Maintenance, Transition and Reversion of the Shoot Apical Meristem during Plant Development

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Abstract The shoot apical meristems (SAM) produce new cells for new organs and tissues continuously, and their activity depends on regulatory genes that balance between proliferation of meristems and organogenesis. Cells originated from SAMs of non-photosynthetic capacity can form vegetative organs of photosynthetic capacity. During the transition from vegetative to reproductive development, SAMs change to influorescence meristems, and ultimately floral meristems. Before the phase of floral determination, the status of SAMs is affected by environmental signals and transcriptional networks largel. Mainly using *Arabidopsis* as a modal plant, the complex and different transcriptional networks with maintenance and transition of the SAM are discussed in this review. In the flower and inflorescence reversion, the positioning of these stem cells within the SAM is also regulated by a set of genes, which display spatially distinct patterns of expression. The transition and harmony of determinate and indeterminate meristems are a major determinant function of organogenesis and of plant architecture.

Key words shoot apical meristem; development; maintenance; transition; reversion

Shoot apical meristems (SAM) have been the focus of many studies during plant development. The SAM make the shoot functions through the following aspects: initiating new organs and tissues, communicating signals to the rest of the plant, and maintaining itself as a formative region. The early state of the apical meristems describes a set of tissues and organs with distinct characteristics. Moreover, processes in vegetative meristems may affect processes in later types of meristems (inflorescence meristems and floral meristems). In the whole development, transcriptional networks are involved in the initiation, maintenance and transition of the SAMs. Because the meristems are able to alter their activity in response to both internal and external factors during growing and development, they provide the developmental flexibility required to deal with continuous diversification. Research over the last decade has led to tremendous advance in the cellular dynamics and characterization and function of the transcriptional networks in the SAM. In this review, encircling the characteristic of the SAM, we provide an overview focusing on maintenance, transition and reversion of the SAM between vegetative and reproductive development, or reversely from floral to vegetative development. Meanwhile its regulation mechanism and function of the SAM are discussed from another angle.

1 Shoot Apical Meristem

The SAM contains a group of pluripotent cells, which generate the daughter cells from the main shoots of the plant. The SAM is typically a small, dome-shaped group of cells. Both the size and shape of SAMs vary greatly at different points in development and among various species.

Two different concepts have been used to define regions of the SAM. One concept is layers and another is zones. The SAM contains three cell layers (Ll, L2, and L3) [1]. As shown in Fig.1, the L1 is the outermost layer, and the L1 forms the epidermis in different parts of the shoot. Cells in the second layer from the surface,

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the L2, divide markedly in the anticlinal plane but also divide in the periclinal plane when organs are forming. Cells in the third layer from the surface, or L3, divide in both anticlinal and periclinal planes and provide cells for the interior of stems and organs. The concept that the SAM have three cell layers has been important for understanding shoot development.

Zones is another concept used to define regions of the SAM. There are three meristem zones: the central zone (CZ), the peripheral zone (PZ), and the rib zone (RZ). The CZ, which is a group of cells located at the end of the apical meristem, includes cells all three layers. Central zone cells are thought to function as stem cells, however, these cells are not permanent unlike mammalian stem cells [2]. Cells in the PZ arise from cells of the CZ. The PZ's main function is forming lateral organs that are positioned at precise points. At the base of the SAM, a transition zone between the apical meristem and shoot, is another set of cells, the RZ. Cells in the RZ are arranged in longitudinal files and contribute to tissues in the center of the stem. Like the cells of the PZ, cells in the RZ are thought to be derived from impermanent initials in the CZ. Two concepts of layers and zones relate to each other, various zones contain cells from all three cells layers.

2 Maintenance of the Shoot Apical Meristem

The SAMs function as the main source of new cells to sustain plant growth. Generally, the SAM is considered to be determinate characteristic. A determinate meristem produces a predictable size and form plant body, such as the flower, whereas indeterminate meristems produce parts of the plant whose size and form depend on the local environment, such as branches and inflorescence that grow to variable lengths. The indeterminate meristems growth is sustained by small groups of self renewing cells that are functionally similar to mammalian stem cells [4]. These cells are located in the CZ, while some of their descendants are displaced to the PZ, recruiting to form new organ primordia. Moreover, L1 has been shown to be necessary for the maintenance of indeterminacy in the underlying layers. The semidominant *Extra cell layers1* (Xcl1) in maize which mutation produces multiple epidermal layers by overproduction of a normal gene [5] may provide a link between L1 division and meristem maintenance. The positioning of determinate and indeterminate meristems varies between species and is a major determinacy of plant architecture.

