



Be my baby: patterning toward plant germ cells

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In flowering plants, germ cells are formed via tightly coordinated patterning processes that facilitate specification of spore mother cells and meiosis during sporogenesis, as well as functional differentiation of germ cells in gametogenesis. Studies using the conventional *Arabidopsis* system and the newly emerged bryophyte system have revealed novel interactions between regulatory factors that restrict the number of spore mother cells, and evolutionarily conserved factors that promote germ cell differentiation. This short review summarizes recent advances in our understanding of the cellular events that lead to the formation of germ cells in plants, and highlights questions that remain to be addressed in the field.

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Introduction

In flowering plants, germ cells are formed via the consecutive patterning events of sporogenesis and gametogenesis [1]. In male sporogenesis, multiple spore mother cells (SMCs; also termed microspore mother cells or pollen mother cells) are specified in anthers, and undergo meiosis to produce microspores (Figure 1a). In gametogenesis, each spore produces a generative cell (GC) and a surrounding vegetative cell (VC). A GC divides further to produce two sperm cells either before or after pollination depending on plant species (Figure 1a) [2]. In female sporogenesis, a single subepidermal cell is specified as an SMC (more specifically termed a megaspore mother cell, MMC) and undergoes meiosis (Figure 1b). In contrast to pollen, only one daughter cell survives as a functional megaspore (FM). In gametogenesis, an FM differentiates into a seven-celled embryo sac (ES) composed of one egg, one central cell, two synergids, and three antipodal cells. Of these, only the egg cell transmits

genetic information to the next generation and hence is considered a germ cell.

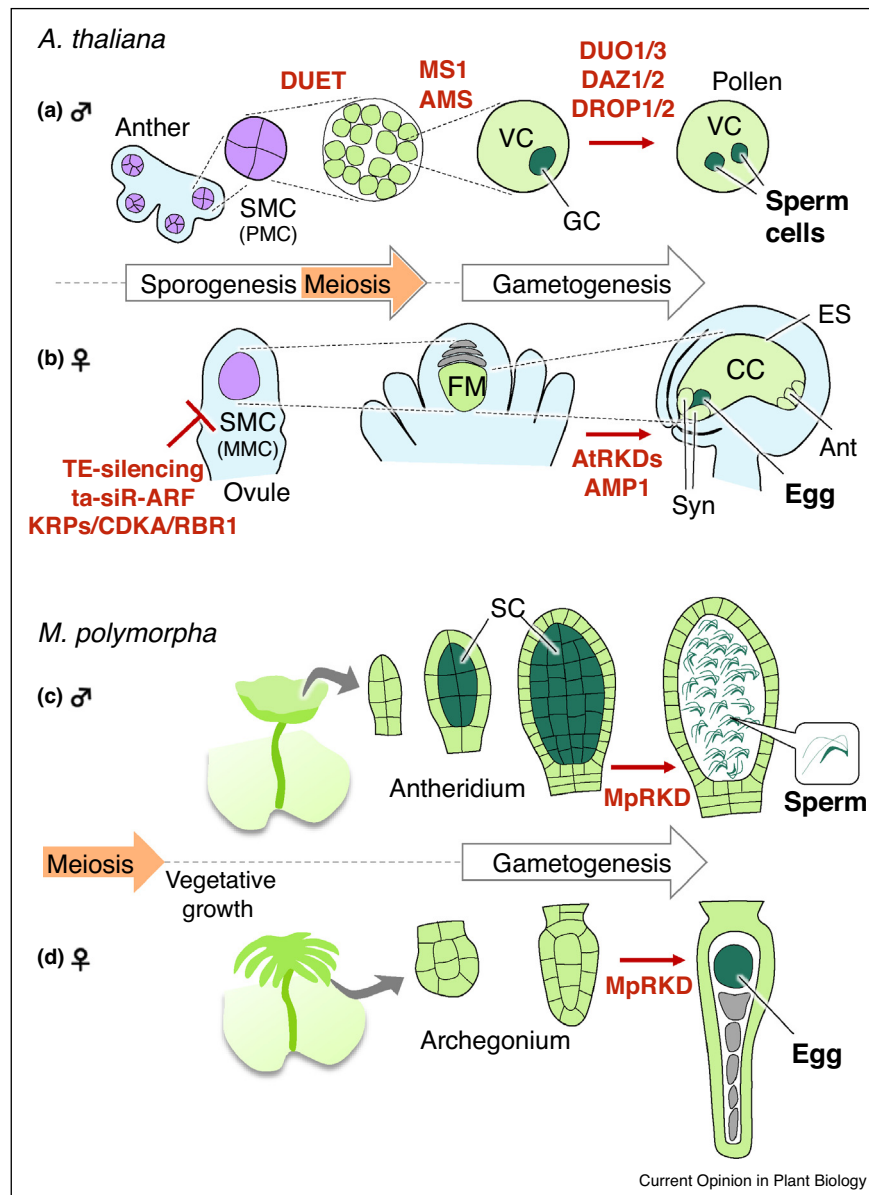
The tightly coordinated cell division and differentiation that occur during plant sporogenesis and gametogenesis suggest that elaborate inter- and intracellular signaling pathways regulate these processes, similar to the pathways that direct somatic organ patterning. However, as germ cells form deep inside floral organs, their patterning mechanisms are difficult to investigate. Recent advances in imaging and sequencing techniques have made it possible to detect weak and low-penetrant phenotypes and to identify their causal mutations. In addition, studies of model bryophyte species, such as *Physcomitrella patens* [3] and *Marchantia polymorpha* [4,5,6^{**},7^{**},8^{*}], have revealed evolutionarily conserved regulatory factors. This short review provides an overview of recent advances in molecular genetic studies of the tissue patterning leading to germ cell formation in plants.

