

# UC Davis

## UC Davis Previously Published Works

### Title

The ULT trxG factors play a role in arabidopsis fertilization

### Permalink

<https://escholarship.org/uc/item/0z50007g>

### Journal

Plant Signaling & Behavior, 9(12)

### ISSN

1559-2316

### Authors

Monfared, Mona M  
Fletcher, Jennifer C

### Publication Date

2014-12-02

### DOI

10.4161/15592324.2014.977723

Peer reviewed

## The ULT trxB factors play a role in arabidopsis fertilization

Mona M Monfared<sup>†</sup> and Jennifer C Fletcher\*

Plant Gene Expression Center; USDA-ARS/UC Berkeley; Albany, CA USA and Department of Plant and Microbial Biology; University of California; Berkeley, CA USA;

<sup>†</sup>Present Address: Santa Clara University Department of Biology; Santa Clara, CA USA

**T**rithorax group (trxB) and Polycomb group (PcG) proteins are epigenetic modifiers that play key roles in eukaryotic development by promoting active or repressive gene expression states, respectively. Although PcG proteins have well-defined roles in controlling developmental transitions, cell fate decisions and cellular differentiation in plants, relatively little is known about the functions of plant trxB factors. We recently determined the biological roles for the *ULT1* and *ULT2* trxB genes during *Arabidopsis* vegetative and reproductive development. Our study revealed that *ULT1* and *ULT2* genes have overlapping activities in regulating *Arabidopsis* shoot and floral stem cell activity, and that they have a redundant function in establishing the apical-basal polarity axis of the gynoecium. Here we present data that *ult1* and *ult1 ult2* siliques contain a significant proportion of aborted ovules, supporting an additional role for *ULT1* in *Arabidopsis* fertility. Our results add to the number of plant developmental processes that are regulated by trxB activity.

Plant development occurs in distinct embryonic, vegetative and reproductive phases that are driven by coordinated changes in global gene expression patterns. The cellular memory of stable gene expression states during development is mediated by the opposing activities of Polycomb group (PcG) factors and trithorax group (trxB) factors. PcG factors maintain their target genes in a silenced state by depositing repressive histone methylation marks, whereas trxB factors sustain

target gene transcription by depositing activating marks.<sup>1,2</sup> In *Arabidopsis*, 3 distinct PcG complexes play key roles in mediating developmental phase transitions.<sup>3,4</sup> Among these, the FERTILIZATION INDEPENDENT SEED (FIS) complex is required for female gametophyte and early seed development.<sup>5,6</sup> In contrast, little is known about the contribution of trxB factors to these essential developmental functions.

*ULT1* and the closely related *ULT2* gene encode SAND domain proteins that function as trxB factors. *ULT1* regulates the expression of hundreds of downstream target genes during vegetative and reproductive development.<sup>7</sup> *ULT1* activity counteracts the deposition of repressive H3K27me3 marks by CURLY LEAF-containing PRC2 complexes,<sup>8</sup> as well as EMBRYONIC FLOWER1-containing PRC1 complexes.<sup>7</sup> *ULT1* also promotes the deposition of active H3K4me3 marks, although the protein itself does not contain a methyltransferase domain.<sup>9</sup> *ULT1* and *ULT2* are both expressed in the shoot and floral meristems as well as in developing rosette leaves, stamens and carpels.<sup>9</sup> Consistent with their expression domains, the 2 genes have overlapping roles in restricting shoot and floral stem cell accumulation and promoting basal carpel polarity.<sup>10</sup>

During gamete formation, both *ULT1* and *ULT2* are expressed in the tapetum tissue of the anthers and in ovules,<sup>9</sup> but no role for these genes in gametogenesis has yet been described. To address the question of whether the ULT trxB factors contribute to *Arabidopsis* fertility, we analyzed silique morphology and seed formation in wild-type *Ler* and *ult* homozygous

**Keywords:** *Arabidopsis*, development, fertility, ovule, Polycomb group, trithorax group, ULT

This article not subject to US copyright law

\*Correspondence to: Jennifer C Fletcher; Email: [jfletcher@berkeley.edu](mailto:jfletcher@berkeley.edu)

Submitted: 08/28/2014

Accepted: 09/08/2014

<http://dx.doi.org/10.4161/15592324.2014.977723>



**Figure 1.** Developing seeds within (A) wild-type Ler, (B) *ult1-2*, (C) *ult2-3*, and (D) *ult1-2 ult2-3* siliques. Arrows indicate the positions of aborted ovules. Scale bar, 0.5 mm.

single and double mutant plants. Both *ult1-2*, an EMS-induced null allele of *ULT1*,<sup>9</sup> and *ult2-3*, an EMS-induced null allele of *ULT2*,<sup>10</sup> were used in the experiments. Siliques from Ler, *ult1-2*, *ult2-3* and *ult1-2 ult2-3* plants grown at 21°C under constant light conditions were harvested 11–13 d after pollination, manually dissected to display the developing seeds, and visualized using a Zeiss Axio-phot microscope.

We observed that both *ult1* and *ult1 ult2* siliques had normal morphology but contained aborted ovules. In wild-type and *ult2-3* siliques, 2 rows of developing green seeds filled the siliques without gaps between them (Fig. 1A and C). In contrast, *ult1-2* (Fig. 1B) and *ult1-2 ult2-3* (Fig. 1D) siliques contained aborted ovules, seen as small white structures, at multiple positions along the apical-basal axis. Aborted ovules were distributed throughout the carpels, rather than being found primarily at the apex or base (Fig. 1B and D).

