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Mini Review

Sculpting the meristem: The roles of miRNAs in plant stem cells

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ABSTRACT

The whole structure of higher plants is generated dynamically throughout the life cycle by the activity of stem cell niches at the apex of shoot and root. Hormone molecules and many transcription factors cooperate to balance the stem cell maintenance and differentiation. It is becoming increasingly clear that microRNA (miRNA) molecules are also participants in these processes. Here, we highlight the advances that have been made in regarding the roles of miRNAs in plant stem cell control. These advances provide a framework for our understanding of how signals are integrated to specify and position the stem cell niches in plants.

1. Introduction

In contrast to animals, plants possess the ability to continue to produce new organs throughout their life cycle. They are the products of stem cells [1,2]. After a plant seed has germinated, all the new cells in the growing plant are derivated from the pluripotent stem cells located in the shoot apical meristem (SAM) and the root apical meristem (RAM). Plant pluripotent stem cells are defined by their unique capacity for self-renewal and their simultaneous ability to generate cells destined for differentiation [1,3]. The coordination between stem cells maintenance and differentiation is critical for normal plant growth and development. Elements such as phytohormones, transcription factors and some other known or unknown genes cooperate to balance this process [4]. Recent studies also established the involvement of microRNA (miRNAs) in regulating appropriate stem cell activity. The discovery of miRNAs has greatly improved our understanding of molecular mechanism in stem cell function. Furthering exploring the interaction of miRNAs in plant stem cells may represent a novel and feasible approach to disclose the complex regulatory networks of developmental control. Thus, in this review, we summarized the current knowledge of miRNAs in plant stem cell regulation, with an intention to provide new insights into mechanisms of plant development.

2. miRNAs is critical for plant stem cell retaining

The main activities of the angiosperm SAM and RAM throughout development are maintenance of the pluripotent stem cell population while providing founder cells for organ initiation, stem and root production to generate the architecture characteristic of each plant species [4]. The maintenance of stem cell population is intimately balanced with cell recruitment into differentiating through intercellular communication involving a complex signaling network. Recent studies have shown that diverse regulators function in plant stem cell retaining, many of which are supported by miRNAs [5].

3. The role of miRNAs in apical meristem maintenance

In previous study, Willams et al. found that the Arabidopsis *jaba-1D* (*jba-1D*) mutant displays multiple enlarged shoot meristems, radialized leaves, reduced gynoecia, and vascular defects. More intriguingly, these meristem phenotypes require *WUSCHEL* (*WUS*) activity, and directly correlate with a dramatic increase in *WUS* expression levels [6]. Later, it became known that the *jba-1D* phenotypes are caused by over-expression of miR166g, which targets *class III homeodomain-leucine zipper* (*AtHD-ZIP*) family genes [6]. The *HD-ZIP-III* genes include *PHABULOSA* (*PHB*), *PHAVOLUTA* (*PHV*), *REVOLUTA* (*REV*), *AtHB8* and *AtHB15* in Arabidopsis [7]. Overexpression of miR166 results in down-regulation of the *ATHB-9/PHV*, *ATHB-14/PHB* and *ATHB-15* mRNAs, and concomitantly causes an enlargement of SAMs and an enhancement in vascular development [6]. In addition, miR166-resistant icu4-1 and icu4-2 alleles of the *INCURVATA4* (*ICU4*) gene, also known as *AtHB15*, alter leaf phyllotaxis and cell organization in the root apical meristem, reduce root length, and cause xylem overgrowth in the stem [8]. Besides Arabidopsis, miR166 also plays an important role in spatial and temporal restriction of *HD-ZIPIII* mediated enlarged apical meristems in *Nicotiana sylvestris* [9]. All these results demonstrate an indirect role for miRNAs in controlling meristem formation via

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regulation of *WUS* expression, and also reveal complex regulation of the *class III AtHD-ZIP* gene family [6].

Besides miR166, miR165 also target *HD-ZIP-III* gene family. miR165 overexpressors cause a drastic reduction in the transcript levels of all five *HD-ZIP III* genes in Arabidopsis and display prominent phenotypes, including loss of SAM, alteration of organ polarity, inhibition of vascular development and aberrant differentiation of interfascicular fibers [10]. Compared with miR166, we can find that though miR165 and miR166 mediate the degradation of the same genes, they have just reverse effects on stem cell maintenance [10].

