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REVIEW ARTICLE

Emerging concept for the role of photorespiration as an important part of abiotic stress response

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ABSTRACT

When plants are exposed to stress, generation of reactive oxygen species (ROS) is often one of the first responses. In order to survive, cells attempt to down-regulate the production of ROS, while at the same time scavenging ROS. Photorespiration is now appreciated as an important part of stress responses in green tissues for preventing ROS accumulation. Photorespiratory reactions can dissipate excess reducing equivalents and energy either directly (using ATP, NAD(P)H and reduced ferredoxin) or indirectly (*e.g.*, *via* alternative oxidase (AOX) and providing an internal CO_2 pool). Photorespiration, however, is also a source of H_2O_2 that is possibly involved in signal transduction, resulting in modulation of gene expression. We propose that photorespiration can assume a major role in the readjustment of redox homeostasis. Protection of photosynthesis from photoinhibition through photorespiration is well known. Photorespiration can mitigate oxidative stress under conditions of drought/water stress, salinity, low CO_2 and chilling. Adjustments to even mild disturbances in redox status, caused by a deficiency in ascorbate, AOX or chloroplastic NADP-malate dehydrogenase, comprise increases in photorespiratory components such as catalase, P-protein of glycine decarboxylase complex (GDC) and glycine content. The accumulation of excess reducing equivalents or ROS in plant cells also affects mitochondria. Therefore, a strong interaction between the chloroplast redox status and photorespiration is not surprising, but highlights interesting properties evident in plant cells. We draw attention to the fact that a complex network of multiple and dynamic systems, including photorespiration, prevents oxidative damage while optimising photosynthesis. Further experiments are necessary to identify and validate the direct targets of redox signals among photorespiratory components.

INTRODUCTION

Photorespiration can be defined as a process of O_2 uptake and CO_2 release (Fig. 1) that occurs exclusively in the light in photosynthetic tissues. It was earlier described as an inevitable or necessary evil, resulting in significant loss of recently assimilated carbon and a considerable amount of previously captured energy (Edwards & Walker 1983). Photorespiration is the result of the unavoidable oxygenase reaction of ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco). The 2-phosphoglycolate (2PG) generated during the oxygenase reaction of RuBP poses two major challenges: (i) both 2PG and glycolate are toxic and need to be removed from the cell, and (ii) about 30–50% of recently assimilated carbon escapes from the Calvin cycle (Kobza & Edwards 1987; Bauwe *et al.* 2012; Busch *et al.* 2012). The process of photorespiration meets both of these challenges by effectively ensuring the metabolism of 2-PG *via* 3-PGA into the Calvin cycle, and by limiting the loss of carbon through the photorespiratory cycle to about 25% (Bauwe *et al.* 2012; Raghavendra & Sunil 2012).

Reactive oxygen species (ROS) are generated as by-products of various metabolic reactions and bioenergetic pathways. Being readily diffusible and highly reactive, ROS can affect a variety of targets. Therefore, ROS in all forms act as signalling molecules that regulate many cellular processes, such as plant growth/development and acclimation responses to stress (Apel & Hirt 2004; Foyer & Noctor 2005; De Gara *et al.* 2010). Plasma membrane NADPH-dependent oxidases play a key role in ROS generation in cell signalling processes, mainly for biotic stress impact. Although much attention has been given to NADPH oxidases, metabolic processes in chloroplasts, mitochondria and peroxisomes are also important sources of ROS production (Kangasjärvi *et al.* 2012). During periods of biotic or abiotic stress, ROS levels rise significantly, potentially leading to oxidative stress and damage to cell components (Apel & Hirt 2004). However, plants possess an extensive spectrum of antioxidants and antioxidative enzymes to manage this situation and ensure optimal cellular ROS concentrations to avoid damage while allowing signalling events. This defence and signalling system is highly dynamic and involves both generation and scavenging of ROS so as to retain balanced levels of ROS in plant cells (Mittler *et al.* 2004, 2011).

The photosynthetic electron transport (PET) chain is a major source of ROS in plant cells. During photosynthesis, ROS are predominantly produced when CO_2 is limiting, *e.g.*, under drought stress when stomata are closed (Cruz de

