OPINION PAPER

Photorespiratory bypasses: how can they work?

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Abstract

Photorespiration has been suggested as a target for increasing photosynthesis for decades. Within the last few years, three bypass pathways or reactions have been designed and tested in plants. The three reactions bypass photorespiration either in the chloroplast or in the peroxisome, or oxidize glycolate completely to CO2 in the chloroplast. The reactions differ in their demand for energy and reducing power as well as in the catabolic fate of glycolate. The design, energy balance, and reported benefits of the three bypasses are compared here, and an outlook on further optimization is given.

Key words: CO2 refixation, bypass, energy balance, glycolate oxidase, photorespiration, synthetic biology.

Introduction

The dual function of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and the associated carbon and nitrogen losses in the course of the photorespiratory cycle were discovered in the 1970s and 1980s (Ogren, 1984). Much of this research was motivated by the hope that a reduction of photorespiration could improve plant photosynthesis and yield (Zelitch and Day, 1973). This idea was first challenged by the conditionally lethal phenotypes of photorespiratory mutants and by the unavailability of second-site suppressor mutants that would identify alternative catabolic routes for photorespiratory metabolites (Somerville and Ogren, 1982; Somerville, 2001). The prevailing view on photorespiration has completely changed since the pathway is recognized today as an integral element of primary carbon metabolism that interacts with many other pathways (Maurino and Peterhansel, 2010; Bauwe et al., 2012). One important step towards this change in perspective was the unexpected finding that photorespiration is essential for the survival of all organisms that use Rubisco for CO2 fixation (Nakamura et al., 2005; Eisenhut et al., 2008; Zelitch et al., 2009). Previous to these studies, the low rates of photorespiration observed in photosynthetic organisms with carbon-concentrating mechanisms such as C4 plants and most green algae and cyanobacteria were assumed to be insignificant. Moreover, important functions were assigned to photorespiration in the protection of plants from excess light (Kozaki and Takeba, 1996) or in supplying reducing power for nitrate assimilation (Rachmilevitch et al., 2004; Bloom et al., 2010).

Independently of this new positive reputation of photorespiration, three different principles for the reduction of photorespiratory losses by genetic engineering were suggested and two of them proved to be successful, at least in the model system Arabidopsis (Kebeish et al., 2007; Carvalho et al., 2012; Maier et al., 2012). In this review, we discuss the strengths and weaknesses of the different approaches and speculate about the physiological basis of the observed growth improvement.

Three bypasses have been suggested

In 2007, our group proposed a bypass to photorespiration in the chloroplast with the objective of reducing photorespiratory losses (Kebeish et al., 2007). The strategy is shown as bypass 1 on the background of photorespiration in Fig. 1. Key enzymatic reactions are explained in Table 1. The pathway starts with glycolate and ends with glyceraldehyde. Thus, it diverts metabolites from photorespiration, but also feeds back into this cycle. Glycolate is oxidized by a glycolate dehydrogenase (GlycolateDH) from E. coli that uses organic co-factors instead of oxygen as electron
Table 1. Comparison of the enzymatic reactions of photorespiration and the three bypasses

<table>
<thead>
<tr>
<th>Reaction</th>
<th>Photorespiration</th>
<th>Bypass 1</th>
<th>Bypass 2</th>
<th>Bypass 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Phosphoglycolate dephosphorylation</td>
<td>PGLP</td>
<td>PGLP</td>
<td>PGLP</td>
</tr>
<tr>
<td>2a</td>
<td>Glycolate oxidation</td>
<td>GO</td>
<td>GlycolateDH</td>
<td>GO</td>
</tr>
<tr>
<td>2b</td>
<td>H$_2$O$_2$ detoxification</td>
<td>CAT</td>
<td>–</td>
<td>CAT</td>
</tr>
<tr>
<td>3</td>
<td>Transamination</td>
<td>GGAT</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>4a</td>
<td>Decarboxylation</td>
<td>GDC, SHMT</td>
<td>GCL</td>
<td>GCL</td>
</tr>
<tr>
<td>4b</td>
<td>NH$_3$-release</td>
<td>GDC, SHMT</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>5</td>
<td>Transamination</td>
<td>SGAT</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>6</td>
<td>Reduction</td>
<td>HPR</td>
<td>TSR</td>
<td>HPR</td>
</tr>
<tr>
<td>7</td>
<td>Glycerate phosphorylation</td>
<td>GK</td>
<td>GK</td>
<td>GK</td>
</tr>
<tr>
<td>8</td>
<td>Other</td>
<td>MS</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

