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Relative dependence: Autophagy in the mother plant and the embryo contributes to Arabidopsis seed development

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ABSTRACT

Our study focused on the role of autophagy in seed development and its impact on nutrient remobilization from the mother plant and seed physiology. By conducting reciprocal crosses between wild-type (WT) and autophagy-deficient (*atg* mutant) *Arabidopsis thaliana* (Arabidopsis) plants, we differentiated between autophagy in the maternal tissue and the embryo. We found that autophagy in the maternal tissues did not affect embryo development, yet led to reduced growth of etiolated F1 *atg* maternal plants, possibly resulting from altered protein accumulation in the seeds. Surprisingly, F1 seeds from maternal *atg* mutants showed faster germination due to altered seed coat structure, which probably reduced seed longevity. Our results highlight the tissue-specific functions of autophagy, providing insight into the various roles of autophagy in seed development.

Abbreviations: Arabidopsis: *Arabidopsis thaliana; ATG*: autophagy-related; WT: wild-type.

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Seeds are a crucial source of food and feed, providing around 70% of the world's human caloric intake. They contain storage compounds such as starch, storage lipids, and storage proteins, which contribute to their nutritional value. During germination, these storage compounds are broken down to support seedling growth until photosynthesis can sustain the plant. Beyond nutrient content, the availability of these compounds affects seed longevity, which refers to the viability of seeds after dry storage. Those features are essential for germination, crop productivity, and food security.

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Generally, nutrient trafficking and partitioning between source and sink tissues play an essential role in seed development. Nutrients from source tissues (which assimilate compounds from the environment) are utilized for organ growth and then transported to sink tissues (which use nutrients) through catabolism and recycling. The nutrient demands of sink tissues can influence the export from the source. The relationship between plant sources and sinks has been extensively studied, although there is still a debate regarding the primary factor/s controlling plant growth and yield. In annual plants, seed development is accompanied by nutrient remobilization, with both carbon (sucrose) and nitrogen (glutamine and asparagine) transported from the mother plant (source tissue) to the developing seeds (sink tissue).

Macroautophagy (hereafter autophagy) is an important cellular process in eukaryotes that facilitates the recycling and utilization of nutrients. Overexpressing *autophagy-related* (*ATG*) genes in *Arabidopsis thaliana* (Arabidopsis) has been shown to enhance seed yield and increase fatty acid content. Conversely, autophagy-deficient (*atg)* mutants display heightened sensitivity to carbon and nitrogen starvation, premature senescence, reduced crop yield, delayed germination, and impaired seedling establishment. Autophagy-mediated nutrient remobilization is essential for optimizing plant growth, development, and reproductive success. Manipulating *ATG* genes holds the potential to improve crop productivity. Autophagy also plays a dual role in seed development, affecting nutrient mobilization from the mother plant to the seed, and influencing storage protein content and processing.

To further investigate the role of autophagy in seed development, we recently conducted reciprocal crosses between wild-type (WT) and *atg* mutant (*atg5-1* or *atg7-2*) Arabidopsis plants to distinguish between the role of autophagy in the mother plant (source tissue) and the embryo (sink tissue). Through that, we generated a heterozygote embryo, covered by a mutant seed coat, and grown in a mutant mother plant (Figure 1A). We found that autophagy in the mother plant did not significantly affect embryo development and seed weight. Moreover, the F1 progeny displayed functional autophagy, as they exhibited a response to carbon starvation similar to WT plants (Figure 1B). Interestingly, etiolated seedlings from maternal *atg* mutant plants had shorter hypocotyls, suggesting altered storage compound deposition. However, lipidomics analysis did not reveal significant differences in lipid content between WT and *atg* mutant maternal seeds. In contrast, we found that F1 seeds from maternal mutants had reduced protein levels, indicating impaired nitrogen but not carbon remobilization from the mother plant (Figure 1C). Interestingly, we did not observe differences in storage protein processing, suggesting that this phenotype is specifically affected by autophagy deficiency in the embryo or endosperm. Further research is

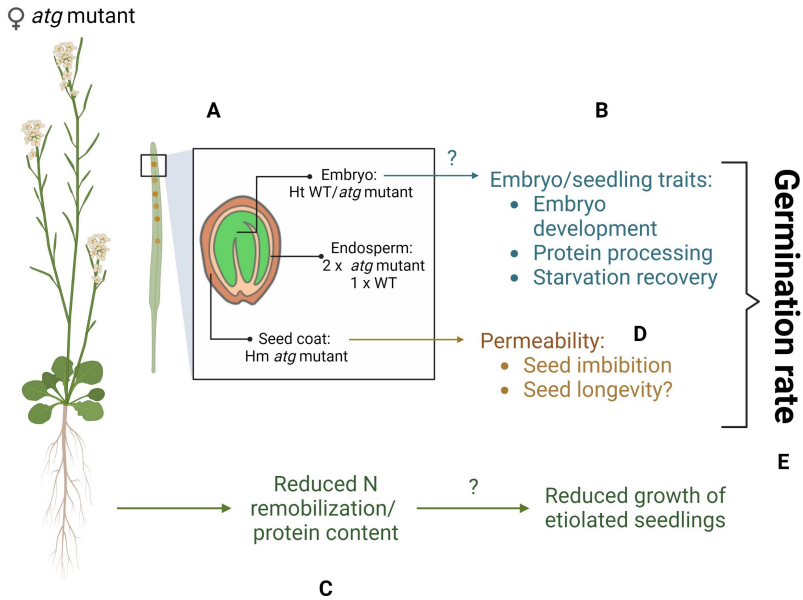

Figure 1. Autophagy plays a complex role in seed development, depending on the tissue in which it functions Seeds generated by a cross between an *atg* mutant plant and WT pollen exhibit distinct genotypes in different tissues (A). The phenotypic characteristics of *atg* mutant seeds are influenced by the genotype of the embryo in some aspects (B), while in others, they depend on nutrient supply from the mother plant (C) and the structure of the seed coat (D). The combined rates of radicle protrusion and seed permeability are assumed to determine the germination rate (E). Created with BioRender.com

needed to explore the role of autophagy in storage protein accumulation in seeds.

Surprisingly, while *atg* mutant seeds showed a delay in germination, F1 seeds from maternal *atg* mutant plants exhibited earlier germination, compared to WT seeds, potentially due to increased water permeability combined with a normal autophagy in the embryo (Fig. 1D, E). Seeds from maternal *atg* mutants displayed reduced mucilage content and experienced structural changes at both the cellular and overall organ levels, as indicated by seed coat analysis. Artificial aging experiments supported a link between the altered seed coat and reduced seed longevity in *atg* mutants (Fig. 1D). Overall, our findings suggest that autophagy in the mother plant influences protein content, seed coat properties, and germination characteristics in the progeny, while the lipid content remains largely unaffected.

In conclusion, our study suggests that the seed phenotype of *atg* mutants is a complex phenotype resulting from the lack of autophagy in both the mother plant and the embryo. In addition, it demonstrates

how autophagy deficiency in one organ can cause opposite effects than in the whole plant. This emphasizes the importance of studying autophagy in a tissue-specific manner while considering the overall plant context, mainly when investigating source-sink aspects. Generating plant lines with selective downregulation of autophagy in specific tissues or at particular time points will provide a valuable tool for further investigation. One example is downregulating autophagy in the embryo to understand its role in generating the compound phenotype of *atg* mutant seeds [1].

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Reference

[1] O. A. Erlichman *et al*., "Autophagy in maternal tissues contributes to Arabidopsis seed development," *Plant Physiol*., Jun. 2023, doi: 10.1093/PLPHYS/KIAD350.