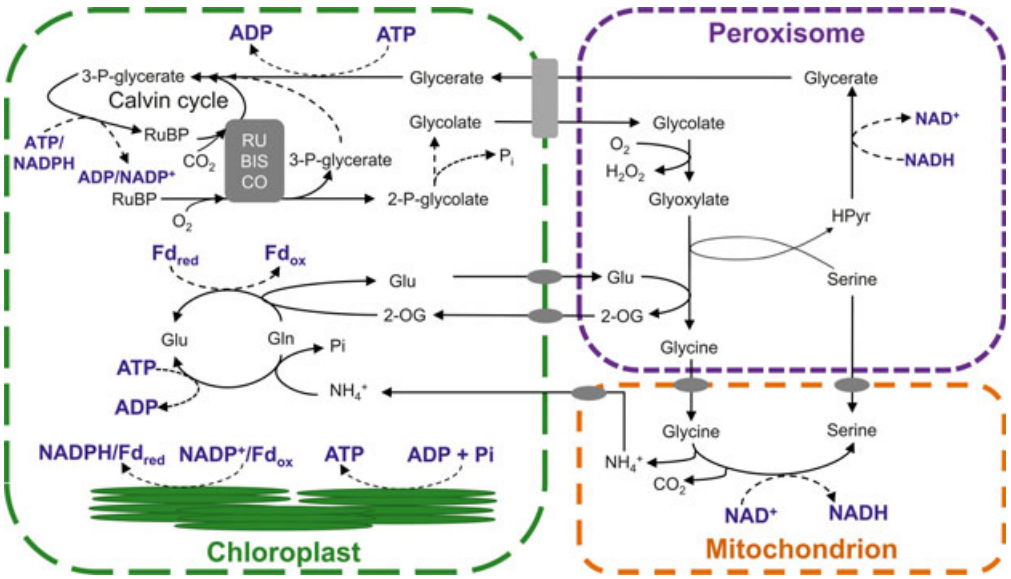

Fig. 1. Reaction scheme of photorespiration (adapted from Heldt & Piechulla 2010). Photorespiration is a consequence of the oxygenase reaction of Rubisco and involves reactions located in chloroplasts, mitochondria and peroxisomes. In contrast to photosynthesis, during photorespiration, O_2 is fixed by Rubisco while CO_2 and H_2O_2 are produced during detoxification of glycolate. In addition, photorespiration requires reducing equivalents (NAD(P)H, Fd_{red}) and energy (ATP), and two important amino acids – serine and glycine – are synthesised. Glu = glutamate; Gln = glutamine; 2-OG = 2-oxoglutarate; HPyr = hydroxypyruvate; Fd_{red} = reduced ferredoxin; Fd_{ox} = oxidised ferredoxin.

Carvalho 2008) or in high light (Mittler *et al.* 2004). Plants can progressively acclimate to deal with such stress situations, ranging from prevention of acceptor limitation to down-regulation of photosynthetic electron flow, in order to prevent irreversible damage from ROS (Scheibe *et al.* 2005; Scheibe & Dietz 2012).

Photorespiration itself is one of the major metabolic processes leading to ROS production. In peroxisomes, large amounts of hydrogen peroxide (H_2O_2) are formed from not only glycolate oxidase (GOX; Foyer *et al.* 2009) but also from other ROS-generating systems, such as xanthine oxidase (del Rio *et al.* 2006; Corpas *et al.* 2008). Photorespiration-linked changes in redox cycling could also alter NAD(P)/H redox states in chloroplasts and mitochondria because photorespiration involves inter-compartment cycling through redox shuttles (Igamberdiev & Gardeström 2003; Hanke *et al.* 2009). Thus, factors that alter the rate of photorespiration could influence levels of intracellular ROS in plants cells by both increasing and decreasing ROS production (Scheibe *et al.* 2005; Foyer *et al.* 2009).

The process of photorespiration helps to minimise ROS production by directly or indirectly using ATP and NADPH. The re-assimilation of NH_4^+ arising from glycine decarboxylation consumes reducing equivalents from ferredoxin and/or NAD(P)H as well as ATP. Similarly, conversion of glycerate to PGA consumes ATP and regenerates ADP. The requirement of NADH for hydroxypyruvate reduction would provide an additional sink for reducing equivalents, which can originate from chloroplasts *via* the malate valve or from the mitochondrial TCA cycle. Thus, photorespiration is a significant and important component of processes involved in minimising ROS production (by dissipating excess reducing equivalents as well as energy), although at first sight it is itself a source of H_2O_2.

In this mini review, we attempt to highlight the dynamic and multifunctional nature of photorespiratory reactions and their responses to different stress situations. We emphasise that photorespiration not only responds to mild disturbances in the redox state of plant cells. We discuss the contributions of photorespiration as part of a hierarchically acting photosynthetic stress response because of sustained acceptor limitation. We propose that photorespiration can play an important role in maintaining optimal redox state, despite being a source of H_2O_2.

PHOTORESPIRATION AS PART OF THE STRESS RESPONSE TO PREVENT EXCESS ROS ACCUMULATION

Light energy is used for photoreduction of $NADP^+$ and to establish a proton gradient, which drives ATP production. Most of the generated NADPH and ATP are used for CO_2 assimilation in the Calvin cycle; but this pathway is not the only sink for photosynthetic energy. Metabolic pathways requiring reducing equivalents and ATP are located in different compartments within the cell. Transport of the products of photosynthetic light reactions is in most cases indirect, *via* shuttle systems, mainly transporting malate across membranes as a carrier of reducing equivalents (Scheibe 2004). In different environmental situations, the metabolic demand of the cell for reducing equivalents and ATP in the different compartments fluctuates (Hanke *et al.* 2009); the flexible adjustment of their production relative to consumption is a major task controlled through various regulatory mechanisms.