PGLP, phosphoglycolate phosphatase; GO, glycolate oxidase; CAT, catalase; GGAT, glutamate:glyoxylate aminotransferase; GDC, glycine decarboxylase; SHMT, serine hydroxymethyltransferase; SGAT, serine:glyoxylate aminotransferase; HPR, hydroxypyruvate reductase; GK, glycerate kinase; GlycolateDH, glycolate dehydrogenase; GCL, glyoxylate carboxylase; TSR, tartronic semialdehyde reductase; ME, malic enzyme; PDH, pyruvate dehydrogenase; HPI, hydroxypyruvate isomerase; MS, malate synthase.

Fig. 1. Scheme of photorespiration (black) and the three bypasses for the reduction of photorespiratory losses (red, numbers in boxes). The arrows indicate enzymatic reactions or transport steps. Enzymatic reactions (numbers in circles) are explained in Table 1. The stoichiometry of the reactions is not included. 3-PGA, 3-phosphoglycerate.
acceptors (Lord, 1972). This allows for the conservation of reducing power associated with this reaction as reducing equivalents. Similar to photorespiration, two C2 compounds (glyoxylate) are merged to one C3 compound [here tartronic semialdehyde (TS)] with the release of CO2 (note that stoichiometries are not included in the figure). CO2 release is shifted from mitochondria to chloroplasts and catalysed by a glyoxylate carboligase (GCL) also derived from E. coli (Chang et al., 1993) in plants over-expressing this bypass. The product of the decarboxylation reaction is then reduced to glyceraldehyde by tartronic semialdehyde reductase (TSR). Similar to the major pathway, three-quarters of the glycolate fed into this bypass are re-converted into Calvin cycle intermediates. This reduces carbon outflow from the cycle caused by RuBP oxygenation. A major difference from photorespiration is that ammonia release is avoided and therefore refixation is not required. Concomitantly with the first publication introducing this bypass, it became evident that the photosynthetic cyanobacterium Synechocystis can use the same pathway as an alternative to photorespiration (Eisenhut et al., 2006).

Bypass 2 (Fig. 1) resembles bypass 1 in that it starts with a photorespiratory intermediate and produces another photorespiratory intermediate (Carvalho et al., 2012). The decarboxylation reaction is catalysed by the same enzyme as in bypass 1, but targeted here to the peroxisome. The resulting tartronic semialdehyde is fed back into photorespiration by an isomerase reaction (HYI). In this bypass, ammonia release is abolished and three-quarters of the carbon from glycolate is converted to 3-PGA. This balance is identical to the balance of bypass 1. Organisms using this pathway for photorespiration have not yet been identified, but the reactions of bypass 2 might be involved in glycolate or glyoxylate metabolism of E. coli (Ashiuchi and Misono, 1999).

Bypass 3 is not a true bypass as there is no reconnection to the major pathway (Fahnenstich et al., 2008; Maier et al., 2012). Instead, this pathway completely oxidizes glycolate to CO2 by a combination of endogenous and newly introduced enzymes. Glycolate oxidation in this pathway is catalysed by a plant glycolate oxidase (GO) that was relocated from the peroxisome to the chloroplast. As this enzyme produces equimolar amounts of H2O2 during glycolate oxidation, an additional catalase (CAT, also from the peroxisome) is required for detoxification. Together with acetyl-SCoA, glyoxylate resulting from glycolate oxidation is converted to malate by malate synthase (MS), thus, two C2 compounds are metabolized to one C4 compound here. The malate synthase reaction is normally part of storage lipid mobilization in glyoxysomes of young plants (Kindl, 1993; Cornah et al., 2004). In E. coli, the gene for malate synthase is part of the operon encoding the subunits of GlycolateDH (Pellicer et al., 1996) suggesting an additional role in glycolate metabolism in prokaryotes. The remainder of the pathway is supposed to be catalysed by endogenous enzymes. Decarboxylation of malate to pyruvate by malic enzyme (ME) is the first CO2 release reaction. Further oxidation of pyruvate to CO2 by pyruvate dehydrogenase (PDH) produces acetyl-SCoA as a by-product that can be used for the next formation of malate from glyoxylate. Both endogenous reactions of bypass 3 result in the formation of reducing equivalents and shift CO2 release reactions from the mitochondrion to the chloroplast. Experimental evidence for the presence of the required enzyme activities in chloroplasts is available (Johnston et al., 1997; Maier et al., 2011). In total, the net reaction balance of bypass 3 is the conversion of glycolate and O2 to CO2 and H2O accompanied by the formation of reducing equivalents. Noteworthy, the reaction depletes the Calvin cycle from intermediates when compared with photorespiration or the two other bypasses as no 3-PGA is recycled.

