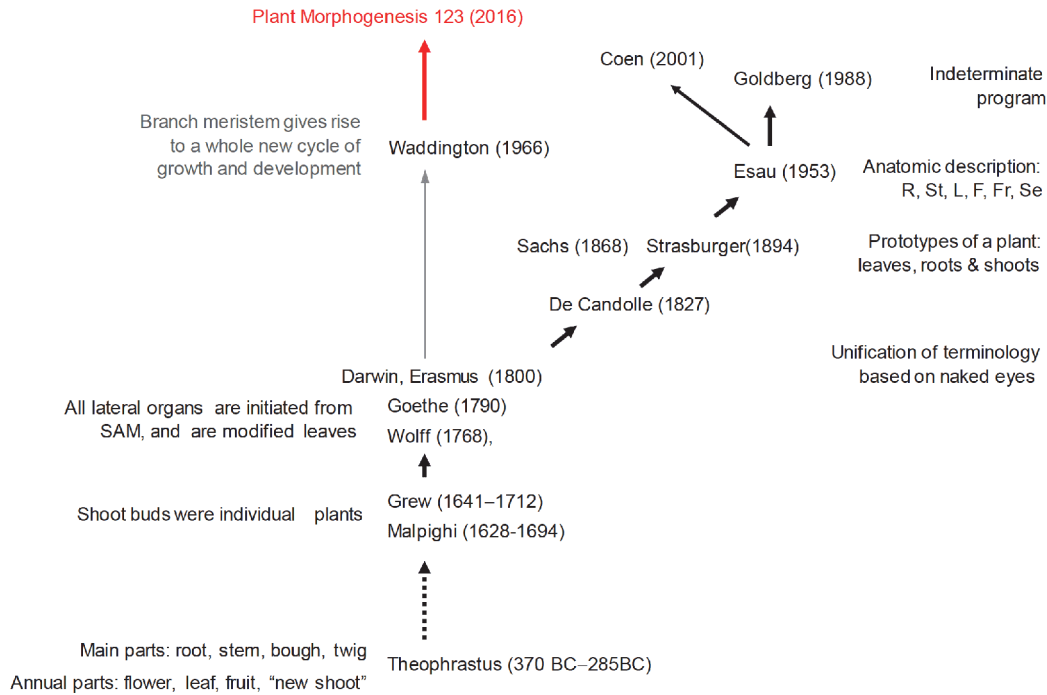
### **Fundamental but previously neglected questions: a perspective**

Under the current mainstream conceptual framework of plant morphogenesis, a plant is a combination of different types of organs, as roots, leaves, stems, flowers, fruits and seeds.

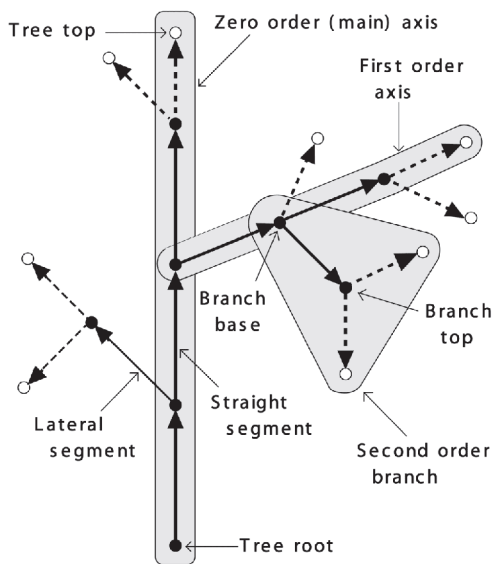
Investigations therefore mainly focus on how these organs are formed, along with the detailed mechanisms underlying the differentiation of tissues such as meristems, vascular, epidermis, and so on. Among these topics of investigation, flowering induction and floral organ determination have taken center stage for decades.

However, how are these organs integrated? If they need to be integrated, is there a general controller overseeing the diverse aspects of these differentiation mechanisms to ensure that they are functionally coordinated? From the perspective of PM123, an alternative concept underlies the morphogenetic process: multicellular structures (MCSs) are interpolated into the intervals of the unicellular SRC. These MCSs are derived from zygotes to form diploid sporophytes and from meiotically produced cells to form haploid gametophytes. Over the generations, MCSs have evolved from simple cell clusters in the first interval of the SRC, such as the capsule in moss, to diversified structures with genetically stable characteristics in both form and function. This viewpoint underlies the recently proposed “function-based evolutionary perspective” (Bai, 2017).

Currently, the “axial tree” concept proposed by [Prusinkiewicz and Lindenmayer \(1990\)](#) is the best model describing this plant morphogenesis concept from both the phylogenetic and ontogenetic perspectives. According to the “axial tree” concept ([Figure 5](#)), both diploid and haploid MCSs develop from a single cell through axial growth. The key events in plant morphogenesis can therefore be categorized into three axis-centered events: (i) growth of the main axis, (ii) branching to multiply the axes, and (iii)



**Figure 4** (Color online) A summary of the evolution of conceptual frameworks on plant morphogenesis. Main information adopted from Arber (1950). Additional references: Bai, 2016; Coen, 2001. The abbreviations “R, St, L, F, Fr, Se” used in “Anatomic description” refer to “root, stem, leaf, flower, fruit, seed”, respectively.



**Figure 5** An axial tree. Open circle, terminal node; filled circle, branching point; dashed arrow, apex; solid arrow, internode. Modified from Prusinkiewicz and Lindenmayer, 1990.

