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IN BRIEF

Phytol from Degradation of Chlorophyll Feeds Biosynthesis of Tocopherols

Tocopherols, a subclass of tocochromanols that contain a phytol attached to the head group, act as antioxidants to protect lipids from oxidative damage, a particularly important function in chloroplasts and for seed longevity (reviewed in Maeda and DellaPenna, 2007). One pathway for tocopherol biosynthesis involves de novo synthesis from geranylgeranyl-diphosphate; the other pathway uses phytols derived from chlorophyll (see figure). In the latter pathway, the phytol kinase VITAMIN E DEFICIENT5 (VTE5) phosphorylates phytol; the phytyl-phosphate then undergoes a second phosphorylation to form phytyl-diphosphate, which feeds into tocopherol biosynthesis.

The phytyl-phosphate kinase was identified by a phylogenetic approach, comparing the genomic sequences of plants with those of algae and bacteria that contain chlorophyll and conduct oxygenic photosynthesis (Seaver et al, 2014). Here, **vom Dorp et al. (2015)** examine the *Arabidopsis thaliana* gene encoding this candidate kinase, terming it *VTE6*, based on subsequent characterization. Consistent with a role in tocopherol biosynthesis, VTE6 localizes to the chloroplast envelope. Moreover, *vte6* mutants showed increased levels of phytyl-phosphate and severely reduced levels of tocopherol. Plants overexpressing *VTE6* showed increased levels of phytyl-diphosphate and tocopherol. Finally, feeding experiments showed that wild-type plants could convert exogenous phytol to phytyl-diphosphate, but *vte6* mutant plants could not, showing that VTE6 has phytyl-phosphate kinase activity. Also, *Escherichia coli* expressing *VTE5* and *VTE6* could produce phytyl-diphosphate from phytol.

The two pathways for tocopherol biosynthesis could act redundantly, or one pathway could predominate. Indeed, the leaves of *pheophorbide a oxygenase* mutants, which have a block in chlorophyll degradation, show low levels of total tocochromanols, supporting the importance of chlorophyll-derived

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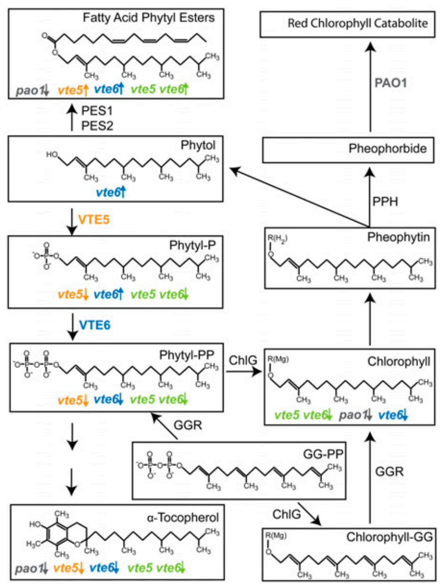

Metabolism of phytols. Degradation of chlorophyll produces phytol; phosphorylation of phytol by VTE5 and VTE6 produces phytyl-diphosphate, a precursor of tocopherol synthesis. Arrows show the changes in levels of each intermediate in the indicated mutants. R(Mg), chlorophyllide; R(H_2), pheophorbide. (*Based on vom Dorp et al. [2015], Figure 9*.)

phytol. These observations indicate that the chlorophyll-derived pathway predominates, as the *vte6* mutant plants show severe deficiencies in tocopherol and suffer severe phenotypic consequences. In addition to having low levels of tocopherol, the *vte6* mutants could not grow photoautotrophically; even on sucrose-supplemented media, the mutant plants were stunted and pale, with weak root systems. Homozygous *vte6* mutants did not set seeds, but in the progeny of heterozygous mutants, the homozygous seeds showed reduced viability after storage. In addition to the effects of tocopherol deficiency, accumulation of the phytyl-phosphate intermediate might negatively affect the *vte6* mutant plants, as, in contrast to *vte6*, other tocopherol-deficient mutants, such as *vte1*, *2*, *4*, and *5*, can grow photoautotrophically. Supporting this idea, the *vte5 vte6* double mutants showed less inhibition of growth compared with the *vte6* single mutants.

As vitamin E, tocochromanols are an important part of the human diet and have commercial uses in preventing oxidation of vegetable oils; therefore, improving the tocopherol contents of plant oils and animal forage remains an ongoing aim (reviewed in Hunter and Cahoon, 2007). The discovery that phytol from chlorophyll degradation feeds the tocopherol biosynthesis pathway has interesting implications for metabolic engineering, as *VTE6*-overexpressing plants show increased tocopherol levels in leaves and seeds. If successful (and lacking detrimental side effects), such engineering will improve food and feed, help enable industrial applications of plant-derived oils, and potentially enhance seed longevity.

Jennifer Mach
Science Editor
jmach@aspb.org
ORCID ID: 0000-0002-1141-6306

REFERENCES

Hunter, S.C., and Cahoon, E.B. (2007). Enhancing vitamin E in oilseeds: unraveling tocopherol and tocotrienol biosynthesis. Lipids **42:** 97–108.

Maeda, H., and DellaPenna, D. (2007). Tocopherol functions in photosynthetic organisms. Curr. Opin. Plant Biol. **10:** 260–265.

Seaver, S., et al. (2014). High-throughput comparison, functional annotation, and metabolic modeling of plant genomes using the PlantSEED resource. Proc. Natl. Acad. Sci. USA **26:** 9645–9650.

vom Dorp, K., Hölzl, G., Plohmann, C., Eisenhut, M., Abraham, M., Weber, A.P.M., Hanson, A.D., and Dörmann, P. (2015). Remobilization of phytol from chlorophyll degradation is essential for tocopherol synthesis and growth of Arabidopsis. Plant Cell **27:** 2846–2859.