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REVIEW

Ten Years of Gene Discovery for Meiotic Event Control in Rice☆

Qiong Luo [a], Yafei Li [b], Yi Shen [b], Zhukuan Cheng [b],*

[a] College of Plant Protection, Yunnan Agricultural University, Kunming 650201, China
[b] State Key Laboratory of Plant Genomics and Center for Plant Gene Research, Institute of Genetics and Developmental Biology, Chinese Academy of Sciences, Beijing 100101, China

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ABSTRACT

Meiosis is the crucial process by which sexually propagating eukaryotes give rise to haploid gametes from diploid cells. Several key processes, like homologous chromosomes pairing, synapsis, recombination, and segregation, sequentially take place in meiosis. Although these widely conserved events are under both genetic and epigenetic control, the accurate details of molecular mechanisms are continuing to investigate. Rice is a good model organism for exploring the molecular mechanisms of meiosis in higher plants. So far, 28 rice meiotic genes have been characterized. In this review, we give an overview of the discovery of rice meiotic genes in the last ten years, with a particular focus on their functions in meiosis.

KEYWORDS: Chromosome pairing; Synapsis; Crossover; Meiosis; Rice

INTRODUCTION

Meiosis is a special kind of cell division that plays significant roles in the life cycle of all sexually propagating eukaryotes. One of the most notable aspects of this process is that meiotic cells undergo a single round of DNA replication and two successive nuclear divisions (meiosis I and meiosis II). Meiosis I is a reductional division, in which homologs segregate away from each other. While in meiosis II, sister chromatids segregate, just resemble that in a haploid mitosis (Gerton and Hawley, 2005). A series of events that arise in the prophase I of meiosis, including homologous chromosomes recognition, pairing, recombination and segregation, are crucial to gamete formation and sexual reproduction (Kleckner, 1996; Zickler and Kleckner, 1999). The entire process of meiosis is shown as Fig. 1 using rice as a model.

In plants, the cytological behaviors of meiotic chromosomes have been analyzed for many decades by a combination of various methods. Cytology, as one of the most commonly used techniques, directly or indirectly showing meiotic chromosomes, mainly relies on different instrument and approaches including bright-field microscopy, electron microscopy (EM), fluorescence *in situ* hybridization (FISH), and protein immunolocalization. Live-cell image using cultured anthers has also been used to illuminate the cell morphology of meiosis in higher plants (Sheehan and Pawlowski, 2009). Recently, new ultra-high-resolution microscopic techniques have been applied to get more superior images of chromatin and chromosome structure during meiosis, especially together with the using of immunolocalization techniques (Carlton, 2008; Shao et al., 2008).

Plants also provide an outstanding system for characterization of molecular mechanisms of major events occurred in meiosis. The expressed meiotic prophase transcripts were well analyzed in lily, which has large reproductive organs and long duration of meiosis to create very specific cDNA libraries (Kobayashi et al., 1993). However, as the model plant for molecular biological research, *Arabidopsis*, even with tiny

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* Corresponding author. Tel: +86 10 6480 6551; fax: +86 10 6480 6595.
E-mail address: zkcheng@genetics.ac.cn (Z. Cheng).

