Preface

Photorespiration: origins and metabolic integration in interacting compartments

This special issue on photorespiration focuses on recent advances in this topic. The majority of the papers summarizes and extends contributions given at the 2nd workshop, ‘Photorespiration–key to better crops’, held in Warnemuende, Germany in June 2015. This was organized by the DFG (German Research Foundation)-supported research network, ‘Photorespiration: origins and metabolic integration in interacting compartments’ (FOR 1186–Promics).

The term photorespiration (PR) describes a light-induced biochemical process that converts 2-phosphoglycolate (2PG) into 3-phosphoglycerate (3PGA) and is accompanied by O$_2$ uptake and CO$_2$ release. It is closely associated with photosynthetic CO$_2$ assimilation and represents one of the major highways of carbon metabolism in most plants. By mass flow, surpassed only by photosynthesis, PR actually constitutes the second most important process in the land-based biosphere. Plants using the most widespread C$_3$ type of photosynthesis for CO$_2$ assimilation display particularly massive photorespiratory CO$_2$ production. PR is initiated by competition of O$_2$ with CO$_2$ at the active site of the universal carboxylating enzyme Ribulose 1,5-bisphosphate Carboxylase/Oxygenase (Rubisco) (Smith, 1976), which produces large amounts of 2PG during the day. Hence, PR essentially acts as a salvage or metabolic repair process that converts the toxic by-product 2PG into the useful Calvin–Benson cycle intermediate 3PGA. It is supposedly the most important ancient ancillary metabolic process that enables plants to thrive in an O$_2$-containing atmosphere (Osmond, 1981). To convert 2PG into 3PGA, the concerted action of many plastidial, peroxisomal, mitochondrial, and also cytosolic enzymes is necessary, which makes this pathway the most prominent example of subcellular metabolic integration in higher plants.

However, PR also leads to the loss of a considerable fraction of freshly assimilated C and N as photorespiratory CO$_2$ and NH$_3$. Quantitatively, PR can decrease photosynthesis by up to 30% under current atmospheric concentrations of CO$_2$ and O$_2$ and even more at elevated temperature (e.g. Sharkey, 1988; Zhu et al., 2004). This substantial decrease of net photosynthesis led to the somewhat misleading view of PR as a ‘wasteful’ process limiting photosynthetic productivity in C$_3$ plants (e.g. Garrett, 1978; Siedow and Day, 2001). However, genetic analysis showed that PR is essential for all organisms performing oxygenic photosynthesis, since mutations of genes encoding for key photorespiratory enzymes always resulted in the photorespiratory phenotype and frequently in lethality (Somerville, 2001), i.e. corresponding mutants of cyanobacteria, red algae (Rademacher et al., this issue), chlorophytes, C$_3$ and C$_4$ plants were not viable in ambient air and could only be rescued under artificially enhanced CO$_2$/O$_2$ ratios (reviewed in Bauwe et al., 2010). Nevertheless, due to the large CO$_2$ and energy losses, PR is seen as a promising target in breeding more productive crops (Ort et al., 2015). For example, attempts have been initiated to introduce photorespiratory bypasses to make the process less energy demanding or to reduce the CO$_2$ release (reviewed in Peterhänsel et al., 2013). Interestingly, it has recently been reported that, instead of decreasing PR an increased PR flux capacity resulted in enhanced growth of Arabidopsis thaliana in ambient air. The independent over-expression of two different proteins of the mitochondrial glycine cleavage system increased photorespiratory carbon flow and also improved Calvin–Benson cycle activity, leading to higher photosynthetic activity and higher biomass production (Timm et al., 2012a, 2015).

