IN BRIEF

A New Chlorophyll Degradation Pathway

Chlorophyll degradation is vital during leaf senescence and fruit ripening, as it allows for recycling of nitrogen and other nutrients and for protection from buildup of phototoxic chlorophyll intermediates (Hörtensteiner, 2006). The first steps in chlorophyll breakdown are the removal of the phytol tail (dephytylation) and the central Mg atom. It has been thought that dephytylation typically occurs first, catalyzed by the enzyme chlorophyllase, which converts chlorophyll to phytol and chlorophyllide. Removal of Mg subsequently converts chlorophyllide to pheophorbide. However, Arabidopsis contains just two known chlorophyllases, CHL1 and CHL2, and it has been shown that neither of these isoforms is localized to plastids, and double knockout mutant plants still are able to degrade chlorophyll during leaf senescence (Schenk et al., 2007). Now, Schelbert et al. (pages 767–785) report the discovery of a novel plastid-localized enzyme, pheophytinase, that is essential for chlorophyll breakdown during leaf senescence.

Based on the results of Schenk et al. (2007), Schelbert et al. set out to discover the true chlorophyllase that functions during leaf senescence, using a combination of bioinformatics and reverse genetics. They reasoned that the protein should contain an α/β hydrolase fold characteristic of enzymes that catalyze an ester hydrolysis. Of 462 such proteins found in the Arabidopsis genome, the search was narrowed to 30 with predicted localization in chloroplasts and no previously defined function, and just three of these corresponded to genes that showed a leaf senescence-related pattern of expression. T-DNA insertion mutants of these genes were obtained, and one of these mutants showed a stay-green phenotype, indicating a lesion in chlorophyll breakdown during leaf senescence (see figure). The authors show that the corresponding enzyme is a pheophytinase (PPH), which specifically dephytylates the Mg-free chlorophyll pigment pheophytin and does not act on chlorophyll. They also found that putative PPH orthologs are common in eukaryotic photosynthesizing organisms, suggesting that the pathway may be highly conserved.

This work indicates that the previously accepted pathway of chlorophyll breakdown must be revised. During leaf senescence, removal of Mg to form pheophytin is likely the first step, followed by removal of the phytol tail, catalyzed by PPH. Chlorophyllide, which is the last precursor of chlorophyll biosynthesis, is most likely not an intermediate of breakdown. Therefore, chlorophyll synthesis and breakdown are metabolically separated during leaf senescence. Based on patterns of expression, chlorophyllase may play a role in chlorophyll breakdown during fruit ripening (Azoulay Shemer et al., 2008) and response to pathogens and wounding (Kariola et al., 2005).

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REFERENCES


Deficiency of PPH causes a stay-green phenotype. Leaves after 5 d of dark-induced senescence are shown, left to right: wild type (Col-0), pph-1 mutant, complementation of the stay-green phenotype of pph-1 with a 3SS-PPH cDNA construct, and lack of complementation using a construct harboring a mutation of the proposed active-site Ser residue (3SS-PPH<sub>5221A</sub>). (Image from Figure 2 of Schelbert et al. [2009].)
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*Plant Cell* 2009; 21:700; originally published online March 20, 2009;  
DOI 10.1105/tpc.109.210313  

This information is current as of January 8, 2018

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