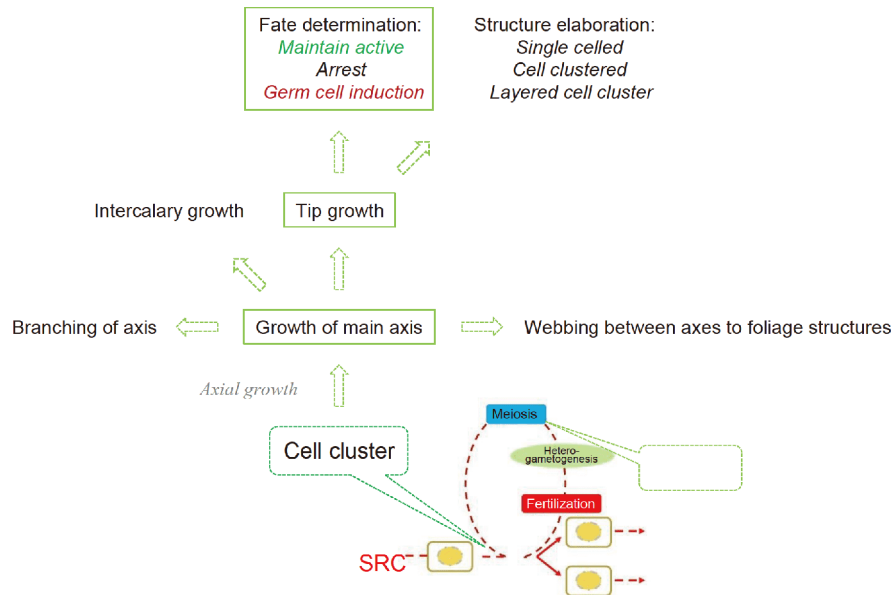
webbing to produce foliage structures. Each event can be further divided into sub-events; for example, axis growth can be sub-categorized into the activities of the growth tip and intercalary growth. Growth tip activity can again be sub-categorized into two events: fate determination, i.e., cells in the growth tip are actively dividing, arrested, or induced to

form germ cells; and structural elaboration, i.e., the process leading from the development of a single cell in the growth tip to a cell cluster and a well-organized multicellular structure, the SAM (Figure 6).

Based on this perspective, many interesting but previously neglected questions about plant morphogenesis emerge. Below is a list of some such questions that can be investigated using currently available technology.

**How did the growth tip evolve from a single cell to a cell cluster, and to a layered structure?**

Wolff first dissected and described the plant growth tip in the 18th century (1759). It is widely accepted that plant morphogenesis follows an additive pattern, with new structures being sequentially added through the activity of the growth tip. The SAM functions at the center of morphogenesis (Wardlaw, 1956), and recent mutant analyses have resulted in the identification of many genes involved in SAM formation (Barton, 2010). According to classic morphological descriptions, however, bryophytes such as *Physcomitrella patens* possess only a single cell, which carries out the function of the growth tip in the gametophyte (Harrison et al., 2009; Kofuji and Hasebe, 2014). In pteridophytes, such as *Marsilea*, *Selaginella*, and *Ophioglossum lusitanicum*, the growth tips consist of one, two, or several cells in sporophytes respectively (Fahn, 1982). In gymnosperms, such as *Ginkgo* and *Pinus*, the growth tip comprises a group of cells in



**Figure 6** Diagram of key events and their possible relationships evolved during the axial growth in diploid multicellular structures.

sporophytes, but no tunica corpus structure forms (Fahn, 1982). These observations suggest that the layered structure of the SAM is specific to angiosperms. Such a structure is important for tip growth in angiosperms, but it is not indispensable for growth tip function in all plants. This leads to a new question: are specific genes required for growth tip function across the bryophytes, pteridophytes, and spermatophytes? If so, what are these genes? If not, how can the function of the growth tip be explained in light of their morphological differences? If specific genes are required, how did the growth tip structures evolve from single cells to cell clusters and from a random to a layered arrangement while maintaining functionality?

### How are foliage structures formed?

Ideally, for multicellular photoautotrophic organisms, the minimum number of cells should be used to build the maximum photosynthetic surface. This concept likely explains the characteristic structure of foliage in plants. However, it is not yet clear how this foliage structure forms.

According to Arber (1950), Sachs proposed the idea that the leaf is derived from the shoot. In 1965, Zimmermann proposed the “telome theory” to explain how both microphylls and macrophylls originated (Kaplan, 2001). According to the “axial tree” concept proposed by Prusinkiewicz and Lindenmayer (1990), two events are required for foliage structure formation: the branching of the axes and the webbing of cells between branched axes.

In angiosperms, all leaves are formed from a cell cluster (the primordium) derived from the SAM. The current conceptual framework is that the primordium undergoes the following developmental stages to form a foliage structure:

(i) primordial specification; (ii) establishment of adaxial-abaxial polarity/axis; and (iii) lateral growth, proximal-distal growth, and tissue differentiation (Freeling, 1992; Waites and Hudson, 1995; Efroni et al., 2010; Tsukaya, 2014). Almost all efforts over the past several decades have been devoted to the identifying genes and regulatory components involved in these events. This viewpoint leaves little room to investigate the “branching axes” suggested by Prusinkiewicz and Lindenmayer (1990). The existence and potential functions of the vascular tissue in foliage structures has also been neglected. However, it is perhaps possible that vascular tissue differentiation functions as the branching axes during leaf morphogenesis (Mattsson et al., 1999; Dkhar and Par- eek, 2014). By contrast, analyzing the mechanisms underlying the formation of foliage structures in non-vascular plants should shed light on the manner in which cell clusters become arranged to form flat structures.

