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Integrated operation of the photorespiratory cycle and cytosolic metabolism in the modulation of primary nitrogen assimilation and export of organic N-transport compounds from leaves: A hypothesis

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ABSTRACT

Photorespiration is generally considered to be an essentially dissipative process, although it performs some protective and essential functions. A theoretical appraisal indicates that the loss of freshly assimilated CO_2 due to photorespiration in well-watered plants may not be as high as generally believed. Even under moderately adverse conditions, these losses may not exceed 10%. The photorespiratory metabolism of the source leaves of well-watered and well-nourished crop plants ought to be different from that of other leaves because the fluxes of the export of both carbohydrates and organic N-transport compounds in source leaves is quite high. With a heuristic approach that involved the dovetailing of certain metabolic steps with the photorespiratory cycle (PR-cycle), a novel network is proposed to operate in the source-leaves of well-watered and well-nourished plants. This network allows for the diversion of metabolites from their cyclic-routes in sizeable quantities. With the removal of considerable quantities of glycine and serine from the cyclic route, the number of RuBP oxygenation events would be several times those of the formation of hydroxypyruvate. Thus, to an extreme extent, photorespiratory metabolism would become open-ended and involve much less futile recycling of glycine and serine. Conversion of glyoxylate to glycine has been proposed to be a crucial step in the determination of the relative rates of the futile (cyclic) and anabolic (open-ended) routes. Thus, in the source leaves of well-watered and well-nourished plants, the importance of the cyclic route is limited to the salvaging of photorespiratory intermediates for the regeneration of RuBP. The proposed network is resilient enough to coordinate the rates of the assimilation of carbon and nitrogen in accordance with the moisture and N-fertility statuses of the soil.

Introduction

Photorespiration has long been an enigma. However, photorespiration is known to play a crucial role in some protective and essential functions of plants (Noctor and Foyer, 1998; Noctor et al., 1998; Wingler et al., 2000; Takahashi et al., 2007). The rate at which photorespiration occurs in C3 crop plants, particularly under high-light, high-temperature, and soil-moisture deficit conditions, has led to the belief that photorespiration considerably lowers the net rate of photosynthesis (through the loss of freshly assimilated CO_2), resulting in a substantial loss of crop yields (Zelitch, 1973). Due to their Kranz anatomy, C4 plants are able to keep the concentration of O_2 low in the vicinity of RubisCO and thus appear to circumvent photorespiration. However, it has been reported that, in maize (a C4 plant), a finite photorespiratory process occurs, which is ordinarily masked by the high efficiency with which photorespiratory CO_2 is recycled (Volk and Jackson, 1972). Photorespiration also occurs in CAM plants (Moradshahi et al., 1977; Lüttge, 2010).

Certain aspects of photorespiration are not congruent with the dissipative nature that is generally attributed to the photorespiratory cycle (PR-cycle); e.g.:

- The dependence of primary nitrogen assimilation on photorespiration (Rachmilevitch et al., 2004);
- The essentiality of the joint operation of the Calvin cycle and the PR-cycle for the sustenance of the normal growth of plants (Zelitch et al., 2008);
- High rates of photorespiration that accompany high rates of photosynthesis in high productivity genotypes and the low-rates of photorespiration that accompany the low rates of photosynthesis in the low productivity genotypes of crop plants (Aliyev, 2012);

Abbreviations: CPS, carbamoyl phosphate synthetase; GS, glutamine synthetase; GS-GOGAT, glutamine synthetase-glutamine 2-oxoglutarate amidotransferase; ICDH, isocitrate dehydrogenase; PGA, 3-phosphoglycerate; PR-cycle, photorespiratory cycle; RubisCO, ribulose bisphosphate carboxylase/oxygenase; RuBP, ribulose-1,5-bisphosphate.

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- The inhibition of both nitrate-assimilation and photorespiration by CO_2-enrichment (Bloom et al., 2010).
- The impairment of the growth of photorespiratory mutants of *Arabidopsis*, a C3 plant (Somerville and Ogren, 1982), and maize, a C4 plant (Zelitch et al., 2008). Thus, the disruption of photorespiration results in strongly retarded growth of mutant plants (Maurino and Peterhansel, 2010) growing under normal air.

Ribulose bisphosphate carboxylase/oxygenase (RubisCO) is the enzyme that catalyses the first step of the Calvin cycle. During catalysis, ribulose-1,5-bisphosphate (RuBP) first binds to the substrate binding site and forms RuBP endiolate. In normal environmental conditions, once RuBP is bound to this site, CO_2 and O_2 molecules compete with each other to react with RuBP endiolate (Bowes and Ogren, 1972; Laing et al., 1974). Reaction with CO_2 results in the formation of two molecules of PGA (a 3-C compound), both of which enter the Calvin cycle, while reaction with O_2 results in the formation of one molecule of PGA and one molecule of 2-phosphoglycolate (a 2-C compound). This dual function of RubisCO is universal in photosynthetic organisms (Anderson, 2008) and explains the inevitability of concurrent carboxylation and oxygenation in the photosynthetic tissues of higher plants.