In general, PET produces more reducing equivalents than required in biosynthetic metabolism relative to ATP (Stitt 1986). CO_2 limitation in the Calvin cycle and lack of $NADP^+$ or other acceptors in photosystem I (PSI) will lead to formation and accumulation of ROS that must be removed by various systems, including the water–water cycle (Asada 1999; Serrato *et al.* 2004; Spinola *et al.* 2008). In situations of enhanced or multiple stresses, *e.g.*, high light stress in conjunc-

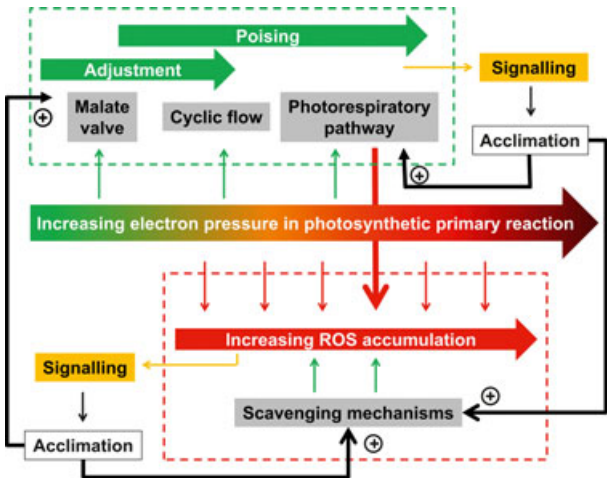

Fig. 2. Scheme of photosynthetic stress response due to increased electron pressure in the photosynthetic primary reaction. During the photosynthetic stress response, four mechanisms act more or less hierarchically: (i) adjusting NADPH/ATP ratio, (ii) preventing ROS accumulation, (iii) scavenging accumulated ROS, and (iv) signalling for acclimation. Within these mechanisms, different reactions take place side-by-side or even build upon each other. Malate valve and cyclic electron flow are important for adjustment and for preventing ROS accumulation by poising. Photorespiration is also an essential factor in poising reducing equivalents and energy, but also produces H_2O_2, which might be an important signalling factor for induction of scavenging mechanisms resulting in increased ROS detoxification.

tion with drought, salt, chilling, etc., severe problems can arise for a cell. Four mechanisms or steps in photosynthetic response to stress can be distinguished: (i) prevent acceptor limitation, (ii) prevent ROS accumulation in cases of acceptor limitation, (iii) detoxify ROS when in excess, and (iv) signal induction for acclimation (Fig. 2). The properties of these hierarchically acting systems are described below.

The malate valve system (Scheibe 2004) is one of the first options used to avoid acceptor limitation at PSI/ferredoxin. Oxaloacetate is reduced to malate through NADP-malate dehydrogenase (MDH) using NADPH from the PET. Malate is then transported *via* dicarboxylate transporters (Taniguchi *et al.* 2002) to the cytosol. Thus the malate valve is a system to adjust the NADPH/ATP ratio, preventing imbalances that restrict photosynthetic electron flow, and redirecting excess reducing equivalents into other compartments for further use (Backhausen *et al.* 1998; Scheibe 2004). The key enzyme of the malate valve, namely NADP-MDH, is light-activated, but $NADP^+$ inhibits activation; therefore, a high $NADP^+$/NADPH ratio decreases the NADP-MDH activation state (Scheibe & Jacquot 1983). This post-translational regulation provides the system with high flexibility and robustness in order to maintain redox homeostasis within the chloroplast under changing conditions (Scheibe *et al.* 2005). It has also been shown that the NADP-MDH capacity increases during ongoing stress when it is fully activated for an extended time period (Savitch *et al.* 2001; Becker *et al.* 2006). However, a gene knockout for NADP-MDH does not lead to significant phenotypic changes under high light stress (Hebbelmann *et al.* 2012). This suggests that the malate valve acts in concert with other systems for flexible adjustment of the ATP/NADPH ratio in order to prevent acceptor limitation at PSI, but is itself not essential to avoid ROS accumulation. These transgenic plants lacking NADP-MDH appear to increase, among other systems, photorespiratory capacity under high light conditions, and other shuttle systems, such as the alternative oxidase (AOX) in mitochondria, might help to consume reducing equivalents (Hebbelmann *et al.* 2012).

Under more severe acceptor limitation at PSI, induced by high light or drought, the importance of cyclic electron flow (CET) is well established for C_3 plants (Munekage *et al.* 2004). In contrast to the malate valve, where excess NADPH is used in other systems, CET decreases the generation of NADPH while simultaneously increasing ATP production. This mechanism allows adjustment of the ATP/NADPH ratio in situations of ongoing acceptor limitation. In addition, there is an increased proton gradient across the thylakoid membrane, resulting in the generation of qE. This indicates the importance of CET under conditions of sustained stress. Several pathways of CET are possible, and it is still debated whether there are specific functions associated with the different pathways in stress response or adjustment of the ATP/NADPH ratio (Miyake 2010). Nevertheless, CET is capable of adjusting the NADPH/ATP ratio to optimise photosynthesis. CET is, however, mainly important in situations of CO_2 limitation and under continued lack of $NADP^+$ as electron acceptor at PSI. Under these conditions, CET prevents uncontrolled ROS formation by (i) cycling electrons back to the components of PET and (ii) building up qE to allow quenching of excess light energy leading to its dissipation as heat (Foyer *et al.* 2012).