### How is shoot branch patterning regulated?

In angiosperms, shoot branches are derived from axillary buds. However, there are two long-held opinions on how axillary buds form, namely the *de novo* and detached concepts. According to the *de novo* concept, the axillary meristem is derived from cells at the base of the leaf primordium. By contrast, the detached concept suggests that the axillary meristem is originally part of the SAM from which the leaf primordium is derived, and detaches from the main SAM to function as an independent meristem (Steeves and Sussex, 1989). Recent evidence appears to support the *de novo* concept (Barton, 2010).

If we broaden our view beyond angiosperms, it is clear that branching is an ancestral phenomenon that occurred in

pteridophytes, bryophytes, and even multicellular green algae prior to the emergence of land plants. There are two main types of branching: dichotomous branching at the growth tip and the lateral initiation of a new growth tip. Considering the evolutionary trends of the growth tip described above, it would be interesting to determine whether there is a conserved rule for branching and if so, whether such a rule has been modified alongside the evolution of the growth tip. If there is such a rule, as described by the “axial tree” concept by Prusinkiewicz and Lindenmayer (1990), what is its molecular basis? If there is indeed an evolutionary trend corresponding to the evolution of the growth tip, how did these diverse modifications emerge?

Several decades of effort focused on understanding branching in angiosperms has yielded little information. Perhaps the issue should be thought of differently, from an evolutionary perspective. Specifically, this might involve using recently established bryophyte model plants to explore the possible conserved rules governing branching, and deciphering the modified strategies used by various plant species.

#### ***How does the fate of the growth tip relate to the SRC?***

Under the scenario in which multicellular organisms originate from the interpolation of multicellular structures into the intervals of the SRC (Figure 2), all multicellular structures are derived from cells generated by the division of the zygote or meiotically produced cells. In animals and fungi, only one multicellular structure is interpolated into either the first (animals) or second interval (fungi), while in plants, two multicellular structures, the sporophyte (diploid,  $2n$ ) and gametophyte (haploid,  $n$ ), are interpolated into both intervals. Accordingly, the strategies used to maintain the SRC differ between animals and plants. In animals, the SRC is carried out via the germline, which originates during early embryogenesis in most animal species (Gilbert, 2010; Juliano and Wessel, 2010) and remains fated to produce gametes. In plants, all cells derived from the zygote, and meiotically produced cells are first committed to form somatic cells. After the formation of multicellular structures, including the sporophyte and the gametophyte, some somatic cells are induced to form germ cells; diploid germ cells are committed to undergo meiosis, and haploid germ cells are committed to undergo gametogenesis (Figure 7). This raises the question of how germ cell induction occurs in plants.

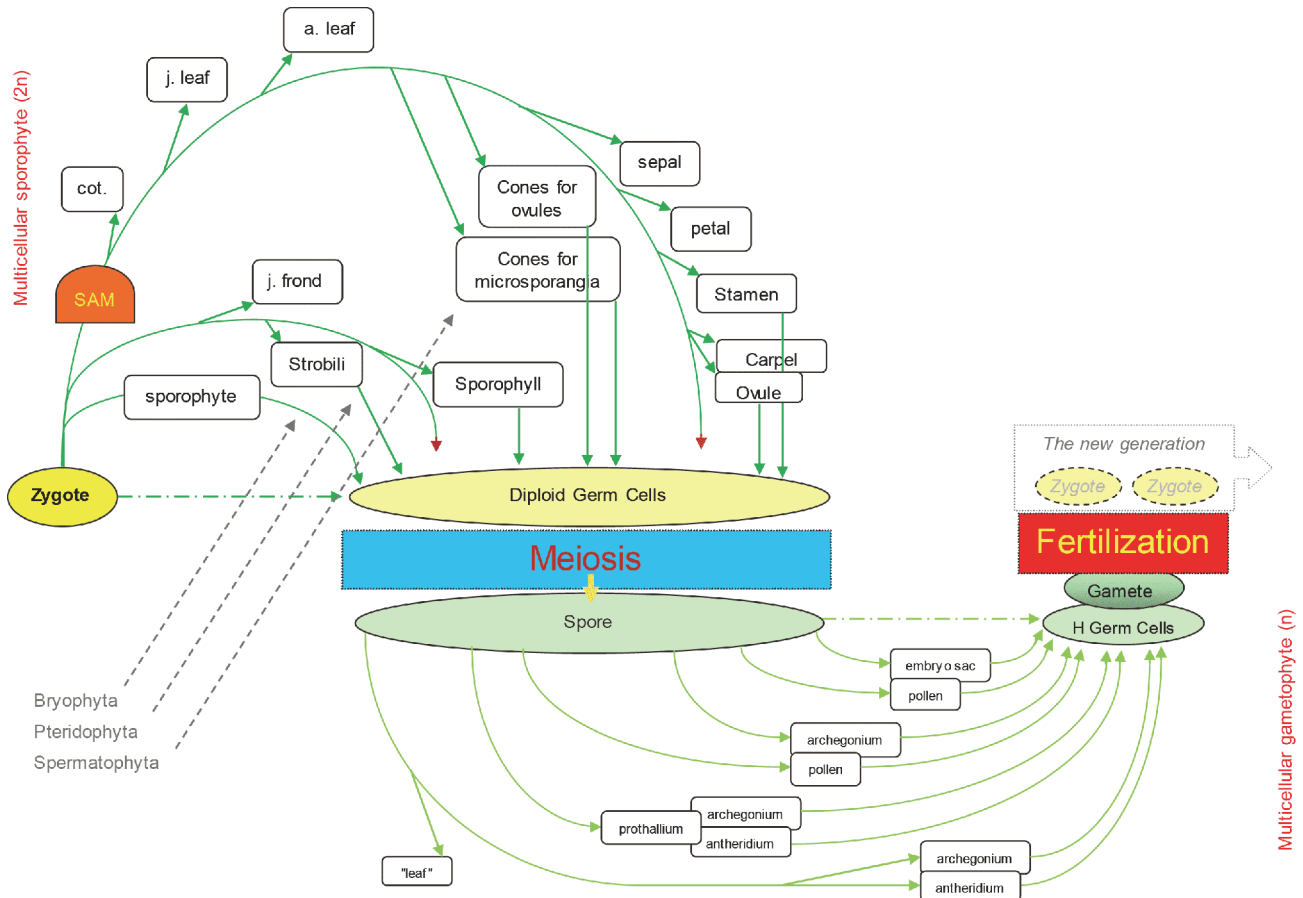
Traditionally, the differentiation of both diploid and haploid germ cells was considered part of the process of cell differentiation; for example, meiotic cells are considered to be produced during stamen and ovule differentiation in angiosperms, and generative cells are considered to be produced during antheridium and archegonium formation in pteridophytes and bryophytes. From a “function-based evo-

