Spindle Positioning, Meiotic Nonreduction, and Polyploidy in Plants

Sebastien Andreuzza, Imran Siddiqi*

Centre for Cellular and Molecular Biology, Hyderabad, India

Polyploidy, the state of having more than two sets of chromosomes, is common in flowering plants (angiosperms), including the major crops [1]. Indeed, it is estimated that 30%–80% of the angiosperms are polyploids [2], and most diploid plant species, including Arabidopsis thaliana, show evidence of genome duplication in their ancestry [3]. Polyploidy is accompanied by genome-wide changes in gene expression and epigenetic modifications, leading to phenotypic diversity and rapid adaptation [4]. Doubling of chromosome number can also rescue and stabilize interspecific hybrids that would otherwise show a high degree of sterility due to failures in meiosis. Thus, polyploidy is thought to be a driving force in plant evolution and speciation [5].

In this issue of PLoS Genetics, d’Erfurth and colleagues report on the molecular characterization of the AtPS1 gene and show that lesions in the gene result in unreduced gametes, which are believed to be an important step in polyploidization [6].

While polyploids can originate by an increase of chromosome number either during somatic growth or during meiosis, the major route is now considered to be via the formation of unreduced gametes [7]. The formation of 2n gametes resulting from failure of reduction during meiosis occurs in several plant species and can give rise to triploids that can serve as a bridge to the establishment of an even set of chromosomes in subsequent generations [8]. Unreduced gametes have also been used in breeding schemes for crop improvement wherein beneficial traits have been introduced from diploid relatives into cultivated polyploid species [9].

The paper by d’Erfurth et al. [6] provides the first molecular insight into high-efficiency unreduced pollen formation in plants based on analysis of mutants in the Arabidopsis gene AtPS1 that produce diploid pollen. A range of meiotic abnormalities can give rise to unreduced gamete formation. These can be broadly classified as first or second division restitution (FDR and SDR, respectively) [2]. The occurrence of parallel spindles at meiosis II, resulting in a single plane of cell division and formation of dyad spores, is a frequently found mechanism for 2n gamete formation and is genetically equivalent to FDR in that it results in retention of heterozygosity for centromeric markers (Figure 1). The parallel spindle 1 (ps1) mutant of potato, which produces unreduced pollen by such a mechanism, was described more than 80 years ago [10] and has been used in potato breeding for introgression of beneficial traits in cultivated strains [11]. While the occurrence of unreduced gamete formation in plants has long been recognized, the molecular mechanisms leading to diploid gamete formation have only recently begun to be uncovered [12,13].

d’Erfurth et al. identified the AtPS1 gene using a novel bioinformatics approach. They looked for genes whose expression pattern in microarrays correlated with that of known meiotic genes. Subsequent analysis showed that T-DNA insertions in AtPS1 result in the production of diploid pollen, and triploidy in as many as 30% of progeny. The authors then show, by elegant genetic and cytological experiments, that the atps1 mutant phenotype results from the positioning of the spindles at metaphase II in a parallel orientation instead of in the normal tetrahedral configuration. In most angiosperms, including Arabidopsis, cytokinesis at the time of meiosis occurs only after the second round of chromosome segregation. The occurrence of parallel spindles at meiosis II in atps1 thus results in the formation of one plane of division, and gives rise to dyads containing diploid spores instead of a tetrad of haploid spores (Figure 1).

Interestingly, AtPS1 is a plant-specific gene that encodes a protein containing an N-terminal Forkhead Associated (FHA) domain. FHA domains are phosphoprotein binding modules and are found in proteins that regulate signal transduction pathways in several different contexts: plant meristem homeostasis, DNA repair, and cell cycle control [14]. The identification of AtPS1 opens a new window on the control of meiosis II, particularly in relation to spindle orientation.

The spindle pole body (SPB) and the centrosome are the yeast and animal microtubule-organizing centers (MTOCs), respectively. MTOCs nucleate microtubules and orient the spindle during cell division [15]. Within the SPB and centrosome is a pair of centrioles that contain γ-tubulin, the site of nucleation of microtubules [16]. Although γ-tubulin is conserved in eukaryotes, land plants lack a conspicuous MTOC in the form of a centrosome. Nucleation of microtubules occurs in the cortical cytoplasm and on the nuclear envelope from sites along existing microtubules that are marked by γ-tubulin [17]. Microtubule nucleation in plants therefore appears to be spatially distributed within the cell. A number of reports point to γ-tubulin as the plant MTOC, but the precise mechanism underlying orientation of the spindle and its relation to spindle biogenesis during cell division in plants remains to be established [18]. The identification of AtPS1 and its role in controlling spindle orientation during meiosis II represents an important step in understanding the control of spindle positioning in plants, and determination of its mode of action would be of continued interest. Importantly, because unreduced gametes are of agronomic value, the discovery of AtPS1 may also benefit crop biotechnology.

