

WHIRLY proteins maintain seed longevity by effects on seed oxygen signalling during imbibition

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The WHIRLY (WHY) family of DNA/RNA binding proteins fulfil multiple but poorly characterized functions in plants. We analysed WHY protein functions in the Arabidopsis *Atwhy1*, *Atwhy3*, *Atwhy1why3* single and double mutants and wild type controls. The *Atwhy3* and *Atwhy1why3* double mutants showed a significant delay in flowering, having more siliques per plant but with fewer seeds per silique than the wild type. While germination was similar in the unaged high-quality seeds of all lines, significant decreases in vigour and viability were observed in the aged mutant seeds compared to the wild type. Imbibition of unaged high-quality seeds was characterised by large increases in transcripts that encode proteins involved in oxygen sensing and responses to hypoxia. Seed ageing resulted in a disruption of the imbibition-induced transcriptome profile such that transcripts encoding RNA metabolism and processing became the most abundant components of the imbibition signature. The imbibition-related profile of the *Atwhy1why3* mutant seeds, was characterised by decreased expression of hypoxia-related and oxygen metabolism genes even in the absence of ageing. Seed ageing further decreased the abundance of hypoxia-related and oxygen metabolism transcripts relative to the wildtype. These findings demonstrate that the WHY1 and WHY3 proteins regulate the imbibition-induced responses to oxygen availability and hypoxia, and protect seeds against ageing.