lutionary perspective” (Bai, 2017), however, the SRC emerged in unicellular eukaryotes; therefore, germ cell induction is ancestral and indispensable, while the surrounding somatic cells of reproductive organs in multicellular eukaryotes were derived later and function to protect and support the germ cells. In other words, by combining the conceptual framework of SRC-derived multicellular organisms and the “axial tree”, an interesting concept emerges: all “reproductive organs”, including both diploid and haploid organs, are indeed located at growth tips consisting of committed germ cells and surrounding somatic cells that support the germ cells. Thus, the question of how germ cells are induced can be phrased as follows: how does the growth tip become committed to form the germ cells?

In unicellular eukaryotes, the initiation of germ cells is always stress induced (Bai, 2015). Similarly, in multicellular bryophytes, the induction of sporangial and gametangial differentiation is stress induced as well (Hohe et al., 2002; Shimamura, 2016). Kofuji et al. (2018) described the process of transition of the apical cell of a *Physcomitrella* gametophore from growth tip to antheridial initial fate. In maize (*Zea mays*) and rice (*Oryza sativa*) stamens, recent evidence suggests that diploid germ cell initiation is also stress induced (Kelliher and Walbot, 2012; Chen et al., 2015). These findings suggest that the concept of stress-induced germ cell initiation applies both to unicellular and multicellular eukaryotes, at least in plants; however, more investigations are needed to determine whether this is indeed a general rule.

#### ***Sequential morphological and functional changes of the lateral organs***

According to Strasburger’s *Textbook of Botany* (Strasburger et al., 1976), first published in 1894, the typical plant body consists of three parts: the shoot, i.e., main stems, leaves, and roots. In the 1960s, although Wardlaw emphasized the study of apical meristem activity, plant morphogenetic research still spanned a wide spectrum, from ferns to spermatophytes, and emphasized the distinction between the leaves and the shoots (Cutter and Wardlaw, 1966). Since the photoperiodic induction of flowering was first described in the 1920s (Garner and Allard, 1922), however, flowering has gradually taken center stage in the study of plant morphogenesis (Bernier et al., 1981; Halevy, 1985). But what is “flowering”? According to Bernier et al. (1981), flowering is a term covering a wide range of morphological changes (Table 1). However, from a practical perspective, flowering is generally described as the transition from “vegetative” to “reproductive” growth (Buchanan et al., 2015; Smith, 2010). In his brilliant study using *Arabidopsis thaliana* as a genetic system to identify the genes controlling flowering, Koornneef et al. (1991) proposed two simple criteria to define the process: the number of leaves produced and/or days before



**Figure 7** Different levels of elaboration around the core processes in the life cycles of the three plant phyla. The sexual reproduction cycle from one zygote to the next generation’s zygotes through meiosis and fertilization is the backbone of the lifecycle for all three land plant groups, Bryophyta, Pteridophyta, and Spermatophyta. Green arrows show the differentiation of various organ types in diploid phase, and light green for organs in haploid phase. Dark red arrowheads indicate unlimited tip growth activity. cot., cotyledons; j. leaf, juvenile leaf (e.g., rosette leaves in *Arabidopsis*); a. leaf, adult leaf (e.g., cauline leaves in *Arabidopsis*). Reprinted from Bai, 2017.

**Table 1** The flowering syndrome<sup>a)</sup>

Relevant traits to flowering	Morphological changes
Internode	Increased internode elongation
Shape of SAM	Broadening and doming of the SAM
Shape of leaf	Changing in leaf shape: petiole and lamina
Axillary buds	Precocious initiation of axillary buds
Leaf growth	Change in leaf growth rate
Plastochron	Plastochron shortening
Phyllotaxis	Change in phyllotaxis

a) Bernier et al., 1981.

the first floral bud is observed after seed germination. The genetic strategy proposed by Koornneef was so successful that all the genes he identified, such as *CONSTANS (CO)* and *FLOWERING LOCUS T (FT)*, were subsequently cloned and have become “star” genes during the past two decades (Andrés and Coupland, 2012).