Following the discovery between 1960 and 1980 of many essentials of the photorespiratory cycle (Olbert, 1971; Ogren, 2003), research interest in this topic declined. However, the recognition of PR as a main crop-breeding target and the development of new tools for plant research resulted in a revitalization of PR research over the last 15 years. Meanwhile most contributing enzymes and genes have been identified at a molecular level and a set of corresponding mutants was generated to investigate the metabolic interaction of PR with the metabolism of the entire plant (e.g. Boldt et al., 2005; Schwarte and Bauwe, 2007; Timm et al., 2008, 2012b). For example, these results showed the close interaction of PR with plant C1-metabolism and with other metabolic pathways (Engel et al., 2007; Ewald et al., 2007). Advanced metabolomic and transcriptomic approaches allowed a system-wide characterization of PR in the wild type and mutants of Arabidopsis (e.g. Fernie et al., 2013). The first candidates for photorespiratory transporters connecting the different interacting compartments such as the chloroplastidial glyceraldehyde/glycolate exchanger were identified by bioinformatics tools and then
biochemically verified (Bordych et al., 2013; Pick et al., 2013). Research on C₄ plants not only showed that PR is essential for these plants (Zelitch et al., 2009), but also provided increasing evidence for the important role of PR in the evolution of C₄ photosynthesis (Sage, 2004). The different location of photosynthetic enzymes in so-called C₃-C₄ intermediate plants generated/established an ancient CO₂ pump based on the transport of glycin and serine, which is also called C₂ photosynthesis, as the precursor for the final dicarboxylic-based C₄ cycle (e.g. Mallmann et al., 2014). Last but not least, the identification of functional photosynthetic processes in cyanobacteria resulted in the view that photorespiration is an ancient process which coevolved with oxygenic photosynthesis (Eisenhut et al., 2006, 2008; Kern et al., 2011, 2013; Bauwe et al., 2012; Hagemann et al., 2013).

The present special issue reports on different aspects of actual PR research. It comprises one insight paper, eight review papers, three opinion papers, and nine original research papers.

The insight paper and three reviews discuss the current view on PR and its evolution. Sage (this issue) summarized the stepwise development of C₄ photosynthesis from C₃ photosynthesis, whereby the localization of photosynthetic enzymes and metabolic fluxes between bundle sheath and mesophyll played a crucial role. Bräutigam and Gowik (this issue) highlight the important role of PR in the evolution of C₄ photosynthesis via intermediary stages, in which the capacity for PR is lost from leaf mesophyll cells and relocated to the bundle sheath cells. As shown by Döring et al. (this issue), in fully evolved C₄ plants such as sorghum, the majority of genes encoding components of PR are also expressed preferentially in bundle sheath cells. Khoshravesh et al. (this issue) highlight the importance of organelle positioning in bundle sheath cells and the relocation of photosynthetic activity to this tissue during the evolution of C₄ photosynthesis in grasses. Hagemann et al. (this issue) review the current position on the continuous coevolution of photosynthesis and PR. The evolution of all photosynthetic enzymes was elucidated and it was revealed that the present-day plant photosynthetic enzymes originated from archaean, bacterial, and cyanobacterial sources, which served as eukaryotic host cell (Archaea), and mitochondrial (proteobacteria) or plastidial (cyanobacteria) endosymbionts, respectively. Moreover, calculating in terms of the geological era, ancient CO₂/O₂ ratios indicated that photosynthetic metabolism existed from the invention of oxygenic photosynthesis and remained necessary in cells evolving different types of carbon-concentrating mechanisms (CCM).