Potential benefits of the three bypasses

From an engineer’s point of view, architecture of the bypasses is much simpler than the circuitous photorespiratory pathway. Particularly, bypasses 1 and 3 avoid any transmembrane transport whereas photorespiration is associated with at least 12 transport processes (Reumann and Weber, 2006). Bypass 2 would also clearly reduce the number of necessary transport steps compared with photorespiration. However, an answer to the question whether reduction of transport steps would improve energetics of the pathway has to await the molecular identification of the transporters involved.

Two potential benefits of the bypasses on plant carbon assimilation are conceivable. Bypass 1 and bypass 3 release CO2 in the chloroplast. This might increase the chloroplastic CO2 concentration and reduce the probability of further oxygenation reactions. From the physiological characterization of bypass 1 plants, there is evidence that such an increase in chloroplastic CO2 indeed takes place based on the reduction of the CO2 compensation point compared with the controls (Kebeish et al., 2007, see also below). For bypass 3, no change in compensation point was reported. From the stoichiometry of the reaction, it would have been expected that the extra release of CO2 (2 CO2/glycolate instead of 0.5 CO2/glycolate in photorespiration) would increase the CO2 compensation point. This has, for instance, been described for Arabidopsis mutants that convert part of the glycolate to CO2 in the peroxisome (Cousins et al., 2008). The apparent absence of such an increased compensation point in bypass 3 over-expressors (Maier et al., 2012) already indicates an improved availability of CO2 in the chloroplast. Efficacy of a chloroplastic CO2 release system would strongly depend on the degree of refixation of CO2 released in the mitochondrion by photorespiration (or in the peroxisome by bypass 2). If the CO2 released outside the chloroplast would be refixed anyway, the location of CO2 release should not matter. It has been suggested that such refixation can be significant if chloroplasts cover the outer surface of cells so that any CO2 released somewhere in the cell has to diffuse through a chloroplast before reaching the intercellular space (Sage and Sage, 2009). Even an active channelling mechanism for CO2 from the mitochondrion to the chloroplast in higher plants has been suggested (Braun and Zabaleta, 2007; Zabaleta et al., 2012). In C4 plants, optimization of CO2 refixation by the restriction of photorespiratory CO2 release to the mitochondria of bundle sheath cells might have been the first dedicated evolutionary step towards an efficient CO2 concentration system (Sage et al., 2012). Thus, there is ample evidence for evolutionary pressure towards the optimization of CO2 fixation. As the efficiency of the endogenous refixation system is still a matter of ongoing debate, the benefit of chloroplastic CO2 release cannot be included in the energy balance of the various pathways, although significant impact can readily be imagined.
The second potential benefit relates to the energy balance of the bypasses. Table 2 shows a calculation of the demand of the different bypasses for reducing equivalents (red. eq) and ATP. This is based on a balance sheet for photorespiration that has recently been published (Peterhansel et al., 2010) and that calculated the energy demand to reestablish the ‘status quo ante’, i.e. completely to resynthesize the RuBP that has been oxygenated by Rubisco. Here, the energy balances of the bypasses are calculated compared with photorespiration using the same assumptions. Note that this calculation is different from the calculation used by Maier et al. (2012), because the costs for the reduction of released CO2 are integrated here. All numbers in the calculation are per molecule glycylate synthesized and therefore per oxygenation event. Several aspects have to be taken into consideration.

