Review

New insights into the regulation of inflorescence architecture

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The architecture of inflorescences displays the spatiotemporal arrangement of flowers and determines plant reproductive success through affecting fruit set and plant interaction with biotic or abiotic factors. Flowering plants have evolved a remarkable diversity of inflorescence branching patterns, which is largely governed by developmental decisions in inflorescence meristems and their derived meristems between maintenance of indeterminacy and commitment to the floral fate. Recent findings suggest that regulation of inflorescence architecture is mediated by flowering time genes, *Arabidopsis LSH1* and *Oryza G1* (ALOG) family genes, and the interaction between the auxin pathway and floral meristem regulators. In this review, we discuss how the relevant new players and mechanisms account for the development of appropriate inflorescence structures in flowering plants in response to environmental and developmental signals.

Diverse inflorescence architectures in flowering plants

During post-embryonic development of flowering plants, the shoot apical meristem (SAM) and root apical meristem (RAM) generate aerial and underground parts, respectively. The SAM gives rise to all aerial organs under a dynamic balance of growth and differentiation. It generates vegetative structures, such as leaves, stems, and axillary meristems, at the vegetative phase and is transformed into the main inflorescence meristem during the floral transition, when environmental and developmental conditions are optimal for plant reproductive success. The main inflorescence meristem either produces flowers or remains indeterminate to produce branch meristems, which could iterate the pattern of the main inflorescence meristem. Various branching patterns and the spatiotemporal generation of flowers from main and branch meristems contribute to a huge variety of inflorescence architectures observed in nature. The optimal inflorescence architecture plays a key part in reproductive success because it affects the ultimate number of flowers that set fruits and the competitive strength of plant individuals in interacting with biotic or abiotic factors, such as pollinators and wind [1–3].

There are three major architectural types of inflorescences based on the termination events on the inflorescence meristems of various orders [4,5]. Plants such as *Arabidopsis* (*Arabidopsis thaliana*) develop the raceme-type inflorescences, in which main inflorescence meristems grow indefinitely and generate either flowers or branch meristems that reiterate the pattern of the main inflorescence meristems (Figure 1). The panicle-type inflorescences are largely characteristic of grasses such as rice (*Oryza sativa*) and oat (*Avena sativa*). Main inflorescence meristems of these plants terminate after producing a series of lateral branch meristems, which eventually terminate in flowers after generating either flowers or higher-order branches (Figure 1). Unlike the raceme- and panicle-type inflorescences, a cyme-type inflorescence, such as the one that develops in tomato (*Solanum lycopersicum*), lacks a main axis and terminates in a flower after generating a new inflorescence meristem that reiterates this pattern (Figure 1).

In addition to the three architectural types and their variations, two basic growth habits, monopodial and sympodial, affect the diversity in inflorescence architecture. During the floral transition, the main SAMs of monopodial plants, such as *Arabidopsis* and rice, develop into the central leader inflorescence shoots while producing other subordinate branches. By contrast, the SAMs of sympodial plants, such as tomato, either terminate in reproductive structures or are aborted after a period of vegetative growth, and their growth continues from new axillary meristems that repeat this process. In tomato, the SAM terminates in a cyme-type inflorescence, and new vegetative growth continues from a sympodial shoot meristem produced from the axil of the youngest leaf [6–8]. The sympodial shoot meristem reiterates the pattern of the SAM to terminate in an inflorescence and initiate the generation of a new sympodial shoot meristem, eventually resulting in elaborate sympodial inflorescence shoots in tomato (Figure 1).

Recent findings from different plant species have demonstrated that the integrated regulatory network that controls inflorescence architecture includes previously unrecognized components, such as flowering time genes and *Arabidopsis LSH1* and *Oryza G1* (ALOG) family genes, and an interaction between the auxin pathway and floral meristem regulators. In this review, we discuss how these new components contribute to the development of appropriate inflorescence architectures in flowering plants to ensure reproductive success under changing growth conditions.

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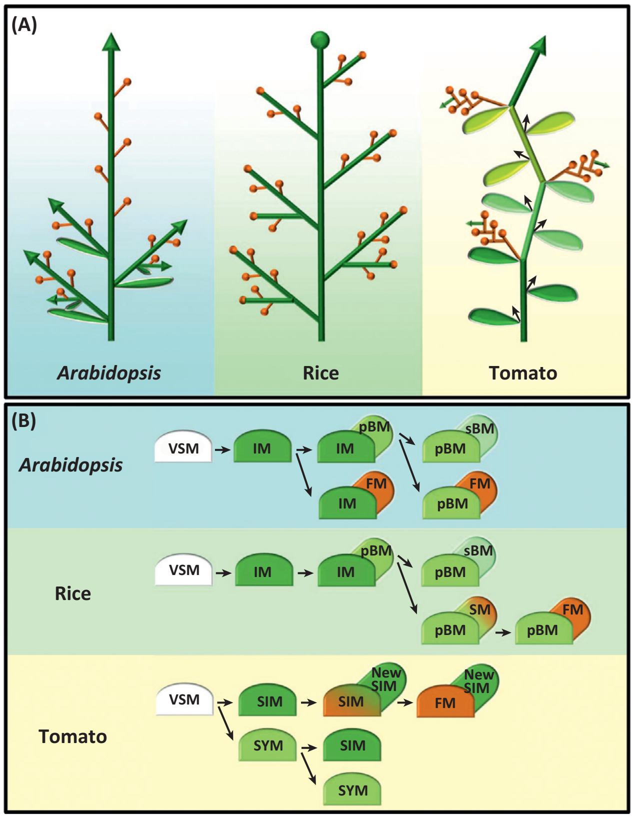