Another set of contributions deals with the intertwining of the photosynthetic pathway with the central metabolism and its significance for engineering plant productivity. For example, Fromm et al. (this issue), by using mutants that lack the activity of mitochondrial NADH dehydrogenase, analysed the role of the mitochondrial electron transport chain in photosynthesis. Using transcriptomic analysis of Lotus japonicus wild type and GS2 mutant plants on a range of different nitrogen concentrations and at ambient and elevated CO₂, Pérez-Delgado et al. (this issue) show that primary nitrogen assimilation and PR are transcriptionally co-regulated. They also identify candidate transcription factors mediating this co-ordinated response. Bettì et al. (this issue) summarize recent advances obtained in photorespiratory engineering and discuss the potential of realizing gains in crop productivity through manipulation of the photorespiratory pathway. Nunes-Nesi et al. (this issue) explore natural genetic variation in yield and photosynthetic capacity and point to the fact that photosynthetic capacity, in part, is genetically determined. Obata et al. (this issue) review the tight integration of PR with other metabolic pathways which reach beyond the recycling of carbon from the Calvin–Benson cycle, a topic that is further extended by Hodges et al. (this issue). Timm et al. (this issue) focus on the still limited understanding of regulatory interactions between plant PR and photosynthesis and discuss its critical impact for successfully engineering photosynthesis. Montgomery et al. (this issue) also explore the regulatory effect of light reactions on PR in their opinion paper. They employ the framework of modularity in the cyanobacterium Fremyella diplosiphon and suggest a highly controlled interplay among light reactions, PR, and CCM. The opinion paper by Orf et al. (this issue) also centres on cyanobacteria. According to their comparative meta-analysis of cyanobacterial and plant metabolite profiles, the authors propose that cyanobacteria can serve as a much simpler surrogate to study the complex, highly compartmentalized, plant PR metabolism.

A deeper understanding of PR requires technology to determine rates of PR and photosynthesis accurately and this is reviewed by Hanson et al. (this issue). Alonso-Cantabrana and von Caemmerer (this issue) report on using carbon isotope discrimination as a tool to quantify C₃-like photosynthesis in C₃-C₄ intermediate species. Labelling with the stable carbon isotope ¹³C also revealed a strong effect of reduced mitochondrial malate dehydrogenase activity on PR (Lindén et al., this issue). Sharwood et al. (this issue) emphasize the importance of standardized and validated protocols for quantifying carbon fixation capacity in plants with differing carbon assimilation strategies, with particular emphasis on quantifying Rubisco activity.

Four papers deal with the specific role of the central enzyme, glycylate oxidase. The biochemistry of this peroxisomal enzyme converting glycolate into glyoxylate is reviewed by Hodges et al. (this issue). Dellero et al. report on the impact of reduced photorespiratory glycylate oxidase activity on leaf metabolism in Arabidopsis (Dellero et al., a, this issue) and review recent advances in the understanding of glycylate metabolism in different plant organs (Dellero et al., b, this issue). Knocking out glycylate oxidase of Cyanidioschyzon merolae resulted in the first mutant with a photorespiratory phenotype among red algae (Rademacher et al., this issue). This finding revealed that the plant-type photorespiratory cycle using a peroxisomal glycylate oxidase evolved before the split of red and green algae, and it represents a further example that organisms, though carrying a CCM, also depend on functional PR.
Concluding remarks
The past decades of research on the process of PR have revealed that this pathway is an indispensable companion to oxygenic photosynthesis and includes photosynthetic organisms that feature highly efficient CCMs such as cyanobacteria, many algae, and C₄ plants. Not only is it essential to support photosynthetic carbon assimilation, it is also heavily intertwined with other metabolic pathways and is the driving force for the evolution of C₄ photosynthesis (Heckmann et al., 2013), the most efficient mode of photosynthetic carbon assimilation in the angiosperms. In extant oxygenic photosynthetic organisms, the only means to reduce the rate of PR and hence enhance photosynthetic efficiency is to increase the concentration of CO₂ at the site of Rubisco. Therefore, future research aimed at increasing the efficiency of photosynthesis in crop plants might want to focus on this aspect. In the short term, perhaps the most promising path towards increased crop efficiency might be founded on a deeper understanding of natural variation in photosynthetic capacity to unravel those genes that determine source strength. Here, a better understanding of PR regulation and its integration into the cellular metabolism via yet unidentified transporters (e.g. exchanging glycine and serine between mitochondria and peroxisomes) would be an important future aim. However, in the long term, it is also envisaged that synthetic pathways for carbon assimilation (i.e. pathways not existing in nature), that are not affected by oxygen, might become a reality (Bar-Even et al., 2010; Ort et al., 2015), thereby enabling hitherto unimaginable gains in productivity.

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Martin Hagemann
Universität Rostock
Andreas PM Weber
Heinrich-Heine-Universität, Düsseldorf
Marion Eisenhut
Heinrich-Heine-Universität, Düsseldorf