IN BRIEF

The Evolution of Photorespiratory Glycolate Oxidase Activity

The first step of photosynthetic carbon fixation is catalyzed by ribulose-1,5-bisphosphate carboxylase/oxygenase, which arose when the atmosphere contained virtually no O_2. The increase of atmospheric O_2 caused by oxygenic photosynthesis gave rise to photorespiratory metabolism, a process whereby O_2 substitutes for CO_2, causing ribulose-1,5-bisphosphate carboxylase/oxygenase to produce the toxic compound 2-phosphoglycolate, which is ultimately recycled into 3-phosphoglycerate (reviewed in Bauwe et al., 2010). This recycling process is vital for the success of photosynthetic organisms under the current levels of O_2 in the atmosphere but also accounts for losses of large amounts of carbon and energy. New work from **Hackenberg et al. (2011)** advances our understanding of the evolution of photorespiration.

During the recycling of 2-phosphoglycolate to 3-phosphoglycerate, glycolate is converted into glyoxylate by glycolate oxidases (GOXs) in plants and by glycolate dehydrogenases in cyanobacteria and green algae. Hackenberg et al. searched for GOX homologs in bacteria, algae, and plants and found homologs of the well-characterized spinach (*Spinacia oleracea*) GOX in cyanobacteria and algae. This result corroborates the recent findings of Kern et al. (2011), who similarly report that GOX-like proteins are found in nitrogen-fixing cyanobacterial species and show that GOX in photosynthetic eukaryotes was in the genome of the cyanobacterial endosymbiont that gave rise to the plastid. However, given that green algae and cyanobacteria use glycolate dehydrogenases instead of GOX for the comparable step of photorespiration, the discovery of genes coding for GOX-like proteins in their genomes raises the questions: What are the cyanobacterial and algal GOX homologs doing? How did they acquire their photorespiratory function in land plants?

Hackenberg et al. purified GOX-related proteins from *Arabidopsis thaliana*, the N_2-fixing cyanobacterium *Nostoc* PCC 7120, and the green alga *Chlamydomonas reinhardtii*. They found that whereas all three proteins displayed oxidase activity, the *Nostoc* and *C. reinhardtii* proteins preferred L-lactate over glycolate and thus are lactate oxidases (LOXs).

A LOX-null *Nostoc* mutant did not display the growth impairment typical of photorespiratory mutants. Instead, LOX appears needed for nitrogen fixation in the presence of oxygen. Hackenberg et al. speculate that LOX functions as an oxygen scavenger that allows the bacteria to use atmospheric nitrogen as their nitrogen source even in high-oxygen atmospheres.

Given the close relationship between nitrogen-fixing cyanobacteria and the plastid endosymbiont, it is reasonable to imagine that after endosymbiosis the plastid-encoded LOX evolved GOX activity and acquired a role in photorespiration, replacing glycolate dehydrogenases. Based on comparisons of the LOX and GOX sequences (see figure), the authors were able to mutate *Nostoc* LOX such that its GOX activity increased at the same time as its LOX activity decreased, making it resemble a GOX. This shows that once LOX was present in the plant genome, it would have been evolutionarily easy to acquire a fully functional GOX protein. The eventual origin of GOX-based photorespiration in the charophyte green algal lineage may have played an important role in the subsequent appearance of land-adapted plants.

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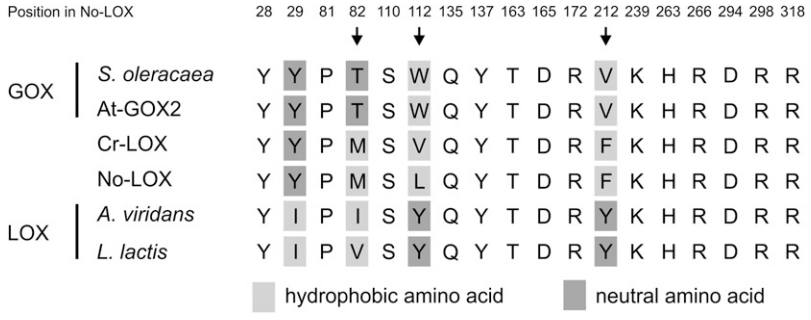

Alignment of the active sites of GOX, LOX, and related proteins. The gray residues are those likely involved in substrate binding. Arrows mark amino acid mutations in *Nostoc* LOX that together switched its activity to GOX. (*From Figure 2 of Hackenberg et al. [2011]*.)

REFERENCES

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