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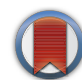

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Article

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Stem cell lineage in body layer specialization and vascular patterning of rice root and leaf

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Abstract Since the first appearance of vascular plants during evolution, the plant body has become specialized for adaption to land conditions. Much of our knowledge of plant body specialization and the origins of tissues from stem cells have been obtained from studies on the dicot *Arabidopsis thaliana*. However, less is known about plant body specialization in monocots, another important branch of angiosperms. In this study, we analyzed stem cell lineage and differentiation during development of the root and leaf of the monocot model plant rice (*Oryza sativa*). Our results showed that three body layers of rice are established from stem cells accompanied by progressively reduced pluripotency. Layer 1 (L1) is a single-cell layer of epidermis; L2 is the cortex/endodermis in the root and the mesophyll in the leaf; and L3 is the site of vascular initiation. At least two common steps in vascular development are shared between rice root and leaf. The preprocambium divides to form the procambium and root pericycle or leaf outer sheath. The procambium further differentiates into the xylem, phloem and circumambient cells. We found that the outer sheath of leaf vascular bundles originates not only from the preprocambium of L3, but also from the mesophyll precursor cells of L2. In addition, *WUSCHEL-RELATED HOMEOBOX* (*WOX*) genes are expressed in not only the stem cell niche but also metaxylem precursor in rice. This pattern differs from that of homologs in *Arabidopsis*, suggesting that *WOX* functions have been recruited in different stem cells in dicots and monocots.

Keywords *Oryza sativa* · Stem cell · Body layer · Preprocambium · Vascular development · *WOX*

Minhuan Zeng, Bo Hu and Jiqin Li have been contributed equally to this work.

SPECIAL TOPIC Plant Development and Reproduction

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1 Introduction

More than 400 million years ago, the colonization of land by plants had a great impact on the evolution of both plants and animals [1–3]. Plant bodies became functionally specialized to adapt to life on land. The vasculature, which is located in the inner center of all organs, is one of those specialized structures. Vascular tissues contain not only the xylem and phloem but also adult stem cells. Together, these tissues and cells function in the long-distance transport of water, nutrients and other substances, in the physical support of the plant body, and in the initiation of de novo organogenesis [1, 4–7].

Specialized tissues originate from stem cells, which are characterized by their ability to both self-renew and differentiate into functional cells [8–11]. Different from

those in animals, stem cells in plants are able to maintain their activity throughout the whole life of the plant to continuously produce organs at the post-embryo stage, allowing some plant species to have almost interminable lives [8, 9]. Stem cells are usually located in the meristem, which comprises the stem cell niche and neighboring transit-amplifying cells [8]. The stem cell niche usually consists of an organizer and its surrounding initial cells. The initial cells usually undergo cell division to form two daughter cells; one daughter cell adjacent to the organizer retains its initial cell identity and the other gives rise to transit-amplifying cells. The primary function of the organizer is to send signals to the initial cells to maintain their undifferentiated state. Transit-amplifying cells can undergo rapid cell division and begin to differentiate into specialized tissues.

The maintenance and differentiation of plant stem cells are controlled by a complex molecular network, in which *WUSCHEL-RELATED HOMEOBOX* (*WOX*) family genes have an essential role [12]. *WOX* genes encode homeodomain transcription factors and are found in a wide range of plant species from green algae to angiosperms [12–17].

A recent study suggested that the origin of angiosperms, the most highly evolved group of vascular plants, was traced back to 225–240 million years ago in the Late to Middle Triassic. The origin of monocots, a subgroup of angiosperms, was estimated to be 154–191 million years ago in the Jurassic [18]. To date, most studies on the mechanism controlling stem cells have been conducted in dicots using the model plant *Arabidopsis thaliana*, and little is known about this mechanism in monocots. However, the organization of the tissue structures differs between monocots and dicots [19–21]. Unraveling the common and diverse mechanisms controlling tissue formation from stem cells in dicots and monocots will improve our understanding of how plant body structures have evolved in angiosperms. In this study, we performed detailed histological and molecular analyses of stem cell lineage in body layer formation and vascular patterning in the monocot model plant rice (*Oryza sativa*).

2 Materials and methods

2.1 Plant materials and growth conditions

Oryza sativa L. *japonica*. cv. Nipponbare was used as the wild-type rice, and Columbia-0 (Col-0) was used as the wild-type *A. thaliana*. Rice plants were grown at 29 °C with a 12-h light (~10,000 lux)/12-h dark photoperiod in a greenhouse or plant chamber.

2.2 Sectioning and microscopy observation

For paraffin sectioning, samples were fixed in FAA solution (v/v: 50 % ethanol, 5 % acetic acid, 3.7 % formaldehyde) at 4°C for 24 h. Samples were dehydrated in a graded ethanol series followed by a graded ethanol/Histo-Clear series with safranin O staining. Then, tissues were embedded in paraffin and cut into 9-µm sections onto poly-L-lysine coated slides. The sections were de-paraffinized in Histo-Clear.

For thin sectioning [22], samples were fixed in FAA solution at 4 °C for more than 24 h. Samples were then dehydrated with a graded ethanol series and acetone, infiltrated in a series of resin and acetone solutions, immersed in resin for 24 h and embedded in Epon 812 resin. After polymerization at 35 °C for 6 h and 60 °C for around 2 days, 3-µm-thick sections were cut using a Leica 2265 microtome (Leica Microsystems GmbH, Wetzlar, Germany). The sections were stained with toluidine blue.

Differential interference contrast (DIC) microscopy observations were performed as previously described [23, 24]. Samples were observed under a Nikon Eclipse 80i microscope (Nikon, Tokyo, Japan).

2.3 In situ hybridization and quantitative reverse transcription-polymerase chain reaction (qRT-PCR)

In situ hybridization was performed according to our previous method [25, 26], and the probes were subcloned into the pGEM-T Easy vector (Promega, USA) using the following primers: 5′-ATGCCTCAGACCCCTTCGAC-3′ and 5′-TTAATTGGTGGAGGTGGAGC-3′ for *OsNAL2*, 5′-ATGAGGCTTCACCATCTGCATG-3′ and 5′-TTAAGCTTTTCCCTGGGGATG-3′ for *OsWOX4*, and 5′-ATGGAGGCTCTTAGCGGGCGAG-3′ and 5′-ACTAGGACTAGGCACAGCGACA-3′ for *OsWOX5*.

RNA extraction and qRT-PCR were performed as previously described [22, 27], using the following gene specific primers: 5′-CCCGTCGGCGGAGCAGATAAAG-3′ and 5′-AGCGTGCTGAGGGTGAGGAGGG-3′ for *OsWOX4*; and 5′-GGTATTGTTAGCAACTGGGATG-3′ and 5′-GATGAAAGAGGGCTGGAAGA-3′ for *OsACTIN*. The qRT-PCR results are shown as the relative expression levels, which were normalized against those produced by the primers for *OsACTIN*.

2.4 Accession numbers

Sequence data of rice *WOX* genes can be found in the Rice Genome Annotation Project under the following accession numbers: *OsWUS* (LOC_Os04g56780), *OsWOX2* (LOC_Os01g62310), *OsWOX3B* (LOC_Os05g02730),

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