(i) All bypasses avoid ammonia release and, thus, do not require ammonia refixation.
(ii) All bypasses circumvent the mitochondrial GDC/SHMT reaction. Absence of NADH synthesis in this reaction has to be accounted for as a penalty in terms of energy balance.
(iii) Bypass 1 uses a glycylate dehydrogenase for glycylate oxidation that synthesizes reducing equivalents instead of transferring electrons to oxygen. This reduces the net consumption of reducing equivalents in this pathway.
(iv) Bypass 3 liberates two CO2 from glycylate that have to be refixed instead of 0.5 CO2 for photorespiration and bypasses 1 and 2. Based on Calvin cycle stoichiometry, we calculate three ATP and two reducing equivalents per CO2 refixation. This makes 4.5 ATP and three reducing equivalents for the extra CO2 released in bypass 3.
(v) Bypass 3 does not produce 3-phosphoglycerate (3-PGA) as part of the glycylate recycling process. Therefore, no costs for the re-reduction of 3-PGA in the Calvin cycle have to be calculated. Moreover, the bypass avoids NADH consumption for hydroxypyruvate (HO-Pyr) or tartronic semialdehyde (TS) reduction, which is integrated in the calculation as an additional advantage.
(vi) Bypass 3 synthesizes NAD(P)H in both the malic enzyme reaction and the pyruvate dehydrogenase reaction. This results in an additional bonus of two reducing equivalents per glycylate.
(vii) When reducing equivalents are used for ATP synthesis in the mitochondrial electron transport chain, an average of 2.5 ATP/NAD(P)H are synthesized (Ferguson, 1986; Hinkle, 2005). This rough estimate is used here to convert reducing power into energy equivalents.

In summary, bypass 1 shows an improved energy balance compared with photorespiration. This is mostly due to the energy gain during glycylate oxidation. The energy consumption of bypass 2 is only slightly lower than the photorespiratory energy demand. Bypass 3 ends up with an increased energy demand relative to photorespiration. Thus, the potential benefit of bypass 3 strongly depends on whether chloroplastic CO2 release improves CO2 refixation and/or reduces the probability of oxygen fixation. Importantly, it is questionable whether an improved energy balance of photorespiration is always desirable for the plant. Oxygen fixation by Rubisco is highest in hot and dry climates (Ku and Edwards, 1977a, b). Under these conditions, energy supply from the light reactions is often not limiting photosynthesis. Instead, strong electron sinks are required to avoid overreduction.

| Table 2. The energy balance sheet of photorespiration and the three bypasses in comparison |
|---------------------------------|-----------------|-----------------|-----------------|-----------------|
|                                 | Photorespiration | Bypass 1         | Bypass 2         | Bypass 3         |
|                                 | Red.eq. ATP      | Red.eq. ATP      | Red.eq. ATP      | Red.eq. ATP      |
| Reduction of 0.5 CO2            | 1 1.5            | 1 1.5            | 1 1.5            | 1 1.5            |
| Re-fixation of 0.5 NH3          | 0.5 0.5          | 0 0              | 0 0              | 0 0              |
| Phosphorylation of 0.5 glycylate| 0 0.5            | 0 0.5            | 0 0.5            | 0 0.5            |
| Reduction of 1 PGA              | 1 1.5            | 1 1.5            | 1 1.5            | 1 1.5            |
| formed by Rubisco               | 0.5 0.75         | 0.5 0.75         | 0.5 0.75         | 0 0              |
| by photorespiration             |                 |                  |                  |                  |
| Bonus for GlycolateDH           | –1              |                  |                  |                  |
| Penalty for missing GDC         | 0.5 0.5          | 0.5 0.5          | 0.5 0.5          |                  |
| NADH synthesis                  |                  |                  |                  |                  |
| Penalty for complete glycylate  | 3 4.5            | 3 4.25           | 3 4.25           | 4 7.5            |
| oxidation (1.5 CO2 extra)        |                  |                  |                  |                  |
| Bonus for no HO-Pyr/TS reduction| 0.5             |                  |                  |                  |
| Bonus for ME and PDH            |                  |                  |                  |                  |
| Total units                     | 3 4.75           | 2 4.25           | 3 4.25           | 4 7.5            |
| Assuming 2.5 ATP/NAD(P)H        | 7.5 5            | 7.5 5            | 7.5 5            | 10 10            |
| Total ATP units                 | 12.25 9.25       | 11.75 17.5       |                  |                  |