Citation: Andreuzza S, Siddiqi I (2008) Spindle Positioning, Meiotic Nonreduction, and Polyploidy in Plants. PLoS Genet 4(11): e1000272. doi:10.1371/journal.pgen.10000272

Published November 28, 2008

Copyright: © 2008 Andreuzza, Siddiqi. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

* E-mail: imran@ccmb.res.in

* E-mail: imran@ccmb.res.in
Figura 1. Formación de hilos paralelos durante la meiosis II en *atps1* da esporas no reductoras. La formación de meiosis II, hilos en un plano paralelo a este, resulta en cada mitad del cuerpo de uno de los dos esporas hermanas. El cizallamiento ocurre solo al final de meiosis II, y los planos de cizallamiento se superponen, resultando en un dyad de esporas diploides. doi:10.1371/journal.pgen.1000272.g001

Referencias

1. Leitch AH, Leitch JJ (2008) Genomic plasticity and the diversity of polyploid plants. Science 320: 481–483.
2. Bretagnolle F, Thompson JD (1995) Gametes with the somatic chromosome number: Mechanisms of their formation and role in the evolution of autotetraploid plants. New Phytologist 129: 1–22.
3. Simillion C, Vandepoele K, Van Montagu M, Zabeau M, Van de Peer Y (2002) The hidden duplication past of *Arabidopsis thaliana*. Proc Natl Acad Sci U S A 99: 13627–13632.
4. Mittelsten Scheid O, Afar K, Paszkowski J (2003) Formation of stable epialleles and their para- mutation-like interaction in tetraploid *Arabidopsis thaliana*. Nat Genet 34: 450–454.
5. Otto SP, Whitton J (2000) Polyploid incidence and evolution. Annu Rev Genet 34: 401–437.
6. d’Enfert I, Jolivet S, Friger N, Catrice O, Nowackova M, et al. (2008) Mutations in ATP5I (Arabidopsis thaliana Parallel Spindle 1) lead to the production of diploid pollen grains. PLoS Genet 4: e1000271. doi:10.1371/journal.pgen.1000271.
7. Harlan JR, deWet JMJ (1973) On O. Winge and a Prayer: The origins of polyploidy. Bot Rev 41: 361–389.
8. Henry IM, Dikkes BP, Young K, Watson B, Wu H, et al. (2005) Aneuploidy and genetic variation in the *Arabidopsis thaliana* triploidal response. Genetics 170: 1979–1988.
9. Ramanna MS, Jacobsen E (2003) Relevance of sexual polyploidization for crop improvement—A review. Euphytica 133: 3–18.
10. Fukuda Y (1927) Cytological studies on the development of pollen grains in different races of solanum. Bot Mag Tokyo 41: 459–474.
11. Peloquin SJ, Boiteux LS, Carputo D (1999). Meiotic mutants in potato. Valuable variants. Genetics 153: 1493–1499.
12. Mercier R, Vezon D, Builer E, Motamayor JC, Sellier A, et al. (2001) SWITHC1 (SWI1): A novel gene required for the establishment of sister chromatid cohesion and bivalent formation at meiosis. Genes Dev 15: 1859–1871.
13. Ravi M, Marimuthu MP, Siddiqi I (2008) Gamete formation without meiosis in Arabidopsis. Nature 451(7182): 1121–1124.
14. Li J, Lee GL, Van Doren SR, Walker JC (2000) The FHA domain mediates phosphoprotein interactions. J Cell Sci 113: 4143–4149.
15. Pereira G, Schiebel E (2001) The role of the yeast spindle pole body and the mammalian centrosome in regulating late mitotic events. Curr Opin Cell Biol 13: 762–769.
16. Job D, Valiron O, Oakley B (2003) Microtubule nucleation. Curr Opin Cell Biol 15: 111–117.
17. Paradies A, Wright A, Ehhardt DW (2006) Microtubule cortical array organization and plant cell morphogenesis. Curr Opin Plant Biol 9: 571–578.