4. miRNAs control axillary meristem retaining

During the process of post-embryogenesis of higher plants, new meristems are also initiated in the axils of leaf primordia, which develop into new axes of growth [11]. In Arabidopsis, the establishment and maintenance of axillary meristem and organ boundary have been verified to be controlled by three partially redundant genes, *CUP-SHAPED COTYLEDON* (*CUC1*), *CUC2* and *CUC3* [12–14]. Recent reports have also shown that transcripts of *CUC1* and *CUC2* are targeted for degradation by miR164 [14,15]. Overexpression of miR164 displayed defects in axillary meristem formation and overexpression of miR164 in the *cuc3–2* mutant caused an almost complete block of axillary meristem formation. Conversely, mir164 mutants and plants harboring miR164-resistant alleles of *CUC1* or *CUC2* developed accessory buds in leaf axils [12,15]. Besides, disruption of *CUC2* regulation by miR164, either by making *CUC2* resistant to the miRNA or by reducing miRNA levels leads to enlarged boundary domains and the enlargement related to the division patterns of the boundary cells [14]. Collectively, these results reveal that redundant functions of *CUC1* and *CUC2* as well as miR164 regulation are required for the establishment of axillary meristems and boundary domain [12]. This implicates miR164 as a common regulatory component of the molecular circuitry that controls the separation of different developing organs [15].

In maize (*Zea mays*), the lateral meristem initiation and maintenance is controlled by TSH4, a gene which was localized throughout the inflorescence stem and at the base of lateral meristems, but not within the meristem itself [16]. *Tsh4* mutants display fewer lateral meristems, altered phyllotaxy and ectopic leaves that grow at the expense of the meristem [16]. In contrary to the expression of *TSH4*, miR156 showed a meristem-specific pattern in maize. Consisting with their complementary expression pattern, *TSH4* is negatively regulated by miR156 [16]. Downregulation of *TSH4* by a miR156 allows the establishment of lateral meristems and the repression of leaf initiation. Therefore, miR156-mediated expression of *TSH4* plays a major role in defining meristem versus leaf boundaries. These results also suggest that the establishment of lateral meristems may lead to the expression of miR156, which in turn downregulates *TSH4* within the meristem, thus restricting *TSH4* activity to the subtending bract, where it suppresses growth [16]. The involvement of miRNAs in SAM and axillary meristem is shown in Fig. 1.

5. miRNAs determine plant stem cell differentiation

Upon plants perceiving the appropriate environmental cues, the shoot apical meristem converts to a reproductively determined inflorescence meristem (FM) [17]. Stem cells in the inflorescence meristem also keep the capacity for self-renewal and generate new cells for giving rise to floral organs, which are the

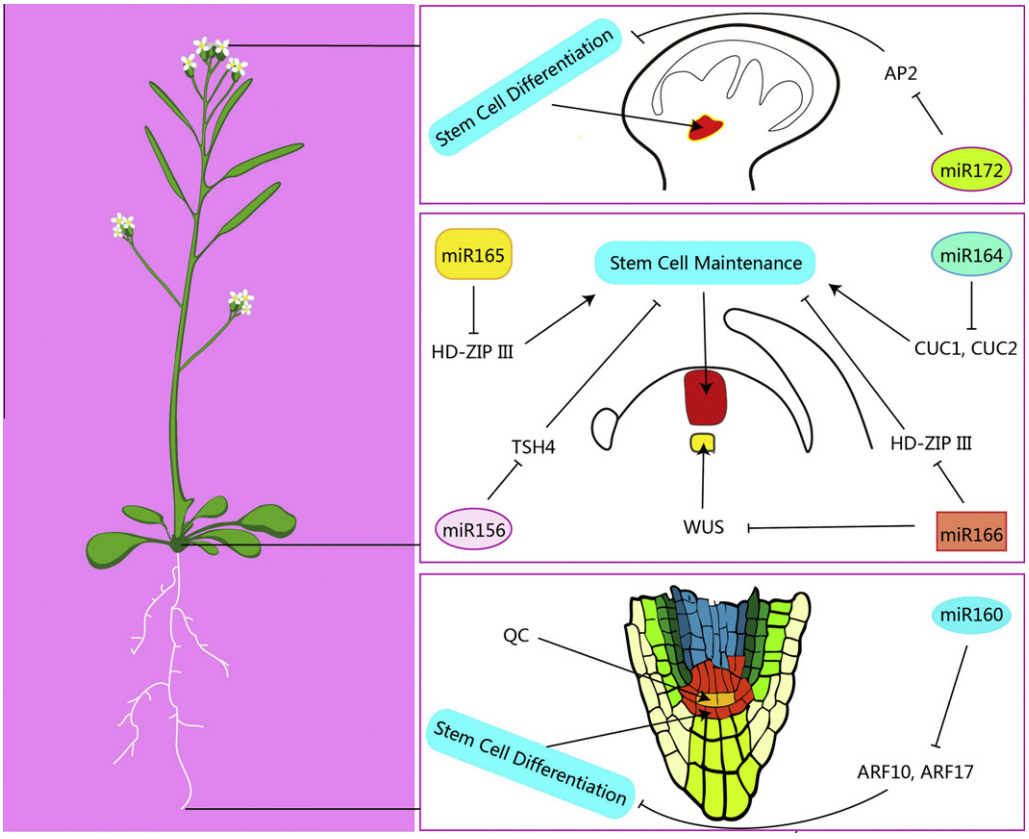

Fig. 1. A diagrammatic representation of the involvement of miRNAs in stem cell maintenance and differentiation. Arrows show simultaneous effect in the pathway while nail shape represents repression.