Photorespiration is a major sink for reducing equivalents as well as ATP in order to regenerate acceptors for the primary reactions (Foyer *et al.* 2009). The connection between photorespiration and CET has been shown in recent studies (Yiotis & Manetas 2010; Foyer *et al.* 2012). In addition, there is evidence for a connection between photorespiratory glycine decarboxylation and activity of the AOX pathway (Bykova *et al.* 2005). A gene knockout for AOX1A results in an increase of various other systems for removal of excess reducing equivalents, including photorespiratory components (Strodtkötter *et al.* 2009). Apparently, the photorespiratory pathway is used in situations of photo-oxidative stress in order to prevent excess ROS formation, when O_2 partial pressure increases in the light while CO_2 partial pressure decreases.

High irradiance, increased temperature and closed stomata cause severe CO_2 limitation for the Calvin cycle, resulting in excess reduction power and energy. Due to increasing acceptor limitation in such situations, classical poising systems are of limited use, because it is not the adjustment of ATP/NADPH but the demand for NADPH and ATP that causes the problem. To prevent oxidative stress under these conditions, photorespiration might assume a more prominent role in consuming reducing equivalents and energy in order to prevent ROS accumulation (Fig. 3). Thus, photorespiration, also known as the oxidative photosynthetic cycle (OPC), will maintain flux through the system when the reductive photosynthetic cycle (RPC or Calvin cycle) is limited by CO_2 supply, while the light reactions are still running (Tolbert *et al.* 1995).

There are direct and indirect possibilities for dissipation of photosynthetic reducing power and energy in the photorespiratory pathway. First, ATP, NADPH and NADH are directly utilised and the acceptors ADP, $NADP^+$ and NAD^+ are regenerated. Furthermore, reduced ferredoxin is used by Fd-GOGAT and H_2O_2 is scavenged by catalase in peroxisomes

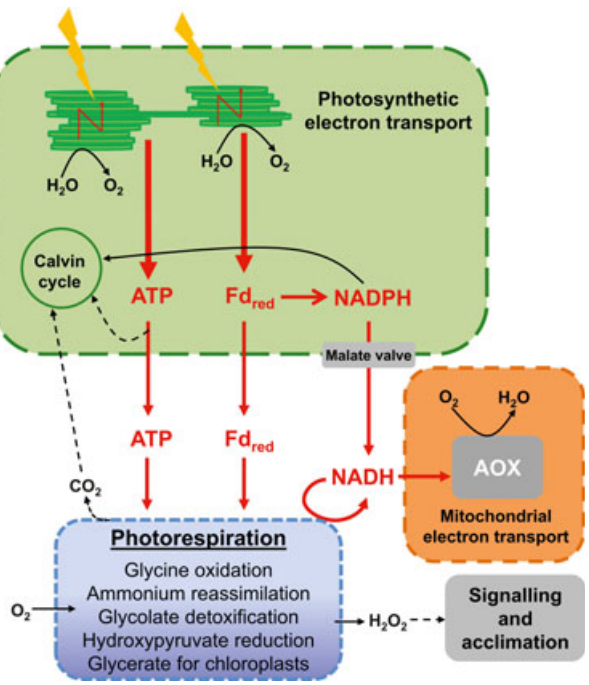

Fig. 3. The function of photorespiration in photosynthetic stress response. Photorespiration is a sink for excess reducing equivalents and energy in order to regenerate free acceptor molecules (ADP, Fd_{ox} and $NADP^+$) at the primary reaction. To achieve this, photorespiration uses different steps (glycine oxidation, ammonium reassimilation, glycolate detoxification and hydroxypyruvate reduction). The produced CO_2 can be reused in the Calvin cycle, thus decreasing the oxygenase reaction of Rubisco. Photorespiratory H_2O_2 release could be a signalling factor to acclimate metabolism to the actual stress situation.

(Foyer *et al.* 2009). In addition, as an indirect effect, the use of NADPH and ATP optimises both linear and cyclic electron flow, the flux through AOX is promoted by photorespiration (Igamberdiev *et al.* 2001; Bykova *et al.* 2005), and release of CO_2 in the photorespiratory pathway can mitigate CO_2 limitation in the Calvin cycle due to its intracellular recycling within the cells (Riazunnisa *et al.* 2006; Busch *et al.* 2012). All these mechanisms, namely the direct and indirect consumption/removal of excess reducing power and energy through photorespiration, are part of photosynthetic stress responses, especially in situations of massive CO_2 limitation for the Calvin cycle (Fig. 3). All these properties turn the photorespiratory pathway into a suitable system to prevent excess ROS accumulation.

Nevertheless, ROS accumulate in situations of ongoing or multiple stress impact (Fig. 2), and the third step of the stress response, namely ROS detoxification, becomes increasingly important to enable sustained photosynthetic performance under such stress conditions. Beside the classical mechanisms for ROS scavenging, such as the Beck–Halliwell–Asada pathway (Asada 1999) and NADPH-thioredoxin reductase (NTRC) system (Serrato *et al.* 2004; Spinola *et al.* 2008), there is evidence for a dynamic role of the photorespiratory pathway in ROS removal under various stress situations. This will be discussed in detail below. The final step in stress response involves ROS signalling (Mittler *et al.* 2011) to achieve rearrangement of metabolism as required for each situation of environmental stress.