Is flowering really such a simple transition from a morphogenetic perspective? George Haughn et al. (1995) first

addressed this issue during the flowering-gene cloning frenzy. He correctly pointed out that the morphogenetic process related to flowering is quite complicated, not a simple switch-like “transition”. After the first floral bud is observed, inflorescence development can exhibit different patterns, and it is therefore difficult to draw a clear line distinguishing “vegetative” from “reproductive” growth. In addition, a flower is essentially a compressed shoot, and from a functional perspective, it is difficult to claim that sepals and petals are “reproductive”. Furthermore, many angiosperms are perennial; for example, many apple tree (*Malus domestica*) shoots grow continuously, with some buds producing flowers and others producing leaves. It is therefore difficult to define a tree as being in the “vegetative” or “reproductive” stage.

After the initial excitement of identifying flowering genes, some of these genes were shown to have additional effects, for example, *CO* and *FT* homologs are also involved in the developmental regulation of storage organs, axillary buds, dormancy, stress responses, and metabolic processes (Chiang et al., 2009; Deng et al., 2011; Lebon et al., 2008; Navarro et



al., 2015; Niwa et al., 2013; Pin and Nilsson, 2012). These findings imply that the functions of so-called “flowering genes” are not actually specific to flowering, so what exactly are the fundamental functions of these genes?

In the early 1950s, Wareing (1959) described how the internal physiological status (“physiological age”) of a plant plays a role in regulating flowering. Since then, juvenility has become a topic of focus in plant developmental biology. Based on years of effort, Wu and Poethig (2006) revealed that microRNA156 is a key component in the determination of juvenility (Poethig, 2010). More interestingly, this component also plays a role in the determination of flowering (Wu et al., 2009) and interacts with sugar signaling during plant morphogenesis (Poethig, 2013). These findings integrate the concepts of internal/external stress responses, juvenility, and flowering induction, but also make the concept of the “transition” from vegetative to reproductive development even less plausible. There is now little room for the idea that flowering represents a simple transition from vegetative to reproductive growth; therefore, an alternative explanation must be developed.

If the concepts of the SRC and PM123 are accepted, diploid multicellular structures derived from the zygote can be considered to represent an interpolation in the interval between the two core cell types, the zygote and meiotic cells. These structures, which are generated by the activity of growth tips as lateral organs in the shoot, sequentially change their morphology and functions in different organ types, such as rosette leaves, cauline leaves, sepals, petals, and carpels in *Arabidopsis*, and they terminate at stamens and ovules, in which the diploid germ cells (meiotic cells) are induced. Clearly, the transition from expansion of MCSs for photosynthesis (vegetative growth) to germ cell induction at the terminal structures such as stamens and ovules (reproductive growth?) is not a simple switch, rather fulfills in a series of sequential changes in organ types. Each change exhibits a balance point shift of the two antagonistic driving forces, photosynthesis (including the metabolism of derived assimilates) and stress responses. This series of sequential changes in organ types occurs in all land plants; however, these changes are most diverse in the angiosperms (Figure 8). This interpretation represents a logically sound alternative to the concept of flowering.

This perspective leads to new questions. Are photosynthesis and stress responses truly the antagonistic driving forces? Are there indeed shifts in the balance point resulting from the two antagonistic driving forces, and do these lead to the sequential changes in organ type? Following this logic, how is germ cell formation induced from somatic cells in terminal structures such as stamens and ovules in angiosperms?

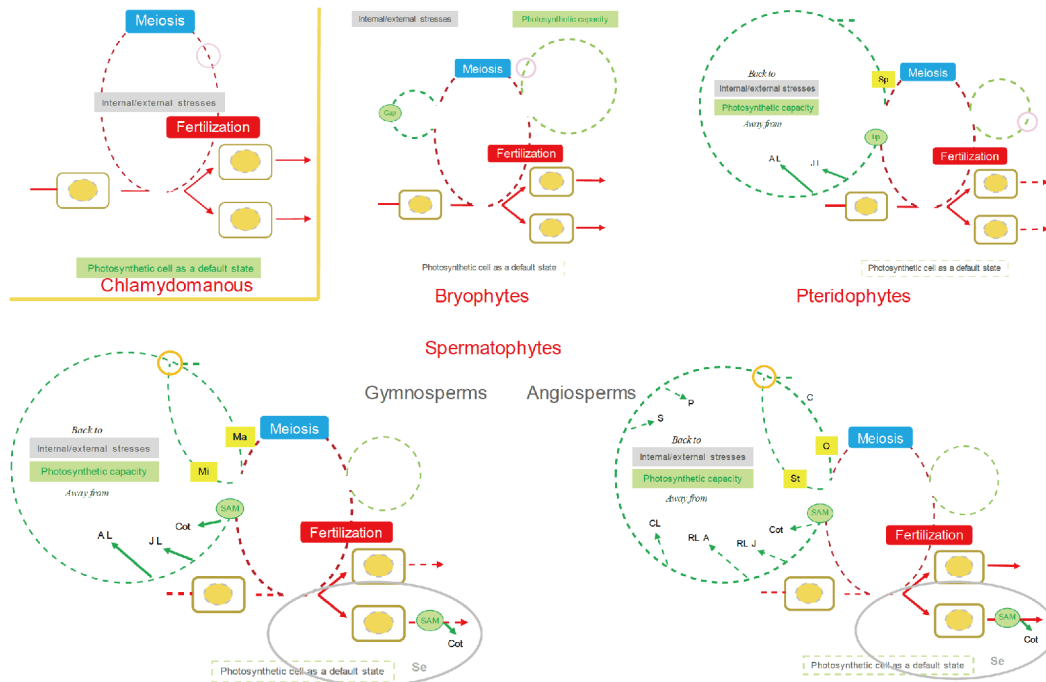
The new perspective discussed here does not exclude the results of traditional studies of flowering, but rather it em-

braces them. Traditional flowering studies demonstrated the importance of using physiological, genetic, and molecular tools to dissect complicated morphogenetic processes. The new perspective promotes the use of techniques that will increase the resolution of observations of the morphogenetic process and integrate the available information into a set of simple but generally applicable principles, such as PM123.

