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A systems approach to understand shoot branching

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ABSTRACT

Shoots are ramifying systems with regular initiation of new growth axils called shoot branches. In seed plants, shoot buds initiate in leaf axils from axillary meristems (AMs) containing stem cells. The activities of AMs and buds play vital roles in plant architecture and crop yield. Whereas recent years have witnessed enormous progress the control of bud outgrowth, our knowledge of AM initiation remains rudimentary. Recently, systems biology approaches have been employed to study AM initiation, and have substantially expanded our understanding of the underlying gene regulatory network (GRN). Systems approaches uncovered transcriptional signatures, predicted cellular functions, and identified new regulators and regulatory relationships. Complementary molecular genetic studies support and extend findings from systems studies.

1. Shoot branching is fundamental to plant architecture

1.1. Branching, plant body plan, and crop yield

Body plan evolution of plants has been distinct from animals since their divergence around 1 billion years ago. Branching is one of the inventions plants made [1]. Whereas branching has also been found in animals in rare cases [2], it is widely adopted by presumably all embryophytes (land plants), including liverworts, hornworts, mosses, pteridophytes (ferns), gymnosperms, and angiosperms [3]. Acquisition of branching is believed to enable plants' adaptation to the changing environment. Because plants maintain apical meristems to keep organogenesis capacity during postembryonic development, multiple apical meristems are favored for the survival of sessile plants. Multiple shoot apical meristems lead to shoot branching and new growth axils.

Different branching systems have been adopted by each group of embryophtes. Mosses, and likely liverworts and horneworts, use mainly terminal branching, in which one shoot meristem, often equally, separates into two [4]. Pteridophytes have most diversified branching systems, including terminal branching, adventive branching, and occasionally axillary branching [5]. Axillary branching, in which branches initiate laterally at some distance away from the shoot apical meristem (SAM), has become the dominant branching system in angiosperms and gymnosperms (Fig. 1A). Although it remains unclear why spermatophytes prefer axillary branching, the axillary position is likely an optimal location for branching. Axillary branches are associated with the phyllotaxis, i.e., the arrangement of leaves on a plant stem. The associated leaf may protect its axillary meristem (AM), which resides in the leaf axil. Molecular evidence suggests that the floral meristem is a type of specialized AM [6].

Shoot branching profoundly affects plant architecture, and is, not surprisingly, a key factor affecting crop yield. In cereal crops, especially grasses, shoot branches during the vegetative stage are termed tillers. The number of tillers determines the number of inflorescences. Each inflorescence further branches one or more times to increase its complexity and finally flower and seed numbers [7]. Thus shoot branching ability during reproductive stage is also critical to final crop yield. In fact, axillary bud activity has long been a target of breeding selection [8], because it significantly affects crop yield by affecting both tiller (and therefore inflorescence) number and inflorescence complexity.

Axillary branch formation can be divided into two steps, the initiation of an axillary bud, and the outgrowth of the bud into a branch [9]. Axillary bud outgrowth is under apical dormancy control, as the main stem shoot apex is dominant over axillary buds' growth. Extensive study has been carried out in recent years on axillary bud outgrowth, as summarized in an excellent recent review [10]. On the other hand, axillary bud formation, i.e., the initiation of an AM, is less studied. We will discuss in this review how systems approaches speed up our understanding of AM initiation.

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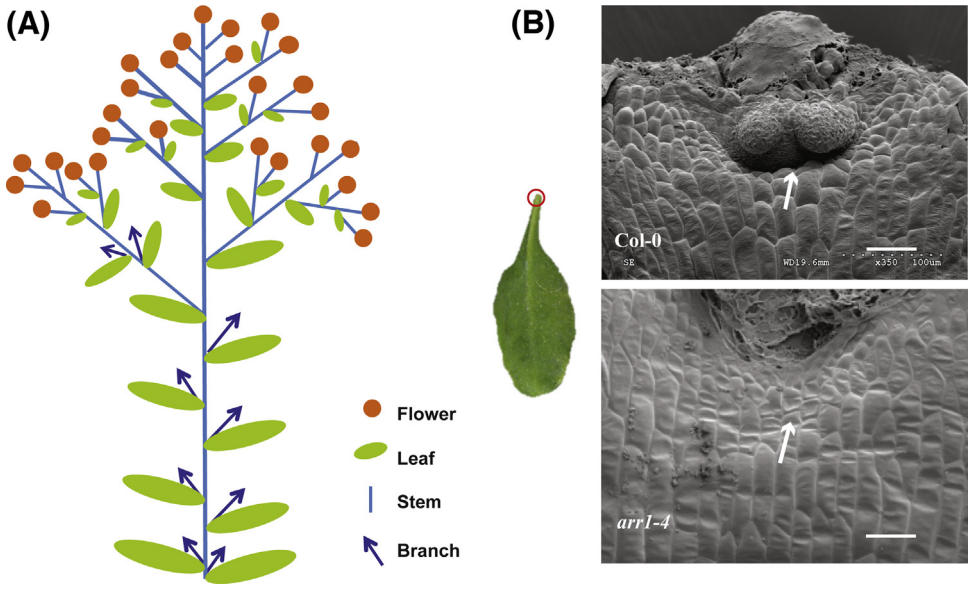

Fig. 1. Schematic representation (A) and morphology (B) of AM initiation. (A) Schematic representation of shoot and inflorescence branching patten in a typical seed plant, showing axillary branching at leaf axils. (B) Scanning electron micrograph of *Arabidopsis* leaf axil with (Col-0) or without (*arr1–4*) an axillary bud. Arrows indicate the position where AM initiates. Bars = 50 μM.