PHOTORESPIRATION MITIGATES OXIDATIVE STRESS UNDER ABIOTIC STRESS CONDITIONS

A marked rise in levels of intracellular ROS is a common feature in response to several types of stress. As described above, ROS scavenging and ROS signalling to achieve acclimation are important parts of the stress response. Photorespiration appears to be a part of the stress response to prevent ROS formation, despite being a source of ROS production in peroxisomes. There is evidence indicating the importance of photorespiratory reactions to keep ROS levels low and thus protect against oxidative damage under a variety of stress conditions (Table 1). We here describe selected examples for the contribution of ROS under different abiotic stress conditions and the involvement of photorespiration in this part of the stress response.

Drought

Drought stress causes stomatal closure, decreases photosynthetic carbon assimilation, causing metabolic disturbances (Umezawa *et al.* 2006; Seki *et al.* 2007; Sirichandra *et al.* 2009; Wang *et al.* 2011; Marshall *et al.* 2012). A decrease in stomatal conductance under water deficit conditions decreases intercellular CO_2 levels within leaves, facilitating an increase in photorespiration. Consequently, photorespiration can act as an effective electron sink in plants during drought stress. For example, in tomato plants, the percentage of photosynthetic electrons dissipated by CO_2 assimilation decreased while the contribution of photorespiration increased from 23% to 40% under water stress (Haupt-Herting & Fock 2002), allowing photorespiration to act as an important energy dissipation pathway for protection of the photosynthetic apparatus from photodamage during drought stress. In another study with four grape varieties, combined measurements of gas exchange and chlorophyll fluorescence demonstrated that photorespiration increased under moderate water stress and helped maintain relatively high photochemical efficiency of PS II and rapid recovery of net photosynthesis after re-watering (Guan *et al.* 2004).

The role of photorespiration during water stress was assessed in barley mutants having reduced activity of the photorespiratory enzymes glycine decarboxylase (GDC) or serine:glyoxylate aminotransferase (SGAT) (Wingler *et al.* 1999). The drought-induced need for increased photorespiratory flux was evident from the increase in glycine (Gly) content in drought-stressed leaves of the GDC mutant. Abogadallah (2011) observed that under moderate stress, photorespiration was quite high, as evidenced by increases in protein levels of GDC-H and SGAT, as well as increased glyoxylate and the Gly/Ser ratio in salt-tolerant *Pancratium maritimum*. Such strong induction of components involved in photorespiration suggests the importance of the photorespiratory pathway in protecting plants from stress-induced damage.

Glycine, generated during photorespiration, is a substrate for biosynthesis of glutathione, a key component of antioxidant defence systems (Foyer & Noctor 2000). Maize, when subjected to drought stress in ambient CO_2, showed a two- to three-fold increase in glycine and serine compared to water-sufficient controls. Such transient accumulation of serine and glycine was not observed under non-photorespiratory conditions. Sicher & Barnaby (2012) hypothesised that moderate drought inhibited

Table 1. The spectrum of protection by photorespiration of plant cells against different abiotic and biotic stresses.

Stress/Plant	Modulated photorespiratory component	References
Water stress		
Tomato	Increased consumption of photosynthetic electrons in photorespiration, offering an alternative energy dissipation pathway to avoid photo-damage during drought stress	Haupt-Herting & Fock (2002)
Grapevine	Increase in rate of photorespiration and high photochemical activity to avoid photo-damage	Guan *et al.* (2004)
Salt/Salinity		
Tomato	Alleviation of oxidative stress in salt tolerant plants by salt induced peroxisomal antioxidant enzymes	Mittova *et al.* (2003)
Pancratium maritimum	Significant increases in photorespiratory components: GDC-H, SGAT and GS2, during moderate water and salt stress	Abogadallah (2011)
Puccinellia tenuiflora	Enhanced expression of glycolate oxidase, catalase and SHMT contributed to salinity tolerance of the halophyte	Yu *et al.* (2011)
Chilling		
Rice	Increased levels of catalase activity was observed in chilling tolerant rice cultivars	Guo *et al.* (2006)
Rice	Enhanced expression of catalase and photorespiratory components such as GDH and SHMT	Cheng *et al.* (2007)
Heavy Metal		
Pea	Increased protein levels of GOX in the isolated peroxisomes from the plants grown with Cadmium	McCarthy *et al.* (2001)
Pea	enhanced activity of peroxisomal HPR, when exposed to Cadmium	Romero-Puertas *et al.* (2002)
Rice	enhanced activity of peroxisomal HPR, when exposed to Cadmium	Cai *et al.* (2011)

GDC = glycine decarboxylase; GS = glutamine synthetase; GOX = glycolate oxidase; HPR = hydroxypyruvate reductase; SGAT = serine-glyoxylate aminotransferase; SHMT = serine hydroxymethyl transferase.

the CO_2 pumping mechanism and activated the photorespiratory pathway even in C_4 plants. Since photorespiration can account for more than 70% of total H_2O_2 generated under drought stress, photorespiratory H_2O_2 can be a major signal of drought that modulates the redox states of antioxidant pools in the leaf (Noctor *et al.* 2002; Scheibe & Beck 2011). In summary, photorespiration appears to be a signal for an adaptation to drought, as the pathway not only generates H_2O_2, but also provides glycine for glutathione synthesis.