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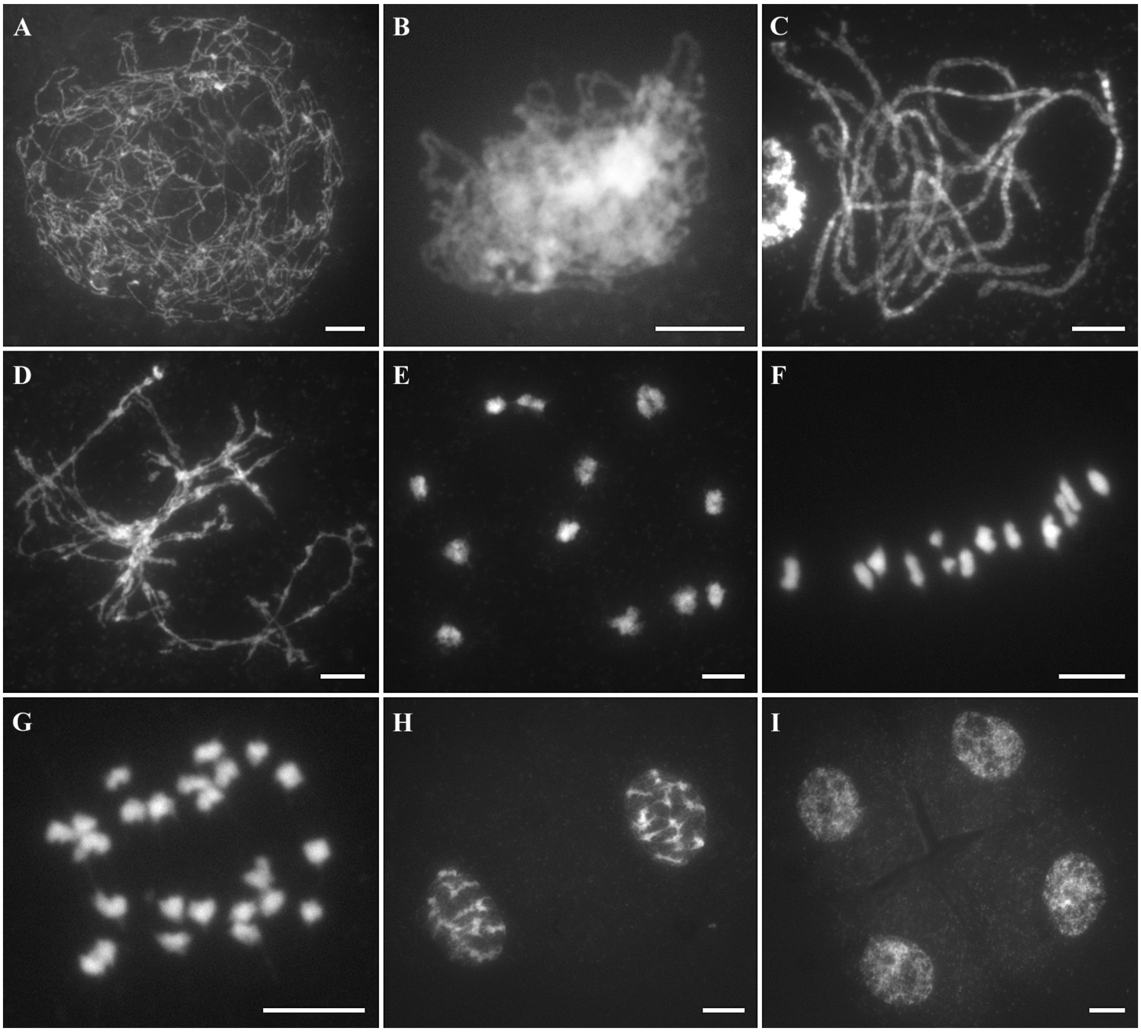

Fig. 1. Male meiosis in the wild type rice.

A: Leptotene, the duplicated sister chromatids start to condense and form thin thread-like structures; **B:** Zygotene, the synaptonemal complexes are to be installed; **C:** Pachytene, the fully synapsed chromosomes appear as a thick thread-like structure; **D:** Diplotene, due to the disassembly of SC, the homologs partially separate except at chiasmata; **E:** Diakinesis, the highly condensed chromosomes show twelve bivalents; **F:** Metaphase I, the homologous chromosomes are pulled by spindle to align along an equatorial plant; **G:** Anaphase I, the homologous pairs are separated toward opposing poles; **H:** Dyad, the haploid sets further condense to form two daughter cells; **I:** Tetrad, meiosis is now completed to produce with four new formed nuclei. Chromosomes were stained with DAPI. Bars, 5 μm.

reproductive organs, has also been fully characterized on molecular mechanisms of the meiotic control due to its well-studied functional genomics. Since the first meiotic gene *AtDMC1* was identified (Klimyuk and Jones, 1997), about eighty meiotic genes have been functionally characterized in *Arabidopsis* (Hamant et al., 2006; Mercier and Grelon, 2008; Osman et al., 2011).

Rice is one of the most significant crops that feed more than 50% of the global population. Besides, the rice genome is ∼430 Mb in size that is smaller than other cereal crops (Eckardt, 2000). With the well-established methods for efficient rice genetic transformation, especially after the completion of rice genome sequencing, rice has become a model organism of molecular biological research. The small size of chromosomes and their moderate number provide advantages for making pachytene chromosome preparations in rice. Thus, rice is also a good model organism for investigating the molecular mechanism of meiosis in higher plants (Cheng, 2013). The first rice meiotic gene, *OsDMC1*, was identified by homologous search (Ding et al., 2001). After that, *PAIR1*, was cloned and functionally characterized by *Tos17* insertion site tagging (Nonomura et al., 2004). The global gene profiling of laser-captured pollen mother cells has also been analyzed to identify the gene subfamilies involved in rice meiosis (Tang et al., 2010). So far, 28 rice meiotic genes have been characterized by *Tos17* or T-DNA insertion site tagging, map-based cloning, as well as RNA interference silence (Table 1). In this review, we give an overview of the discovery of rice meiotic genes in the last ten years, with a particular focus on their functions in meiosis (Fig. 2).

MEIOTIC INITIATION

In eukaryotes, the transition from mitosis to meiosis is the key process of sexual reproduction. Decisive events involved in meiotic initiation occur in G1 phase and is thought to start