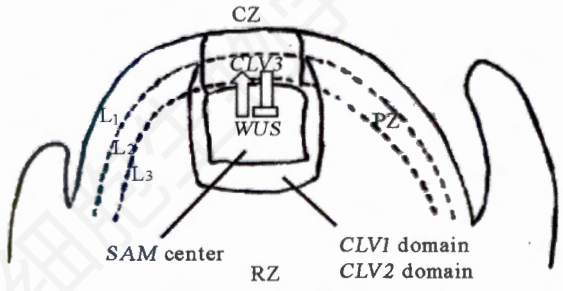

Fig 1 Structure of the SAM and the expression domains of several crucial SAM-related genes [3]

SHOOT MERISTEMLESS (STM) and *WUSCHEL (WUS)* are two central regulatory genes in shoot meristem development. *STM* and *WUS* genes function during meristem development are required not only for the establishment of the shoot meristem during embryogenesis, but also for subsequent meristems maintenance [6–8]. *STM* encodes a homeodomain protein expressed throughout the meristem and delays differentiation to allow enough cells to bulk up before organogenesis [9]. *WUS* also encodes a homeodomain protein and is essential to specify the stem cells in the CZ. *WUS* is required to maintain stem cells in all layers of the CZ, but it is expressed only in a few L3 cells in the CZ [10] (Fig.1). Although both *STM* and *WUS* are essential for meristem maintenance, so far the evidence suggests that *WUS* has a more prominent role and central regulator in the control of meristem size and stability. To balance the recruitment of cells from the meristem with the supply of new meristem cells, a constant and precise pattern of *WUS* expression must be maintained within a group of cells that proliferate continuously, whereas many multiple regulatory genes act to repress *WUS* outside its normal expression domain.

One of the mechanisms that regulate *WUS* expression is the *CLAVATA* (*CLV*) signaling pathway, which represses *WUS* [11]. The signal is the secreted polypeptide *CLV3*, which is produced in the L1 and L2 layers of

the CZ and moves into the inner layers, where it is perceived by a receptor including the *CLV1* and *CLV2* polypeptides (Fig.1). Recent studies demonstrated that a hydroxyl 12-amino acid peptide derived from the conserved CLE [*CLV3/ENDOSPERM SURROUNDING REGION* (*ESR*)] motif of *CLV3* promotes cell differentiation [3]. Along with the *CLV* genes, *WUS* plays a key role in maintaining a group of undifferentiated cells in the shoot meristem [12].

3 Transition of the Shoot Apical Meristem

In the original developmental phase of the shoot meristem, one aspect that has received rather limited attention is that SAM is heterotrophic, in contrast to the majority of cells and tissues which rapidly undergo differentiation to form photosynthetically active, autotrophic organs.

The cells of the SAM are heterotrophic, it is demonstrated that they do not contain chlorophyll under fluorescent illumination [13]. The inability of the SAM performs photosynthesis, but the cells rapidly acquire photosynthetic capacity as they leave the SAM domain, however it is not clear how SAM achieve transition from non-photosynthetic to photosynthetic capacity.

The SAM function is defined a series of transcriptional networks by their spatial and temporal control [14]. The positioning of the stem cells within the SAM is regulated by genes including *WUS* and *CLV* which display spatially distinct patterns of expression [15]. However, none of these patterns directly links to transition by genes from non-photosynthetic to photosynthetic capacity, except increased *CLV3* signaling restricts meristem growth and promotes allocation of peripheral meristem cells into organ primordia [16]. The meristem domain itself is initially defined by expression of *STM-like KNOX* homeobox genes [10] . Repression of *STM-like* gene expression within the SAM is associated with the determinative meristem cells to form a leaf primordium [17]. These transcription factors are not simply linked to the metabolic switch. Furthermore, in a number of SAMs, *STM-like* gene expression can extend into the sub-meristem region of the stem where, for example, chlorophyll is accumulated clearly. So, the transition from heterotrophic to autotrophic growth is not simply regulated by a *KNOX* gene-dependent mechanism. Other genes, such as *AINTEGUMENTA*, are expressed very early in the leaf primordia.

Although SAM cells do not contain chlorophyll, they contain proplastids. Moreover, the transition from meristem to primordium appears to be entwined with plastid differentiation and the acquisition of photosynthetic capacity, suggesting that a switch in carbohydrate metabolism, accompanying with plastid differentiation, might be involved in the change of cell identity. Some data indicated that carbohydrate metabolism is indeed linked with the earliest phase of commitment by meristem cells to form a leaf [18]. In addition, investigations suggest that stem cell niches are characterized by oxidizing enzyme activities, which have been proposed to play a role in the metabolism of growth.