Rivero *et al.* (2009) observed that cytokinin-mediated induction of photorespiration was beneficial in protecting photosynthetic processes during water stress. Transgenic tobacco plants overexpressing P_{SARK}::IPT (isopentenyltransferase under control of the promoter senescence-associated receptor kinase) displayed an increase in peroxisomal catalase and elevated CO_2 compensation point during drought compared to wild-type plants, implying the induction of photorespiration. The contribution of photorespiration to tolerance of the transgenic plants in restricted water regimes was also reflected in an increase of transcripts coding for several photorespiratory enzymes (*e.g.* GOX, GDC and SHMT).

Further, plant peroxisomes are known to proliferate in response to various stress situations (Lopez-Huertas *et al.* 2000; Castillo *et al.* 2008; León 2008). The stress-induced rise in H_2O_2 can be ameliorated by expanding the peroxisome population and thus assist in restoration of the cellular redox balance.

Salinity

Salinity is one of the main environmental factors limiting plant growth and productivity (Allakhverdiev *et al.* 2000). Besides inducing mechanisms to either exclude salt from cells or tolerate its presence within cells, salinity stress can increase photorespiration in plants (Parida & Das 2005). The accelerated generation of ROS under salt and drought stress, along with induction of ROS scavenging systems, has been reported for C_3 and C_4 plants (Miller *et al.* 2010). In all plants, photorespiration can provide a route to rapidly regulate ROS production during adaptive responses to salinity.

Salt-induced oxidative stress in tomato plants results in increased lipid peroxidation and a decrease in reduced ascorbate and glutathione (Mittova *et al.* 2003), probably as a result of increased ROS generation by the peroxisomal GOX. However, there was an up-regulation of the peroxisomal antioxidative enzymes (SOD and catalase) and CuZn-SOD proteins of peroxisomes in leaves of tomato (*Lycopersicon esculentum*) and its wild, salt-tolerant species (*L. pennellii*). Such enhanced activity of antioxidative enzymes in peroxisomes in response to salinity appears to play a role in alleviation of salt-induced oxidative stress in the tolerant tomato species. Further, Redondo-Gómez *et al.* (2010) suggested that photorespiration and CET together protect the halophyte *Arthrocnemum macrostachyum* against excess radiation under high salinity.

Abogadallah (2011) used the salt-tolerant *Pancratium maritimum* L. to assess the contribution of photorespiration to oxidative load during salt stress. In parallel with inhibition of photosynthesis under moderate salt stress, the Gly/Ser ratio and glyoxylate were dramatically enhanced. The increase in Gly/Ser ratio and glyoxylate has been used as an indicator of increased photorespiratory activity under stress conditions (Novitskaya *et al.* 2002; Fahnenstich *et al.* 2008). The strong up-regulation of GDC-H, SGAT and GS2 transcripts further indicates that the photorespiratory pathway is induced under moderate salt stress.

The photorespiratory hydroxymethyltransferases play a critical role in controlling cell damage caused by abiotic stresses such as high light and salt, supporting the notion that photorespiration acts as a dissipatory mechanism in plants to

minimise the production of ROS and mitigate oxidative damage (Moreno *et al.* 2005). *Arabidopsis* mutants deficient in a serine hydroxymethyltransferase gene (*shmt1-1*) show retarded growth and increased accumulation of ROS in the presence of 50 mM NaCl when compared with control plants. The loss of SHMT in these *Arabidopsis* mutants compromised the photorespiratory cycle and led to overproduction of ROS, making the plants susceptible to salt stress (Moreno *et al.* 2005).

Recently, it was shown that the halophytic grass *Puccinellia tenuiflora* develops several ROS scavenging mechanisms to cope with moderate salinity, including enhanced photorespiration (Yu *et al.* 2011), due to a reduction in water availability and CO_2 assimilation during salt treatment (Niyogi 1999). The plants also show enhanced GOX and catalase activity, suggesting increased glycolate oxidation as well as H_2O_2 scavenging. In addition, increased expression of SHMT protein indicated activation of the photorespiratory pathway to ensure salinity tolerance (Yu *et al.* 2011).

Chilling

Low temperature can enhance O_2 uptake processes due to increased O_2 solubility, which could enhance photorespiration (Flexas *et al.* 1999). The chilling-induced physiological imbalance leads to elevated levels of ROS (Suzuki & Mittler 2006; Einset *et al.* 2007). To counter increased ROS levels, antioxidant machinery is induced. During cold stress, catalase is induced, as observed in two chilling-tolerant rice cultivars (Guo *et al.* 2006). Further, using transcriptome analysis, Cheng *et al.* (2007) showed that a ROS-mediated regulatory module functions as an early component of the chilling stress response pathway in rice, including up-regulation of genes such as catalase, indicating the contribution of photorespiration in cold stress situations.