Quantitative analysis revealed that 44.5% of the ovules in *ult1-2* siliques aborted, as compared to 2.5% in wild-type Landsberg *erecta* (Ler) siliques (Table 1). These data indicate that *ULT1* is necessary for normal ovule and/or very early seed development. In contrast, only

5.6% of *ult2-3* ovules aborted (Table 1), suggesting that *ULT2* is unlikely to play a role in fertility. The function of *ULT1* in fertility is also reflected by the high rate of ovule abortion in *ult1-2 ult2-3* siliques (Table 1).

Our data indicate that *ULT1* is necessary for ovules to be properly fertilized and develop into viable seeds. To rule out the possibility that aberrant development of maternal sporophytic tissue is the cause of ovule abortion in *ult1* siliques, we observed the morphology of the mature ovules just prior to fertilization. All *ult1-2* and *ult1-2 ult2-3* ovules had a wild-type appearance, suggesting that malformed integuments were not the cause of the subsequent abortion. Further investigation will be required to determine if aberrant development of the embryo sac is the cause of ovule abortion. Similarly, further experiments are needed to assess if pollen function is compromised in *ult* mutants, contributing to the high rate of ovule abortion.

Our observation of frequent ovule abortion in *ult1* and *ult1 ult2* mutants has uncovered a new function for *ULT1* in *Arabidopsis* development. Our data provide evidence that *trxG* factors, like PcG factors, are required for

successful plant fertilization. As a known *trxG* gene, *ULT1* may be part of a system that counteracts the repressive effects of the PcG proteins that are known to have a role in plant fertility.

#### Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

#### Funding

This work was funded by a grant from the National Science Foundation (IOS-1052050) to J.C.F. Addendum To: Monfared, M.M., Carles, C.C., Rossignol, P., Pires, H.R. and Fletcher, J.C. (2013). The *ULT1* and *ULT2* *trxG* genes play overlapping roles in *Arabidopsis* development and gene regulation. *Molecular Plant* 6: 1564–1579.

#### References

- Schwartz YB and Pirrotta V. Polycomb silencing mechanisms and the management of genomic programmes. *Nat Rev Genet* 2007; 8:9-22; PMID:17173055
- Zheng B. and Chen X. Dynamics of histone H3 lysine 27 trimethylation in plant development. *Curr Opin Plant Biol* 2011; 14, 123-129; PMID:21330185; <http://dx.doi.org/10.1016/j.pbi.2011.01.001>
- Bemer M and Grossniklaus U. Dynamic regulation of Polycomb group activity during plant development. *Curr Opin Plant Biol* 2012; 15:523-529; PMID:22999383; <http://dx.doi.org/10.1016/j.pbi.2012.09.006>
- Holec S and Berger F. Polycomb Group complexes mediate developmental transitions in plants. *Plant Physiol* 2012; 158:35-43; PMID:22086420; <http://dx.doi.org/10.1104/pp.111.186445>
- Chaudhury A M, Ming L, Miller C, Craig S, Dennis ES, Peacock WJ. Fertilization-independent seed development in *Arabidopsis thaliana*. *Proc Natl Acad Sci USA* 1997; 94:4223-4228; PMID:9108133
- Ohad N, Margossian L, Hsu YC, Williams C, Repetti P, Fischer RL. A mutation that allows endosperm development without fertilization. *Proc Natl Acad Sci USA* 1996; 93:5319-5324; PMID:11607683
- Pu L, Liu MS, Kim SY, Chen LF, Fletcher JC, Sung ZR. *EMBRYONIC FLOWER1* and *ULTRAPETALA1* act antagonistically on *Arabidopsis* development and stress response. 2013; *Plant Physiol* 162:812-830;

**Table 1.** Ovule abortion in wild-type *Arabidopsis* and *ult* mutant plants

Genotypes	Normal ovules	Aborted ovules	Total ovules	% aborted
Ler	4176	107	4283	2.5
<i>ult1-2</i>	3215	2574	5789	44.5
<i>ult2-3</i>	1976	118	2094	5.6
<i>ult1-2 ult2-3</i>	3356	2125	5481	38.8

- PMID:23632855; <http://dx.doi.org/10.1104/pp.112.213223>
- 8 Carles CC and Fletcher JC. The SAND domain protein ULTRAPETALA1 acts as a trithorax group factor to regulate cell fate in plants. *Genes Dev* 2009; 23:2723-2728; PMID:19952107; <http://dx.doi.org/10.1101/gad.1812609>
- 9 Carles CC, Choffnes-Inada D, Reville, K, Lertpiriyapong K and Fletcher JC. *ULTRAPETALA1* encodes a putative SAND domain transcription factor that controls shoot and floral meristem activity in Arabidopsis. *Development* 2005; 132:897-911; PMID:15673576
- 10 Monfared M M, Carles CC, Rossignol P, Pires HR and Fletcher JC. The ULT1 and ULT2 trxB genes play overlapping roles in Arabidopsis development and gene regulation. *Mol Plant* 2013; 6:1564-1579; PMID:23446032; <http://dx.doi.org/10.1093/mp/sst041>