The Sounds of Silence: Cell Fate Restriction and RNA Silencing in Plant Ovules

Gamete formation in sexually reproducing plants begins with formation of a “mother cell” that undergoes meiosis to generate haploid spores. Haploid spores further develop into gametophytes within which gametes differentiate. In flowering plants (angiosperms), including crop systems, the female mother cell, called the “megaspore mother cell” (MMC), develops within ovules that grow out of the placenta of carpels. A single MMC forms per ovule from a hypodermal cell located at the apex of the ovule. MMC formation is a key step in plant sexual reproduction as it conditions the production of gametes. Due to its importance as the precursor of the seed, ovule development in angiosperms has been the topic of much research (Drews and Koltunow, 2011). Despite this interest, few factors involved in MMC differentiation remain much of a mystery.

In recent years, identification of new factors involved in MMC differentiation have sparked a renewed interest in ovule development as a model for organ formation and patterning (Pinto et al., 2019). The discovery of a pathway restricting MMC identity to a single cell in ovules in Arabidopsis (Arabidopsis thaliana) was particularly striking (Olmedo-Monfil et al., 2010). The pathway comprises the small RNA processing genes ARGONAUTE9 and RNA DEPENDENT RNA POLYMERASE6 (RDR6). This pathway generates and utilizes 24-nt-long small interfering RNAs that essentially silence transposable elements. In argonaute9 and rdr6 mutants, a proportion of ovules develop more than one enlarged hypodermal cell. However, these extra MMC-like cells largely fail to enter meiosis and rarely produce functional female gametes. Furthermore, the frequency of the phenotype is not fully penetrant in these mutants, suggesting that additional factors remain to be identified.

To identify these factors and characterize the pathway further, the groups of Xuemei Chen and Yuan Qin performed a genetic screen for enhancer mutations in the rdr6 background in the study by Su et al. (2017). They uncovered mutations in TEX1 that encodes a subunit of a conserved complex that exports small RNA precursors out of the nucleus to be processed. They further found that TEX1 represses AUXIN RESPONSE FACTOR3 (ARF3). ARF3 encodes a transcription factor that is activated in the presence of the plant hormone auxin, which is a regulator of cell growth and differentiation. In the wild type, TEX1 restricts ARF3 protein synthesis to the median domain called the chalaza. In absence of the repressive signal, the authors detected ARF3 protein in the apical part of the ovule, called the nucellus. This indicates that ARF3 is sufficient to promote part of the MMC identity program when expressed in the nucellus.

Chen and Qin then sought to identify the cells of the nucellus where ARF3 functions to promote MMC identity. Is it a direct (cell-autonomous) or indirect (non-cell-autonomous) effect? To answer this, Su et al. (2020) used a non-degradable ARF3 mRNA (ARF3m) that enables ARF3 protein synthesis in the nucellus, and which mimicked the tex1 mutant phenotype (Su et al., 2017). Using different promoters to drive ARF3m expression in the wild type, the authors observed that whereas expression or ARF3m in epidermal cells had little effect, expression of ARF3m in hypodermal cells surrounding the MMC triggered MMC identity in these cells (see figure). These results establish that ovule hypodermal cells, but not epidermal cells, are “competent” to acquire MMC fate and that ARF3 functions cell-autonomously. However, using a similar approach, Su et al. (2020) mapped the origin of the small RNA signal to epidermal cells of the nucellus.

The authors thus identify a mobile RNA signal that establishes a boundary between the nucellus and the chalaza; this same signal prevents ARF3 expression in hypodermal cells surrounding the MMC. This work shows that the angiosperm
ovule, contrary to its apparent simplicity, is an intricately patterned and complex organ. Furthermore, Su et al. (2020) identify a direct inducer of MMC identity, suggesting that ARFs and auxin may control early steps of MMC differentiation in plants.

Sebastien Andreuzza
DBT-Cambridge Lecturer
Department of Plant Sciences
University of Cambridge
United Kingdom
Center for Cellular and Molecular Biology

Hyderabad, India
sea60@cam.ac.uk
ORCID ID: 0000-0002-5547-2692

REFERENCES

Drews, G.N., and Koltunow, A.M.G. (2011). The female gametophyte. The Arabidopsis Book 9: e0155.

Olmedo-Monfil, V., Durán-Figueroa, N., Arteaga-Vázquez, M., Demesa-Arévalo, E., Autran, D., Grimani, D., Slotkin, R.K., Martienssen, R.A., and Vieille-Calzada, J.-P. (2010). Control of female gamete formation by a small RNA pathway in Arabidopsis. Nature 464: 628–632.

Su, Z., Wang, N., Hou, Z., Li, B., Li, D., Liu, Y., Cai, H., Qin, Y., and Chen, X. (2017). The THO complex non-cell-autonomously represses female germline specification through the TAS3-ARF3 module. Curr. Biol. 27: 1597–1609.e2.

Pinto, S.C., Mendes, M.A., Coimbra, S., and Tucker, M.R. (2019). Revisiting the female germline and its expanding toolbox. Trends Plant Sci. 24: 455–467.

Su, Z., Wang, N., Hou, Z., Li, B., Li, D., Liu, Y., Cai, H., Qin, Y., and Chen, X. (2020). Regulation of female germline specification via small RNA mobility in Arabidopsis. Plant Cell 32: 2842–2854.
The Sounds of Silence: Cell Fate Restriction and RNA Silencing in Plant Ovules
Sebastien Andreuzza

*Plant Cell* 2020;32;2673-2674; originally published online August 4, 2020;
DOI 10.1105/tpc.20.00599

This information is current as of November 5, 2020

| References | This article cites 5 articles, 1 of which can be accessed free at: /content/32/9/2673.full.html#ref-list-1 |
| Permissions | https://www.copyright.com/ccc/openurl.do?sid=pd_hw1532298X&issn=1532298X&WT.mc_id=pd_hw1532298X |
| eTOCs | Sign up for eTOCs at: http://www.plantcell.org/cgi/alerts/ctmain |
| CiteTrack Alerts | Sign up for CiteTrack Alerts at: http://www.plantcell.org/cgi/alerts/ctmain |
| Subscription Information | Subscription Information for *The Plant Cell* and *Plant Physiology* is available at: http://www.aspb.org/publications/subscriptions.cfm |