### *Sex differentiation*

Sex is a biological phenomenon that can be thought of as a “familiar stranger”; it clearly exists all around us, but its interpretation by scholars has been vague. Table 2 summarizes the current definitions regarding to sex. Bai (2019) recently reviewed the study of sex and classified sex-related phenomena into three essentially different events or processes: (i) sex or heterogametogenesis, (ii) sex differentiation, and (iii) sexual behavior. Heterogametogenesis is one of the three SRC events, together with meiosis and fertilization, which emerged in unicellular eukaryotes and persisted in all multicellular eukaryotes. This event functions to label meiotically produced cells into groups to harness variations and enhance heterogeneity (Bai, 2015, 2019). Such labeling perfectly fits the meaning of the Latin root of “sex”, “*sexus*”, which is perhaps akin to “*secare*”, meaning to “divide”. Sex differentiation emerged in multicellular organisms to ensure heterogametogenesis, including (i) setting the divergence point for the separation of the two gamete types and (ii) providing signals and nutrition for gametogenesis. Sexual behavior also emerged in multicellular organisms, including various mechanisms used in the soma to ensure that the gametes meet and to enhance the selection of adaptive traits (Bai, 2017, 2019).

In animals, since there is only one interpolation of multicellular structures during the first intervals of the SRC (Figure 2), sex differentiation is clearly centered on gonad differentiation. In plants, however, there are two interpolations of multicellular structures during both intervals of the SRC (Figure 2). Bai (2019) referred to the differentiation of archegonium and antheridium during the haploid interval as “real” sex differentiation in plants, because only such differentiation ensures heterogametogenesis. By contrast, the differentiation of stamens and ovules derived from heterosporangia results in divergence to heterosporogenesis, not to heterogametogenesis; therefore, such differentiation should not be considered sex differentiation. In spermatophytes, however, the gametophytes are severely reduced, with few cells fated for archegonium and antheridium differentiation (sex differentiation). Stamen and ovule differentiation carried out the functions of sex differentiation that originally occurred in the gametophytes; therefore, this type of differentiation is considered to represent “pseudo” sex differentiation (Bai, 2019).



**Figure 8** Comparison of the SRC derived “Double-Ring” strategies of morphogenesis in three land plant groups. Symbols and abbreviations: gray circle, heterogametogenesis; pink circle, real sex differentiation; brown circle, pseudo sex differentiation; Cap, capsule; Tip, growth tip; JL, juvenile leaf; AL, adult leaf; Sp, sporangium; SAM, shoot apical meristem; Cot, cotyledon; Mi, microsporangium; Ma, macrosporangium; Se, seed; RL, rosette leaf; CL, cauline leaf; S, sepal; P, petal; C, carpel; O, ovule.

This perspective highlights the need for more research efforts into the differentiation of the archegonium and antheridium as a means of investigating the regulatory mechanisms of real sex differentiation in plants. It would also be interesting to investigate how the capsules in the simple sporophytes of bryophytes evolved into sporangia, which possess more specific tissue differentiation such as the tapetum in the sporophyte of pteridophytes. Future research should also investigate how homosporangia evolved into heterosporangia, and how sporangia with relatively simple morphologies evolved into derived complexes such as the stamen (cluster of sporangia) and the ovule (enclosed sporangium with lateral tissues) (Wang, 2017). Elucidating these mechanisms may reveal the secrets of pseudo sex differentiation, a phenomenon unique to the plant kingdom.

### Sexual behaviors

As mentioned above, sexual behaviors refer to all mechanisms occurring in the soma, which ensure that gametes are combined and which enhance selection for adaptive traits (Bai, 2019). In plants, the mechanisms used to ensure that gametes come together include directional pollen tube growth, the attraction of pollinators, and gamete recognition and fertilization. The mechanisms for enhancing the selection of adaptive traits include various morphogenetic processes and molecular interactions that promote cross-pollination, such as self-incompatibility and unisexual

flower production in angiosperms (Figure 9).

It has been exciting to witness new discoveries about plant sexual behavior in recent years (Higashiyama and Yang, 2017). One intriguing question involves the origin of the pollen tube. After a spore germinates in organisms ranging from bryophytes to spermatophytes, the first structures observed are filamentous: protonema in bryophytes, rhizoids in pteridophytes, and pollen tubes in spermatophytes. The filamentous structure of these tissues clearly alters their function from photosynthesis to a carrier of male gametes, which should be interesting to investigate further.