Reviews published in the last few years (Foyer et al., 2009; Bauwe et al., 2010; Maurino and Peterhansel, 2010; Peterhansel et al., 2010; Peterhansel and Maurino, 2011) have focused on a host of issues in efforts to explain various aspects of photorespiration and to explain the approaches that are adopted to circumvent photorespiration by various means, including the metabolic engineering of plants. In one of these reviews (Peterhansel et al., 2010), several positive aspects of photorespiration have been highlighted, such as the removal of toxic metabolic intermediates, protection from photoinhibition, support for disease resistance and integration with primary metabolism. Using $^{11}CO_2$ and $^{13}CO_2$, Dirks et al. (2012) showed that the metabolites of the photorespiratory pathway are indeed removed in small to large quantities from the cyclic route depending on growth conditions.

The notion that photorespiratory metabolism is restricted to the cyclic flow of metabolites alone (Fig. 1), however, suffers from the following drawbacks:

- The cyclic route does not satisfy the stoichiometry of the exchange of molecules between the cytosol and the other organelles.
- At peak rates of photorespiration, a massive flux of highly cytotoxic NH_4^+ ions from the mitochondria to the chloroplasts would be required for their re-assimilation.
- Two different transaminases (serine:glyoxylate aminotransferase and glutamate:glyoxylate aminotransferase) are required to concurrently catalyse the conversion of glyoxylate to glycine in the peroxisome.
- All of these reactions occur within only three organelles (the chloroplasts, peroxisomes and mitochondria), and photorespiratory metabolites traversing the cytosol remain completely untouched by cytosolic enzymes.

While the possible manifold links between photorespiration and central metabolism have been indicated previously (Peterhansel et al., 2010; Bauwe et al., 2012) and several perspectives on photorespiratory metabolism have also recently been reviewed (Fernie et al., 2013), currently, no attempts have been made to integrate the biochemical steps with the cyclic route of photorespiration to create a network that facilitates the export of metabolites from the source-leaves to the sink tissues in well-watered and well-nourished crop plants. Hence, an expansion of photorespiratory metabolism that extended beyond the cyclic route that highlighted the potential routes of the removal of intermediate metabolites against the back drop of the physiology of the whole plant was needed.

The source-leaves of crop plants export sucrose and organic N-transport compounds to the cells of growing sink tissues. To do this, the cells of the source-leaf need to assimilate the nutrients (especially carbon dioxide and nitrate) in large quantities and convert these compounds into exportable forms. Hence, striking differences ought to exist between the green cells of expanding leaves, mature leaves (or source) and senescent leaves regarding the nature and extent of the interactions between photorespiratory metabolism and other cellular processes.

In the theoretical exercise described here, certain metabolic steps have been identified by surveying the published research on photorespiration and the related processes. These steps were integrated with the PR-cycle, and thus a novel network with several open-ends is proposed to operate in the source-leaves of well-watered and well-nourished crop plants (Fig. 2). This network has the potential to generate organic N-transport compounds for export by diverting the metabolites from the cyclic route and facilitating their transport (along with that of sucrose) for anabolic processes (biomass production) that occur in the sink tissues of growing fruits, tubers, etc. This novel network and the published reports, which support the proposed hypothesis, are both described in this article.

Salient features of the proposed novel network

The identified metabolic steps for integration with the cyclic photorespiratory pathway

- Irreversible decarboxylation of isocitrate in chloroplasts by isocitrate dehydrogenase (ICDH) (EC 1.1.1.42) for generating α-ketoglutarate (2-oxoglutarate) to feed the glutamine synthetase-glutamine 2-oxoglutarate amidotransferase (GS-GOGAT) cycle:

$$\text{isocitrate} + \text{NAD(P)}^+ \rightarrow \alpha\text{-ketoglutarate} + CO_2 + \text{NAD(P)H} + H^+$$

- Incorporation of glycine into γ-glutamylcysteine in the cytosol by glutathione synthetase (EC 6.3.2.3) in an irreversible manner to produce glutathione:

$$\gamma\text{-glutamylcysteine} + \text{glycine} + \text{ATP} \rightarrow \text{glutathione} + \text{ADP} + \text{Pi}$$

- Re-assimilation of photorespiratory NH_4^+ and CO_2 in mitochondria by the combined irreversible action of glutamine synthetase (GS) (EC 6.3.1.2) and carbamoyl phosphate synthetase (CPS) (EC 6.3.5.5):

$$\text{glutamate} + NH_4^+ + \text{ATP} \rightarrow \text{glutamine} + \text{AMP} + \text{PPi}$$

$$CO_2 + \text{glutamine} + 2\text{ATP} \rightarrow \text{carbamoylphosphate} + \text{glutamate} + 2\text{ADP} + \text{Pi}$$

- Deamination of serine by the serine/threonine dehydratase family of enzymes (E.C. 4.2.1.13 and 4.2.1.16) to form pyruvate in an irreversible manner:

$$\text{l-serine} \rightarrow NH_4^+ + \text{pyruvate}$$

In this hypothesis, the step of the conversion of glyoxylate to glycine is identified and proposed to be the crucial step for balancing the rates of the cyclic (futile) and open-ended (productive) flow of photorespiratory metabolites.