Similarly, Hoshida *et al.* (2000) found that transgenic rice over-expressing chloroplastic glutamine synthetase (GS2) shows increased tolerance to chilling stress by virtue of increased capacity for photorespiration. Photorespiratory GOX activity is affected by low temperatures (Streb *et al.* 2005); short-term (4 h) chilling stress in the evergreen plant *Pachysandra terminalis* activates photorespiration, as evidenced by up-regulated expression of GOX and HPR genes (Zhou *et al.* 2006).

Heavy metals

Exposure of plants to elevated levels of heavy metals results in oxidative stress due to enhanced ROS accumulation within the cells. If damage is not fatal, an increase in ROS can initiate a signalling cascade that mediates the overall stress adaptation responses as a specific defence. For example, cadmium (Cd) induces a concentration-dependent oxidative stress in pea plants (Sandalio *et al.* 2001); at the subcellular level, Cd alters oxidative metabolism in peroxisomes and induces senescence in these organelles (McCarthy *et al.* 2001).

Romero-Puertas *et al.* (2002) found enhanced activity of HPR in pea plants exposed to 50 μM Cd, indicating increased photorespiration. In another recent study, Cai *et al.* (2011) used proteome analysis of leaves from rice genotypes varying in Cd tolerance and accumulation to dissect genotypic differences in Cd toxicity. The Cd-tolerant (cv. Bing97252) rice genotype showed increased expression of hydroxypyruvate reductase (HPR) protein, whereas the Cd-sensitive (cv. Xiushui63) rice had decreased HPR expression. The response of photorespiratory enzymes in this case underlines the importance of photorespiration during heavy metal toxicity, particularly Cd.

From all the above results it can be concluded that photorespiration is an important pathway in the direct response to stress. There is also evidence for the involvement of photorespiration in the next steps of the stress response, resulting in signalling and acclimation to cope with even more stressful conditions, as already discussed.

DISTURBANCE IN REDOX STATE CAUSES UP-REGULATION OF PHOTORESPIRATORY ACTIVITY: TRANSGENIC APPROACHES

Photosynthesis and photorespiration are high flux pathways that involve redox exchange between intracellular compartments. Photorespiration facilitates NADH production in the mitochondria and uses NADH in the peroxisomes, while promoting the export of both NADPH and ATP from the chloroplast and thus facilitating energy dissipation. This shows that photorespiration may exhibit tight cross-regulation with other metabolic pathways so as to maintain redox homeostasis under oxidative stress conditions (Foyer *et al.* 2009). Analysis of mutants lacking components of the photorespiratory pathway and related metabolism revealed a very complex picture of a network designed to optimally balance any deviation from a steady-state in redox and provide protection from damage caused by ROS in photosynthesising plant cells (Hanke *et al.* 2009).

The developmental state of a plant is also of importance as far as the type of response is concerned since long-day plants induced to flower early show a completely different response to high light stress than plants growing in short-day conditions (Becker *et al.* 2006) reflecting the different requirements of basic metabolism. For example, lack of the chloroplast NTRC system results in an increase of photorespiration, but also interferes with plant performance under short-day conditions (Lepistö *et al.* 2009), indicating that there is a link between sensing the photoperiod and the respective metabolic and protective pathways that are active in these different developmental stages. As another example, importance of the redox state for cross-talk between day length-dependent development and photorespiration was shown in *Arabidopsis* mutants lacking the photorespiratory *Cat2* gene (Queval *et al.* 2007).

Because of the crucial nature of photorespiration, mutants deficient in certain photorespiratory enzymes (located in chloroplasts, mitochondria or peroxisomes) are often quite sensitive to stress (*e.g.*, catalase, see Mhamdi *et al.* 2010). Similarly, a deficiency in any key redox modulating component of not only the chloroplast but also mitochondria and peroxisomes could result in up-regulation of photorespiration, as an obvious strategy to keep ROS levels low (Table 2).

Chloroplastic NTRC belongs to the thioredoxin system that controls metabolic and regulatory pathways in plants (Serrato *et al.* 2004). T-DNA insertion lines of NTRC plants (*ntrc* mutants) grown under short days (SD) show decreased CO_2 assimilation, associated with enhanced rates of photorespiration. Transcript profiling of SD-grown plants revealed increased expression of photorespiratory transcripts such as

Table 2. Examples of enhanced photorespiratory activity/components, as a result of redox disturbance in different compartments of the cell.