Red. eq., reducing equivalents; PGA, 3-phosphoglycerate; GlycolateDH, glycylate dehydrogenase; GDC, glycine decarboxylase; HO-pyr, hydroxypyruvate; TS, tartronic semialdehyde; ME, malic enzyme; PDH, pyruvate dehydrogenase. Positive numbers refer to requirements and negative numbers to produced red. eq. or ATP.
of the chloroplastic electron transport chain and generation of reactive oxygen species (ROS) (Demmig-Adams and Adams, 1992; Murata et al., 2007). Perhaps it is one of the benefits of the peroxisomal glycolate oxidase that ROS are generated under controlled conditions in the peroxisome allowing for efficient detoxification. In line with this argument, there is evidence that both glycolate dehydrogenases and glycolate oxidases, respectively, were used for glycolate oxidation in different evolutionary lineages of cyanobacteria and unicellular photosynthetic eukaryotes (Kern et al., 2011). It seems reasonable that higher plants preferred a glycolate oxidase rather than a glycolate dehydrogenase for oxygen fixation because this enzyme burns excess reducing power instead of producing even more. This effect would even be amplified if excess glyoxylate produced by glycolate oxidase would leak out of the peroxisome into the cytoplasm where it could be reduced back to glycolate by a cytosolic glyoxyxalate/hydroxybutyrate reductase (Givan and Kleczkowski, 1992; Timm et al., 2008). This could establish a cycle that efficiently oxidizes excess reducing equivalents. Similar to the CO2 refixation argument above, the actual benefit will strongly depend on environmental and metabolic parameters.

**Reported benefits of the three bypasses**

Data on the characterization of transgenic plants over-expressing one of the three bypasses have now been published. Bypass 2 was partially established in tobacco (Carvalho et al., 2012). Whereas the first introduced enzyme, GCL, was highly expressed in peroxisomes, HYI expression was undetectable probably due to co-suppression of RNA accumulation (Eamens et al., 2008). GCL over-expressors exhibited chlorosis and stunted growth when grown in ambient air, but not at elevated CO2 levels. This phenotype was reminiscent of classical photorespiratory mutants and indicated that conversion of glyoxylate to tartronic semialdehyde in the peroxisome without further metabolism to hydroxy-pyruvate might be deleterious for the plant, perhaps because it provides a metabolic dead-end. This observation already suggests caution when manipulating photorespiratory fluxes, probably because of the above-mentioned intimate integration of photorespiration in primary plant metabolism (Bauwe et al., 2012).

Bypass 1 and bypass 3 have been established in Arabidopsis. Besides over-expression of the complete pathway, transgensics over-expressing components of the pathways were also studied (Kebeish et al., 2007; Fahnstich et al., 2008; Maier et al., 2012). Both studies indicated that the bypasses led to enhanced growth under the test conditions (8h days and approximately 100 µE light) with reported maximum biomass increases of 30–50% at the end of the growth period. Even in Arabidopsis, photosynthesis is definitely light-limited under these conditions suggesting an energy advantage as a basis of the growth effect. However, as our calculation does not reveal any energy advantage for bypass 3, the more probable interpretation is that enhancement of chloroplastic CO2 concentrations might control enhanced growth. Both studies also mention that enhanced biomass accumulation was absent under long-day conditions. This could be interpreted as another argument for improved energy balance as the major factor controlling enhanced growth. However, it should be taken into consideration that the vegetative growth period of Arabidopsis is very short in long days. A small increase in daily photosynthesis by over-expression of a bypass might result in a small increase in leaf area compared with the wild-type at the end of the day. This would again increase the leaf area that is available for photosynthesis during the next day and would result in an exponential relationship between daily carbon gain and final biomass (assuming that no other factors are limiting). In this scenario, the short vegetative period might not allow for the detection of growth increases although photosynthesis might be enhanced.