Suppression of transposable elements restricts the number of SMCs

In most flowering plant species, a single subepidermal cell in the distal ovule domain is specified as an MMC (Figure 1b). Recent studies have highlighted the role of small interfering RNA (siRNA)-dependent suppression of transposable elements (TEs) in MMC specification [9,10]. Mutations in genes encoding components of siRNA biogenesis and function, including *ARGONAUTE9* (*AGO9*), *RNA-DEPENDENT RNA POLYMERASE6* (*RDR6*), and *SUPPRESSOR OF GENE SILENCING3* (*SGS3*), result in the formation of multiple MMCs per ovule [11]. In *Arabidopsis* gynoecia, AGO9 mainly binds to 24-nt siRNAs derived from TEs located in the pericentromeric region [12], and indeed, various TE loci were activated in *ago9* ovules, suggesting that AGO9 acts to silence TEs [11,12]. Within ovules, AGO9 was previously shown to be expressed exclusively in the epidermis at both the mRNA and protein levels, and hence was thought to function non-cell-autonomously [11]. However, a recent immunohistochemical analysis revealed that AGO9 proteins transiently accumulate in MMC nuclei, suggesting that they also function in a cell-autonomous fashion [13].

siRNA-dependent TE silencing also operates in pollen development. In the pollen VCs, centromeric heterochromatins are decondensed and TE-derived 24-nt siRNAs accumulate in the cytosol. While these siRNAs were thought to silence TEs in a non-cell-autonomous fashion in sperm cells [14], experimental evidence for this was lacking. By specifically expressing siRNA molecules in

Figure 1



Patterning toward germ cell formation in *Arabidopsis* and liverworts. (a, b) In *Arabidopsis*, SMCs (purple) are specified in anthers and ovules (blue). SMCs undergo meiosis and the resulting daughter cells produce multicellular gametophytes (light green). (a) In anthers, multiple SMCs (or PMCs) are specified per anther. Each SMC undergoes meiosis to give rise to four haploid daughter cells, which all undergo mitosis to produce a generative cell (GC), the germline progenitor (dark green), within a vegetative cell (VC). The GC further divides to produce two sperm cells. Note that in most angiosperms, generative cells divide in growing pollen tubes [2]. Several regulatory factors are known to function in distinct steps toward germ cell differentiation [46–56]. (b) In ovules, a single SMC (or MMC) is specified per ovule, likely by the independent actions of siRNA-dependent TE silencing, ta-siRNA-mediated ovule patterning, and the interplay between cell cycle regulators. The SMC undergoes meiosis to yield four daughter cells, only one of which survives and differentiates into a functional megaspore (FM). After three rounds of syncytial divisions and cellularization, an embryo sac (ES) composed of one central cell (CC) enclosing one egg, two synergids (Syn), and three antipodal cells (Ant) is formed. Only the egg cell can transmit genetic information to the next generation, and hence is considered a germ cell (dark green). Some *AtRKD* genes act after meiosis to produce and arrange the cells in embryo sacs. (c, d) In liverworts, where gametophytes (green) constitute the main plant body, germ cell formation is uncoupled from meiosis. Upon the transition to the reproductive phase, umbrella-like branches with distinct sexual morphologies are formed. (c) In a male branch, reproductive organs termed antheridia form and their inner cells (spermatogenous cells, SCs) constitute the germline (dark green). SCs divide synchronously to produce numerous motile sperm (for simplicity, only a few sperm cells are drawn here). Transcriptome analyses of antheridia revealed expression of conserved factors with those known to regulate pollen and gamete development in *Arabidopsis* [8*]. (d) In a female branch, the most proximal cell of the central cell file divides asymmetrically and the proximal daughter differentiates into an egg (dark green), while the other cells degenerate to form a passage for sperm. MpRKD functions in antheridia and archegonia to promote sperm and egg formation, respectively. Arrows and T-bars indicate activation and inhibition, respectively.

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