It is clear that the SAM is metabolically distinct from the adjacent tissue. The mechanism controlling the switch of metabolism is unclear. The advent of highly sensitive and powerful tools for the analysis of extremely small samples means that it is possible to attempt to answer these fundamental questions.

4 Transition from Vegetative to Floral Meristems

During early plant growth, leaf primordia are produced on the periphery of a vegetative meristem. When the shoot apex of a plant is induced to flower, the apical meristem switches to become an inflorescence meristem. Then, floral meristems are produced as small bulges on the periphery of the inflorescence meristem. The balance between shoot meristem activity and organ initiation is maintained during most of the plant's growth, but it is eventually inclined to organogenesis during floral development [19].

Flowering plants have two types of inflorescence: indeterminate inflorescence, in which the inflorescence grows indefinitely, and determinate inflorescence, in which a terminal flower is produced. The indeterminate type is thought to have evolved from the determinate. It is worthy to mention that soybean (*Glycine max*) is attributive to indeterminate inflorescence, and inflorescence

meristems come of the SAM of stem shoot, but, strictly speaking, it has the two or three distinct types of stem shoot in the different species synchronously. The time of keeping vegetative development of the SAM in the indeterminate stem termination of soybean is longer than that of determinate stem termination type. Soybean variety with indeterminate stem termination produces new leaves in the terminal after flowering, so during maturation its terminal does not produced pods generally, but soybean with determinate stem termination terminates development in the way of producing pods in the terminal. So, different podding-habits are distinguished in soybean.

In *terminal flower 1* in *Arabidopsis* and *centroradialis* in *Antirrhinum*, inflorescences that are normally indeterminate are converted to a determinate architecture. *CENTRORADIALIS* (*CEN*)[20] and *TERMINAL FLOWER 1* (*TFL1*)[21] were shown to be homologous, however, unlike *CEN*, *TFL1* is also expressed during the vegetative phase, where it delays the commitment to inflorescence development and thus affects the timing of the formation of the inflorescence meristem.

The suppression of indeterminate growth during floral development depends on floral specific regulatory genes, whose expression is embedded within a network of gene expression that is initiated at the transition of reproductive development. The transition from vegetative to reproductive development is controlled by multiple environmental and endogenous signals that ultimately converge on key regulators of floral identity: *APETALA1* (*AP1*)/*CAULIFLOWER* (*CAL*) and *LEAFY* (*LFY*) [22,23].

AP1 and *CAL* are necessary for the transition from inflorescence to floral meristem. Consistent with their role in floral meristems, *AP1* and *CAL* are expressed as soon as the floral primordium emerges from the inflorescence meristem [24]. *LFY* also encodes a transcriptional regulator that specifies floral identity and consequently promotes determinacy [25]. *LFY* accelerates the transition from inflorescence to floral meristem largely by activating *AP1* [26], but subsequently has a central and *AP1*-independent role in controlling floral development. In addition to being activated by *LFY*, *AP1*/*CAL* are redundantly activated by the *FLOWERING LOCUS T* (*FT*) gene [27]. Recent evidence suggests that *FT* in *Arabidopsis* is expressed in leaves and that its protein is transported to the apex as a mobile flowering signal that is produced in response to long days [28]. To maintain the indeterminate inflorescence meristem, the expression of *LFY* and *AP1*/*CAL* in the inflorescence meristem is prevented by *TERMINAL FLOWER* (*TFL*), which encodes a homologue of *FT* but has the opposite function, i.e. it antagonizes floral development [29,30].

The interactions among *FT*, *AP1*/*CAL*, *LFY*, and *TFL* not only divide where floral meristems develop, but also establish regulatory programme that ensure a sharp and stable transition to floral identity. After the initial activation by *FT*, *AP1*/*CAL* and *LFY* reinforce each other's expression by antagonizing *TFL* [31]. However, activity of *LFY* and *AP1* is not directly inhibited by *TFL1*, but their up-regulation is markedly delayed [32].

5 Flower and Inflorescence Reversion

Flower and inflorescence reversion are defined a switch from floral development back to vegetative development, thus rendering flowering an ongoing growth pattern rather than a terminal act of the meristem.

There are three distinct types: (1) inflorescence reversion in which vegetative development occurs after, or within inflorescence development; (2) flower reversion, in which the form of the flower itself is altered and incomplete, with some parts replaced with leaves, or there may be proliferation after the formation of the normal floral organs; and (3) whole-plant reversion (WPR), in which the plant as a whole can be reversed from reproductive to vegetative status even it has bloomed [33,34].