Interestingly, both studies also report that leaves of transgenic plants had a tendency for flatter and thinner growth. These results might indicate links between physiological and anatomical adaptations that have to be followed up in further studies.

Both papers used glycine levels and/or glycine/serine ratios (Novitskaya et al., 2002) to estimate the flux through photosynthesis in the presence and absence of the respective bypass. Reported reductions range from 2-fold to 5-fold under conditions of high photosynthetic flux indicating that a significant part of glycolate is catabolized in chloroplasts in transgenic plants. This is also consistent with post-illumination CO2 burst values (Atkin et al., 1998) that are reduced in plants over-expressing bypass 1. Moreover, plants over-expressing an incomplete bypass 3 without a catalase for H2O2 detoxification showed stunted growth (Maier et al., 2012). This also indicated that appreciable amounts of glycolate were oxidized in the chloroplast and produced damaging concentrations of H2O2. Although these estimates apply to the same direction, final accurate numbers about metabolic flow through the bypasses probably require the use of metabolic flux labelling with heavy isotopes of CO2, O2, or glycolate (Fernie et al., 2005; Hasunuma et al., 2010).

Gas exchange measurements indicated that both bypasses enhance the photosynthetic rate when calculated per leaf area (for bypass 1, Kebeish et al., 2007) or per mol chlorophyll (for bypass 3, Maier et al., 2012), respectively. Only for bypass 1, a reduction of the CO2 compensation point was reported (Kebeish et al., 2007), suggesting better CO2 refixation. As stated above, even an unchanged compensation point in bypass 3 over-expressors argues for better refixation because of the different stoichiometry of CO2 release.

**Outlook**

Our theoretical calculations and the experimental results indicate that photorespiratory bypasses can enhance plant productivity. Whether this is due to better CO2 availability for refixation as compared with photosynthesis or caused by improvements in the energy balance of the pathway still remains to be shown. It is therefore important to learn more about the degree of refixation of photorespiratory CO2 in wild-type plants. Moreover, growth studies with bypass plants under different combinations of varying CO2 supply and limited illumination (Poorter and Pérez-Soba, 2001) will help to elucidate the bottleneck that is overcome by bypass installation.

Bypass 1 still suffers from unequal transgene expression and the multiple proteins necessary for establishment of the pathway.
This is exemplified by the linear dependence of the growth effect on the expression of subunit F of E. coli GlycolateDH that is much lower than the expression of the other genes. However, physiological measurements and growth assays with plants over-expressing GlycolateDH alone suggested that glyoxylate synthesis in the chloroplast is already sufficient to induce the growth effect and partly to reduce flux through photorespiration (Kebeish et al., 2007; Peterhansel and Maurino, 2011). It was speculated that endogenous enzymes are capable of oxidizing glyoxylate to CO₂ at low rates. This is consistent with experimental results describing CO₂ release from glycolate or glyoxylate in chloroplast extracts (Kisaki and Tolbert, 1969; Zelitch, 1972; Kebeish et al., 2007). The carbon and energy balance of such a pathway would be similar to what has been described here for bypass 3. More knowledge about the endogenous enzymes involved in bypass 3. More knowledge about the endogenous enzymes involved in downstream reactions is necessary for improving the efficiency of this pathway by genetic engineering.

The combination of glycolate oxidase and catalase enzymes for glycolate oxidation in the chloroplast requires sophisticated balancing of both activities to avoid deleterious side-effects. GlycolateDH enzymes might be better suited for this function, but the E. coli enzyme used for bypass 1 is made up from three subunits complicating the genetic approach. A single-subunit E. coli GlycolateDH enzyme has been identified in a mutational screen in Synechocystis (Nakamura et al., 2005). Also the Synechocystis homologue to subunit D of E. coli GlycolateDH seems to exhibit GlycolateDH activity (Eisenhut et al., 2006). Such enzymes may also provide superior starting points for the efficient establishment and characterization of photorespiratory bypasses in crop plants. However, as both green algae and cyanobacteria express efficient CO₂ concentrating mechanisms (Price et al., 2007; Spalding, 2007) and photorespiratory flux rates are low, the enzymatic proficiency of these enzymes will have to be studied in more detail.

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