1.2. Genetic analysis of axillary meristem initiation

AM specification occurs during modular plant growth into phytomers, which consists of a leaf, an AM on the adaxial side of leaf base, and a stem segment. As its name suggests, AMs arise on the adaxial side (i.e., the upper side) of the subtending leaf base (Fig. 1B). AM initiation is closely associated with the adaxial leaf fate, because abnormal leaves with altered adaxial development has compromised AM initiation [11,12], and ectopic AMs arise on the abaxial side of fully adaxialized leaves [13]. Clonal analysis indicated that the AM and the subtending leaf share a common pool of ancestral cells [14,15].

Two models have been proposed to explain the origin of AMs. In the "detached meristem" model, a small number of stem cells detach from the SAM and associate with the leaf axil as the leaf differentiates from the SAM. In the "de novo induction" model, an AM initiates from leaf cells which have lost stem cell identity and have differentiated to be leaf cells. It remains to be tested which model better explains the AM initiation process [6].

Genetic studies have identified a small number of transcription factor encoding genes affecting AM initiation. *LATERAL SUPPRESSOR* (*Ls* or *LAS*) of tomato and *Arabidopsis*, and their homolog in rice *MONOCULM1* are the first identified AM initiation regulators [16–18]. *Arabidopsis las* mutants are specifically defective in AM initiation, and its orthologs in tomato and rice also affect flower development. *LAS* encodes a GRAS family transcription factor and its downstream targets are largely unknown. Another group of transcription factors specifically affecting AM initiation are the R2R3 MYB-family *Blind* gene of tomato and its homologs *REGULATORS OF AXILLARY MERISTEMS1–3* (*RAX1–3*) in *Arabidopsis* [19–21]. This *Blind*/*RAX* pathway affects vegetative AM initiation in *Arabidopsis* and vegetative and reproductive branching in tomato. It has also been found that a bHLH family transcription factor, LAX PANICLE1 (LAX1) in rice, barren stalk1 in maize, and REGULATOR OF AXILLARY MERISTEM FORMATION (ROX) in *Arabidopsis*, affects AM initiation [22–25]. Whereas severe vegetative and reproductive branching defects are found in rice and maize, the *Arabidopsis* ortholog only has marginal effect on vegetative stage branching. The *CUP-SHAPED COTYLEDON* (*CUC*) genes encode NAC domain transcription factors [26]. In addition to their roles in embryonic shoot meristem formation, phyllotaxis patterning, and lateral organ boundary specification, *CUC2* and *CUC3*, as well as *CUC1*, play partially redundant roles in AM initiation in *Arabidopsis* [27,28]. All these above mentioned transcription factor-encoding genes are specifically expressed in the axils of leaves from which new AMs initiate. On the other hand, more broadly expressed HD-ZIP III transcription factor *REVOLUTA* (*REV*) also affects AM initiation [29]. Consistent with its broad expression in leaves, stems and roots [30], development of all these tissues is compromised in *rev* mutants. The *PINHEAD/ZWILLE/AGONAUTE10* (*PNH*) gene also has pleiotropic effects on *Arabidopsis* development, including AM initiation [12]. Recent studies have shown that *PNH* encodes a member of the AGO proteins, which are involved in small RNA biogenesis, and that PNH specifically binds to and sequesters micro RNAs miR166/165, which promote *REV* and related HD-ZIP III transcripts degradation [31]. It is thus conceivable that reduced *REV* level in *pnh* is likely responsible for its AM initiation defects.

Identification of additional regulators of AM initiation by forward genetic approaches has been difficult, because strong apical dormancy in the model plant *Arabidopsis* significantly inhibits axillary bud outgrowth. In addition, using molecular genetic approaches to resolve the gene regulatory network (GRN) underlying AM initiation is labor-intensive and time consuming. Systems biology approaches allow high-throughput integrated and comprehensive research to resolve interactions of multiple components of biological systems, such as GRNs. We have recently combined two genome-wide study approaches to tackle the GRN underlying AM initiation and associated organ boundary formation. A first glimpse of the GRN not only identified new directions for further study, but has also successfully connected known regulators and identified novel regulators for AM initiation.

2. Gene expression pattern specified in organ boundary

2.1. Cell type-specific transcriptomes to identify expression patterns

With the rapid development of microarray and, more recently, next generation sequencing technologies, transcriptome analysis has been widely adopted in biological research. For the study of