### Roots

It appears that there is no room for roots in the conceptual framework of PM123. Indeed, roots are not needed for the completion of the life cycle of bryophytes. In vascular plants, however, roots evolved as a derived axial structure (Raven and Edwards, 2001; Kenrick and Strullu-Derrien, 2014). While little is known about the evolutionary origin of roots at the mechanistic level, the available data from studies involving root regeneration from tissue culture (Schivavone and Racusen, 1991; Sena et al., 2009), auxin flow (Tromas and Perrot-Rechenmann, 2010; Druete et al., 2016), and the gene regulatory network (Vernoux and Benfey, 2005; Crawford et al., 2015) suggest that the unique pattern of axial growth resulting in root morphogenesis is induced by a particular microenvironment in which auxin plays a key role. If this is

**Table 2** Definition or description of sex in authorized resources

Types	Years	Definition or description	Authors	Resource
Encyclopedia	2017	Sex, the sum of features by which members of species can be divided into two groups—male and female—that complement each other reproductively.	N.J. Berrill	<a href="https://www.britannica.com/science/sex#toc29374">https://www.britannica.com/science/sex#toc29374</a>
	2017	Organisms of many species are specialized into male and female varieties, each known as a sex.		<a href="http://en.wikipedia.org/wiki/Sex">http://en.wikipedia.org/wiki/Sex</a>
Textbooks	2005	Sexual reproduction is the creation of offspring by the fusion of haploid gametes to form a zygote, which is diploid.	Campbell and Reece	<i>Biology</i> 7th ed.
	2000	It should be noted that sex and reproduction are two distinct and separable processes. Reproduction involves the creation of new individuals; sex involves the combining of genes from two different individuals into new arrangements.	S. F. Gilbert	<i>Developmental Biology</i> 6th ed.
Monograph	1982	—Sex is a composite process in the course of which genomes are diversified by a type of nuclear division called meiosis, and by type of nuclear fusion called syngamy, or fertilization.	G. Bell	<i>The Masterpiece of Nature: The evolution and genetics of sexuality</i>
		Sex and reproduction are quite distinct processes: sex is a change in the state of cells or individuals, whilst reproduction is a change in their number.		
	1983	—Fisher, 1930: No practical biologist interested in sexual reproduction would be led to work out the detailed consequences experience by organism having three or more sexes, yet what else should he do if he wishes to understand why the sexes are, in fact, always two? —Sex is defined as gender, male or female. Sex development refers collectively to the various molecular, genetic, and physiological processes that produce a male or a female from a zygote of a given genotype and parents in a given environment.	J. Bull	<i>Evolution of Sex Determining Mechanisms</i>
	2014	Sex is defined by the occurrence of meiosis.	Beukeboom and Perrin	<i>The Evolution of Sex Determination</i>
Review articles	2002	True sex—syngamy, nuclear fusion and meiosis—is found only in eukaryotes.	Cavalier-Smith	Origins of the machinery of recombination and sex
	2013	The core features of sexual reproduction involve: (i) ploidy changes from diploid to haploid to diploid states, (ii) the production of haploid mating partners or gametes from the diploid state via meiosis which recombines the two parental genomes to produce novel genotypes and halves the ploidy and (iii) cell-cell recognition between the mating partners or gametes followed by cell-cell fusion to generate the diploid zygote and complete the cycle.	Heitman et al.	

the case, it would be interesting to compare the micro-environments during early embryogenesis in pteridophytes and induced root regeneration in angiosperms, both *in vitro* and *in vivo*. These investigations might help untangle the mystery of the root origin.

### Stems and other structures

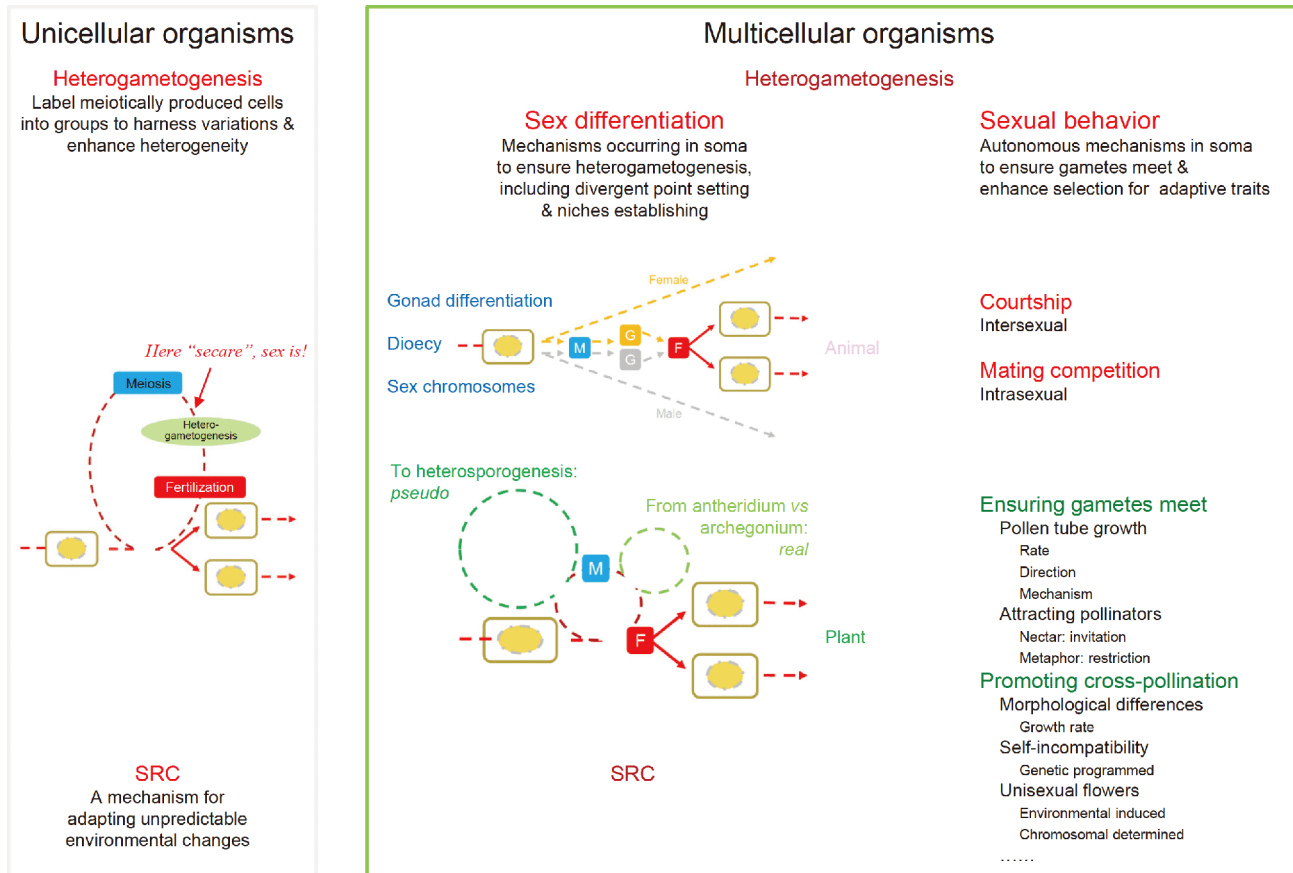
Stems are another hallmark structure of plant morphology. Functionally, the stem is a supportive structure that increases the photosynthetic surface area in the aerial space. Morphogenetically, however, the stem represents a modification of axial growth, but more in the radial direction, with an emphasis on strengthening its supportive features. In addition to stems, numerous morphological variations have evolved to provide plants with a wide range of adaptations to their habitats, such as tubes, tendrils and cups of pitcher plants (Bai, 2017). While these colorful variations have traditionally attracted the attention of plant scientists, many are highly specific to particular species. To understand the essential regulatory mechanisms of plant morphogenesis,

