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IN BRIEF

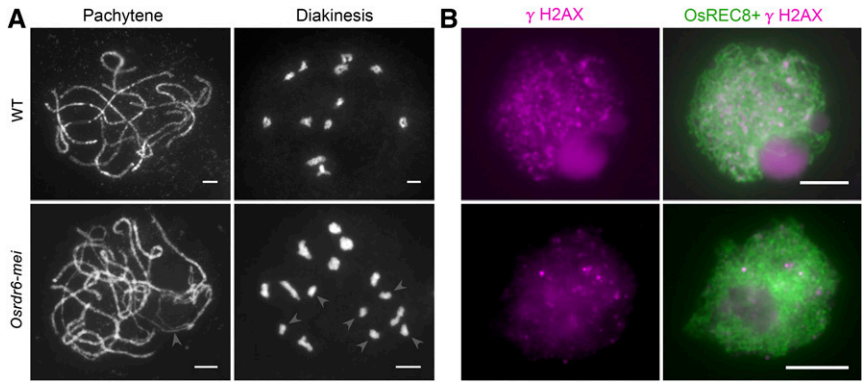
RDR6 Is Essential for Double-Strand Break Formation during Male Meiosis in Rice[OPEN]

Plant RNA-dependent RNA polymerases (RDRs) are essential for the biogenesis of small interfering RNAs (siRNAs). These polymerases function by converting single-stranded RNA transcripts into double-stranded RNAs, which are processed by Dicer-like ribonucleases into 21- to 24-nucleotide siRNAs (reviewed in Borges and Martienssen, 2015). RDR6 in rice (*Oryza sativa*) has been shown to be required for shoot apical meristem and floral organ development (Nagasaki et al., 2007; Song et al., 2012). However, its role in meiosis remains uncharacterized.

Liu et al. (2020) identified a rice mutant that is male- and female-sterile, producing no viable pollen or functional embryo sac. The phenotype is recessive and is controlled by a single nuclear gene. The authors showed that the underlying mutation is a missense point mutation in the *OsRDR6* gene, and this new *Osrdr6* allele was named *Osrdr6-mei* based on the defects in meiosis. A genetic complementation analysis verified *OsRDR6* as the causal gene of the reproductive defects.

To understand the role of OsRDR6 in meiotic progression, the authors examined chromosome behavior during male meiosis in the *Osrdr6-mei* mutant. In the wild type, all homologous chromosomes in meiocytes are paired at prophase I, whereas in the mutant, some homologous chromosomes are not paired. Furthermore, the authors showed that the formation of DNA double-strand breaks (DSBs), which are crucial for crossover formation during meiosis, is perturbed in the *Osrdr6-mei* mutant (see figure).

RNA sequencing detected hundreds of differentially expressed genes between wild-type and *Osrdr6-mei* anthers. Among the downregulated genes, three genes (*OsSDS*, *P31^{comet}*, and *CRC1*) have previously been shown to be essential for meiotic DSB formation in rice. The authors speculated that OsRDR6 regulates meiotic DSB formation by modulating the expression levels of these genes.



OsRDR6 Is Necessary for Meiotic DSB Formation.

(A) Chromosome behaviors at pachytene and diakinesis. Bars = 5 μm.
(B) Detection of DSBs by immunostaining of phosphorylated histone H2AX. WT, wild type. Bars = 5 μm.
(*Adapted from Liu et al. [2020], Figures 1B and 2A.*)

The authors further showed that the abundance of 21-nucleotide small RNAs (21-mers) is dramatically downregulated in the mutant, whereas the abundance of 24-mers is upregulated, suggesting that small RNA biogenesis or turnover processes are dysregulated in the mutant. The 24-nucleotide siRNAs in plants are known to direct DNA methylation. Whole-genome bisulfite sequencing showed upregulation of methylation levels at transposable element loci and regions surrounding non-transposable element genes in the mutant anthers, suggesting that OsRDR6 plays a repressive role in the regulation of DNA methylation.

Based on the collective data, the authors proposed a model whereby the *Osrdr6-mei* mutant accumulates excessive 24-nucleotide small RNAs, which mediate the silencing of genes involved in DSB formation. Since RDR6 is known as a canonical biogenesis factor of multiple types of small RNAs in plants (Borges and Martienssen, 2015), the challenge now is to identify the specific small RNAs, if any, that regulate meiotic DSB formation and to understand how they function during meiosis.

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