TRENDS in Plant Science

Figure 1. Comparison of the inflorescence architecture of *Arabidopsis*, rice and tomato. **(A)** Schematic diagrams depicting the inflorescence structures of *Arabidopsis*, rice, and tomato. Brown circles, green arrows, and a green circle represent flowers, indeterminate shoots, and a determinate shoot, respectively. Black arrows indicate canonical axillary shoot meristems in tomato. **(B)** Sequential development of shoot meristems contributes to different inflorescence structures in *Arabidopsis*, rice, and tomato. In monopodial plants such as *Arabidopsis* and rice, during the floral transition the vegetative shoot meristem (VSM) is transformed into the main inflorescence meristem (IM) that subsequently generates all of the other branches and flowers. *Arabidopsis* develops the raceme-type inflorescence, in which a main IM grows indefinitely and generates either floral meristems (FMs) or primary branch meristems (pBMs) that reiterate the pattern of the main IM to produce either secondary branch meristems (sBMs) or FMs. In the panicle-type inflorescence of rice, the main IM terminates after the production of several pBMs that generate sBMs or spikelet meristems (SMs), each of which is transformed into a single FM. sBMs usually reiterate the pattern of pBMs to give rise to SMs and FMs. Tomato is a typical sympodial plant, in which the VSM terminates in a sympodial IM (SIM), whereas new vegetative growth continues from a sympodial shoot meristem (SYM) produced from the axil of the youngest leaf. The SYM reiterates the pattern of VSM to terminate in a SIM and initiate the generation of a new SYM. The SIM generates a new SIM before terminating in a FM, and reiteration of this pattern forms the cyme-type inflorescence in tomato.

Regulation of meristem identity determines inflorescence architecture

Although a remarkable diversity of inflorescence architectures has evolved in flowering plants (Figure 1), the inflorescence branching pattern is mainly dependent on developmental decisions that take place in inflorescence meristems and their derived meristems; within each meristem, a decision is made between the maintenance of indeterminacy and commitment to the floral fate.

Previous studies in *Arabidopsis* have suggested that an antagonistic interaction between the shoot identity gene *TERMINAL FLOWER 1* (*TFL1*) and floral meristem identity genes, such as *LEAFY* (*LFY*) and *APETALA1* (*AP1*), regulates the inflorescence branching pattern [9–11]. *TFL1* is specifically expressed in the center of the main inflorescence meristem and lateral branch meristems [10,12], whereas *LFY* and *AP1* are strongly expressed in young floral meristems [13–16]. Loss of function of *TFL1* results in early flowering and the conversion of the main inflorescence meristem and lateral branch meristems into floral meristems, which is accompanied with ectopic expression of *LFY* and *AP1* in these meristems [9,17–19]. By contrast, the opposite phenotypes of late flowering and highly branched inflorescences are observable in transgenic plants overexpressing *TFL1*, in which upregulation of *LFY* and *AP1* during the floral transition is delayed [12]. These results suggest that *TFL1* activity is responsible for indeterminate growth of inflorescence meristems partly through preventing the meristems from acquiring the floral identity promoted by *LFY* and *AP1*. Conversely, floral meristem identity genes, such as *LFY*, *AP1*, and two *AP1* homologs, *CAULIFLOWER* (*CAL*) and *FRUITFULL* (*FUL*), are required to repress *TFL1* expression in floral meristems [10,11,19–21]. In the absence of these floral meristem identity genes, ectopic and/or upregulated expression of *TFL1* contributes to the conversion of floral meristems into inflorescence shoots. Thus, *TFL1* and floral meristem identity genes contribute to shaping the inflorescence architecture in *Arabidopsis* through antagonizing each other to determine the identity of inflorescence meristems and their derived meristems (Figure 2A).

LFY encodes a plant-specific transcription factor, the orthologs of which are present as single-copy genes in most land plant species [22]. Although *LFY*-like genes share two highly conserved domains, their expression patterns and functions are diverse in various plants [23–27]. For example, unlike its counterpart in *Arabidopsis*, the rice ortholog of *LFY*, *ABERRANT PANICLE ORGANIZATION 2*/*RICE FLORICAULA* (Table 1), is not expressed in floral meristems and has a role in suppressing the transition from inflorescence meristems to floral meristems [28–30]. It has been proposed that *LFY*-like genes might have two functions: an ancestral role in promoting meristematic growth and a novel role in mediating floral identity [24]. These two functions might exist with different strengths under different regulatory contexts in most flowering plants, thus contributing to various inflorescence structures observed in nature. Whereas *LFY*-like genes occur in most land plants, *AP1* orthologs belong to the *euAP1* gene clade of MADS-box genes and are only present in the core eudicots that comprise the majority of extant angiosperm species [31]. The expression and function of *AP1*-like genes are usually related to flower development [4], whereas their functional modes differ in various plants. For example, *AP1* is required for establishment of floral meristems in *Arabidopsis*, whereas the counterparts in rice, *OsMADS14*, *OsMADS15*, and *OsMADS18* (Table 1), are involved in specifying inflorescence meristems rather than floral meristems [32].

TFL1 is a member of the CETS (CENTRORADIALIS, TFL1, and SELF-PRUNING) family proteins that have homology with highly conserved phosphatidylethanolamine-binding proteins (PEBPs) in eukaryotes [33,34]. So far, investigations on *TFL1* orthologs in various plant species have shown that these genes have a relatively conserved role in affecting inflorescence architecture through preventing shoot meristems from differentiating