more attention should be devoted to the core or commonly shared events or processes described by PM123.

### Epilogue: Why do people study plants?

What would be your answer to the question “why do people study plants”? One answer I have heard is that “I grew up on a family farm with various plants, so it is natural for me to be interested in plants”. Another answer is that “we need food, and plants provide us with food”. One interesting answer is “well, I’ve never thought about it”.

We humans are newcomers to the Earth’s biosphere. As a biological species in the animal kingdom, we require natural resources for our survival. As intelligent animals, we can learn to better use natural resources by understanding them. Nevertheless, using and understanding are two separate issues. Yes, the ultimate purpose of understanding nature is to improve the chances of human survival; however, many investigations do not have direct practical applications. All the plants we utilize are the heritage of long journeys in evolu-



**Figure 9** A diagram of three key concepts of sex, sex differentiation and sexual behavior from the perspective of SRC. Reprinted from Bai, 2019.

tion. Without first understanding how the plants evolved to their current stage, how can we better use them? Just as a curious child who wants to build a car should first disassemble one to understand how the car works, so plant scientists seek to understand how plants work. Indeed, this common-sense concept applies more broadly to the roles of science and technology throughout contemporary society.

Historically, two main driving forces prompt people to study plants. One is to satisfy their curiosity; some wealthy people spend their money on the study of plants to satisfy their curiosity. Another is to increase food production. Currently, the study of plants, like other scientific endeavors, is so expensive that it mainly relies on public funding. This brings up an interesting point: is it reasonable to ask taxpayers to pay scientists to study whatever they are interested in simply to satisfy their own curiosity? It is easy to obtain public support to study plants for increased food production; however, in wealthy countries, there is no urgent need for food. This means that whenever the economy is bad, research funds for plant science are among the first to be cut. In poor countries, there is an urgent need for food but insufficient funding for plant science. Often, it seems that the public and governments have little desire to fund investigations that are not aimed at quickly providing information of practical va-

lue. Unfortunately, if plant scientists focused on food production alone, investigations would be rapidly narrowed down to practical elements, leaving no room for solving other problems.

Many fundamental problems in plant science remain elusive. In the case of interpreting plant morphogenesis, it remains difficult to interpret the developmental status (vegetative or reproductive) of perennial plants. As outlined above, this problem arose from the description of a plant as a whole organism in the early 19th century, although much evidence supports the notion that each bud is a unit with a complete life cycle. Should we ignore this problem, hang onto the traditional explanation, or devise a better interpretation? If one is convinced by the above analysis and perspectives derived from PM123, all that is needed for a renaissance is encouragement!

From a broader perspective, the revival of the viewpoints of the founding fathers of modern botany would not only raise new questions whose answers would increase our understanding of plants, but it would also provide plants with a new role in the study of the fundamental principles used to understand multicellular organisms. From the perspective of the SRC, animals and plants share common principles, although their morphogenetic strategies are diverse. These

common principles include stress-induced multicellular structures, physical principles underlying the morphogenesis of multicellular structures, and the integration of multicellular structures with the unicellular SRC (Figure 7). Only by using plants for comparison is it possible to identify the common principles governing the morphogenesis of all multicellular organisms and the specific adaptive mechanisms of a particular species. To date, plants have played only a marginal role in life sciences, while humans have played a central role. Now, from the perspective of the SRC-derived PM123, the analysis of plants could change the human-centered study of life sciences from a solo endeavor to a pas de deux (duet dance) of plants and animals.

**Compliance and ethics** *The author(s) declare that they have no conflict of interest.*

**Acknowledgements** *I would like to sincerely thank Prof. Manyuan Long (Chicago University) for inviting me to write this article. This invitation gave me the opportunity to propose some new questions about plant morphogenesis which I feel are worthy of investigation.*

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