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### Paternal genomic imprinting in plants

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#### Abstract

Expression of paternal alleles for 20 loci expressed during early seed development in *Arabidopsis* was undetectable during early embryo and endosperm development, suggesting the presence of imprinting of the paternal genome.

# Significance and context

Studies in embryogenesis and seed development in plants have a long history, yet the underlying mechanism for the transition from the maternal (haploid egg) to the zygotic (diploid sporophyte) phase, along with many other events that follow to make an embryo in the seed, remains largely unknown. Vielle-Calzada *et al.* raise the interesting possibility that the paternal genome may be silenced and genomic imprinting may be occurring during early embryo and endosperm development in *Arabidopsis*. Imprinting is a process by which the expression of the maternal or paternal allele at a locus in the embryo is suppressed epigenetically by chromosomal modification that reflects the parent of origin. In plants, only a few genes so far are known to be imprinted in the endosperm; the *R* locus in maize, which controls anthocyanin production, is a well-known example. In *Arabidopsis*, the maternal-effect mutation at the *MEDEA* locus appears to depend on genomic imprinting. Vielle-Calzada *et al.* have attempted to determine whether other loci may be imprinted during seed development in *Arabidopsis*. Although this work raises more questions than it answers, it provides a good framework in which ideas can be rigorously tested in the study of this fascinating aspect of plant development.

#### Key results

To screen for loci that are expressed during early ovule and seed development, Vielle-Calzada *et al.* used enhancer-detector lines that contain *Ds* mobile elements linked to a *uidA* gene, which encodes  $\alpha$ -glucuronidase (GUS). They identified 19 lines that show GUS expression in the developing embryo and/ or endosperm tissue after fertilization. To determine whether the expression pattern is the result of transcription from one or both of the parental alleles, reciprocal crosses were performed. When wild-type pollen was crossed to the transposant lines, all of the progeny showed GUS expression patterns identical to the self-fertilized transposant lines. In contrast, when transposant pollen was crossed to wild-type lines, GUS expression was undetectable. To confirm that the GUS expression pattern reflected the expression of endogenous genes, *in situ* hybridization was performed using an RNA probe specific for a

gene tagged by one of the *Ds* elements in one transposant line. Additionally, to determine whether other genes that are expressed during early embryogenesis could have paternal allele silencing, single-nucleotide polymorphism (SNP) in the *PROLIFERA (PRL)* and *EMB30/GNOM* genes was exploited to detect allele-specific transcripts in whole siliques (seed pods) using reverse transcription polymerase chain reaction (RT-PCR). The assays showed that the transcripts from the maternal allele were present, but that transcripts from the paternal allele were not detectable.

# Links

Enhancer and gene trap lines from a number of sources are available from the *Arabidopsis* Biological Resource Center (ABRC) through the *Arabidopsis* information management system and the Nottingham *Arabidopsis* Stock Centre. The *Arabidopsis* Information Resource provides access to approximately 39,000 SNPs and insertions/deletions (INDELs), including the Cereon *Arabidopsis* polymorphism collection generated by Cereon Genomics and SNP sequences generated by the Stanford Genome Center (GSC).

### Reporter's comments

This paper provides a fascinating example of a biological question that can be addressed by exploiting all the great tools developed and data obtained in the past few years, such as enhancer/gene trap lines, microarrays and SNPs. But some of the supporting data in the paper may need to be verified. For instance, the only example of an *in situ* hybridization experiment illustrated in the paper shows a relatively weak signal, and appropriate negative controls are not shown. The authors will have a much stronger case if *in situ* hybridization for all the loci confirms the GUS expression pattern. Similarly, the RT-PCR experiments were performed on whole siliques, where the amount of maternal DNA relative to paternal (pollen-derived) DNA is quite large. Although the control titration experiment showed that 1:100 dilution of Columbia ecotype:Landsberg erecta ecotype DNA still allowed detection of both polymorphic PCR products, it is not quite comparable to using a single genetically homogeneous tissue, such as the embryo or endosperm, and the RNAs extracted from it. Performing the titration using RNA from a tissue in which transcripts are not silenced would also have been a good positive control for the reciprocal cross experiments. Alternatively, RT-PCR on isolated embryos, rather than on whole siliques, might have provided stronger support. The possibility of paternal genome silencing during early embryogenesis is interesting, and seems worth pursuing if imprinting at all the loci tested in this work is confirmed and if more loci that might be imprinted can be identified and studied. One possibility would be to exploit microarray analysis using pollen, ovule and embryo/endosperm tissue as a primary screen for this class of genes.

# Table of links

#### Nature

Arabidopsis information management system

Nottingham Arabidopsis Stock Centre

The Arabidopsis Information Resource

Cereon Arabidopsis polymorphism collection

SNP sequences

#### References

1. Vielle-Calzada J-P, Baskar R, Grossniklaus U: Delayed activation of the paternal genome during seed development. Nature. 2000, 404: 91-94. 0028-0836