Flowering reversion has been studied in detail in at least three plant species. The first is *Arabidopsis thaliana*. Reversions seen in this species are from flower to inflorescence development and are not true reversions to leaf production, mechanism of floral maintenance derived from this concept are relevant to studies of reversion to leaf production in any of the conditions. The second species is *Impatiens balsamina*, in which

the terminal flower reverts to leaf production consistently when transfering from inductive short days (SD) to long days (LD). One difference between *A. thaliana* and *I. balsamina* reversions is the expression pattern of *LFY* and its Impatiens homologue *IMP-LFY*. *IMP-LFY* is not up-regulated during flowering and the expression level remains constant through vegetative growth, flowering, and reversion. The low level expression may be insufficient either to activate or to repress the Impatiens homologues of *AGAMOUS* (*AG*) [35], and a low level of *LFY* expression is key to a number of the instances of reversion. The third species is *Glycine max*. The similar reversion phenomenon emerges in the special varieties when inductive flowering conditions are removed [36,37]. Flowering reversion in *Glycine max* can be partitioned WPR and partial reversion (PR)[37], PR include floral reversion (FR) and inflorescence reversion (IR), sequentially IR consists of terminal inflorescence reversion (TIR) and lateral inflorescence reversion (LIR). Branches and leaves were produced in the trifid bract of reversed inflorescence where produced customary flowers. With the increment of days of LD treatment, reversed terminal inflorescence have more nodes, and produce flowers with prominent and numberous leave-like bracts, it maybe result that vegetative development and reproduced development compete one another.

The reason why reversion occurs during plant development has three aspects: First, the different parts of the flower organs are equivalent to the branches and the leaves of a shoot. Second, the induction of these new meristem types depends on many environmental signals. Third, the transition to flowering is the culmination of a complex interaction of genes. Thereinto, the flowering time genes control the response to the environmental, endogenous and hormonal signals. The reverted meristem, whilst producing leaves, retains some level of floral determination, and rapid re-flowering occurs on when it is transfered back to inductive conditions [38]. The leaves act as a source of determination signal to the SAM and this signal is constantly necessary up to a certain stage. Meristems not receiving enough signal from the leaves will revert to vegetative growth [39]. Thus, both the flowering and reverting lines require the leaf-derived signal to complete action.

Most species are less prone to reversion because signals from the leaf are always constant, and the pathways inducing flower development have a high level of redundancy that generates the meristem autonomy even when leaf-derived signals are weak. Therefore, suboptimal signal levels do not result in reversion rather slower flowering and abnormal flowers.

Reversion requires a flexibility of plant to switch from floral to vegetative or inflorescence development. Moreover, reversion is always to a distinct, specific and not mixed meristem type [40]. In these instances reversion has been proposed to regular plant development and plays a crucial role in the research of plant architecture and genes function.

6 Conclusions

Maintenance, transition and reversion of the SAM during development are determinative for plant architecture and are dependent on genetic control. In previous studies, genetic control of vegetative and reproductive meristem are main questions of researching development at all times, what is more, genes that affect the key aspects of flowers have been isolated and studied in *Arabidopsis* in detail. However, physiological and biochemical studies of gene action are still unknown, many new problems have been raised by these investigations. For example, how are environmental signals connected to the activation of meristem identity genes? In addition, the mechanisms of molecular level and signal conduction with reversion should be useful to further investigate.

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茎顶端分生组织在植物发育过程中的保持、转变和逆转

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摘要 顶端分生组织(shoot apical meristems, SAM)为产生新的器官和组织而不断提供新的细胞, 它的活性依赖于平衡分生组织细胞的增殖和器官发生之间关系的调控基因。来自不具备光合能力的顶端分生组织的细胞可形成具有光合能力的营养器官。在从营养生长到生殖发育的转变过程中, 茎顶端分生组织, 转变为花序分生组织, 最终形成花分生组织。在进入开花决定状态以前, SAM 的状态很大程度上受到环境信号和转录调控因子的影响。以模式植物拟南芥为主, 对在顶端分生组织的保持和转变中复杂同时又有差异的基因调控网络进行讨论。在花和花序分生组织逆转过程中, SAM 中的细胞也受到相关基因的调控, 且表达方式存在明显的时空差异。因此, 具有决定性的和未决定性双重特性的分生组织之间的转变和相互协调, 对于器官发生和形态建成起到至关重要的作用。

关键词 顶端分生组织; 发育; 保持; 转变; 逆转

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