Plant	Modulated redox component	Response of photorespiration	References
Chloroplast			
Arabidopsis (*ntrc* mutant)	chloroplastic NADPH-thioredoxin reductase	Enhanced expression of photorespiratory genes (CAT2, GGT1, HPR, SHM1, GDC-P1 and Fd-GOGAT1) under short day conditions	Lepisto *et al.* (2009)
Arabidopsis (*pgr5* mutant)	deficient in cyclic electron flow (*proton gradient regulation*) around PS I	Evidence for PS I protection by enhanced photorespiration in high light	Munekage *et al.* (2008)
Arabidopsis (*nadp-mdh* mutant)	knockout of chloroplastic NADP-MDH	Enhanced expression of GDC-P protein and shift in Gly/Ser ratio under high light. Preference for photorespiratory conditions for sustained photosynthesis	Hebbelmann *et al.* (2012)
Mitochondria			
Arabidopsis (*aox-1A* mutant)	mitochondrial alternative oxidase type 1A	Enhanced photorespiration as indicated by increased Gly/Ser ratio and increased expression of GDC-P protein	Strodtkotter *et al.* (2009)
Tobacco (CMSII mutant)	deficiency in mitochondrial complex I	Increased photorespiratory flux and increased glycolate oxidase (GO)	Priault *et al.* (2006)
Cucumber (MSC16: Mosaic mutant)	dysfunctional mitochondrial complex I	Increased photorespiration due to decreased stomatal and mesophyll conductance to CO_2	Juszczuk *et al.* (2007)
Peroxisome			
Arabidopsis (*cat2* mutant)	knock-out of *CATALASE2*	Increased photorespiratory H_2O_2, marked perturbation of intracellular redox state and activation of oxidative signaling pathways (eg. glutathione redox ratio)	Queval *et al.* (2007)

CMSII = cytoplasmic male sterile II; GO = Glycolate oxidase; GDC = glycine decarboxylase; Gly = glycine; Ser = Serine; *nadp-mdh* = NADP- dependent malate dehydrogenase mutant; CAT2 = *catalase2*; GGT1 = *Alanine-2-oxoglutarate aminotransferase*; HPR1 = *Hydroxypyruvate reductase*; SHM1 = *Serine hydroxymethyl transferase*; GDC-P1 = *Glycine decarboxylase-P protein*; Fd-GOGAT = plastidic *Ferredoxin dependent glutamate synthase*.

those coding for catalase, GDC-P protein and hydroxypyruvate reductase (HPR), and exhibited multiple signs of metabolic imbalances (Lepistö *et al.* 2009). The authors suggested such increased photorespiration was a means to dissipate excess light energy in SD leaves to protect the photosynthetic machinery from damage (Kozaki & Takeba 1996; Lepistö *et al.* 2009). In another study, with *pgr5* (proton gradient regulation 5) mutants of *Arabidopsis*, enhanced photorespiration was found to be necessary for photoprotection of PSI under high light (Munekage *et al.* 2008). The *pgr5* mutants do not perform cyclic electron flow around PSI, leading to a decrease in the ATP/NADPH ratio during photosynthesis and causing over-reduction of the stroma. These mutants also showed decreased CO_2 assimilation under high light conditions (Munekage *et al.* 2004; Nandha *et al.* 2007).

In a recent study with the *nadp-mdh* mutant of *Arabidopsis* (Hebbelmann *et al.* 2012) there was an increase in the components of photorespiration, besides NTRC-related components, that helped to sustain high photosynthetic rates even under excess light. The mutant plants showed decreased photosynthesis under non-photorespiratory conditions and also increased expression of GDC-P protein under high light conditions. There was a shift in the glycine-to-serine ratio, suggesting altered patterns of photorespiration of these *nadp-mdh* mutants.

An increase in photorespiratory components was also observed in the *aox-1A* mutant of *Arabidopsis* (Strodtkötter *et al.* 2009). Application of antimycin A (cytochrome pathway inhibitor) led to leaf tissue damage caused by increased ROS accumulation (two- to nine-fold) and Gly/Ser ratio (seven-fold) as compared to wild-type control plants. By blocking the cytochrome pathway, the NADH from glycine decarboxylation cannot be re-oxidised, and this NADH build up leads to increased Gly/Ser ratios, indicating that the carbon flux through GDC may have been affected. It appears that *aox1a* mutants increase their capacity for photorespiration to compensate for the loss of AOX1A.

Priault *et al.* (2006) showed that the cytoplasmic male sterile II (CMSII) mutant of tobacco lacking mitochondrial complex I has increased photorespiration. Using isotopic mass spectrometry, these authors showed that increased photorespiration was a consequence of increased internal resistance to CO_2 diffusion. The retarded leaf growth and lower photosynthetic activity were largely overcome when plants were grown under elevated CO_2, and this shows the importance of enhanced photorespiration in suppressing carbon assimilation in mutant plants. Juszczuk *et al.* (2007) analysed the effects of dysfunctional mitochondrial complex I on photorespiration using the mosaic mutant of cucumber (MSC16). Similar to CMSII mutants of tobacco (Priault *et al.* 2006), MSC16 mutants also show a significant increase in photorespiration as a result of a large decrease in mesophyll and stomatal conductance to CO_2 when compared to the wild type.

During photorespiration, H_2O_2 is obligatorily produced at high rates in the peroxisomes, where it is metabolised primarily by catalase (Queval *et al.* 2007). The catalase-deficient *Arabidopsis* mutant *cat2* shows conditional oxidative stress dependent on photorespiration. These mutants show stress phenotypes when grown in ambient air at moderate irradiance but not in elevated CO_2 conditions (Queval *et al.* 2007). The retarded growth of the mutants is associated with induction of H_2O_2-responsive transcripts. When plants were transferred from high CO_2 conditions to ambient air, accumulation of oxidative mar-

ker transcripts resumed, indicating the important role of catalase in redox homeostasis under physiological conditions.

In a reversal of roles, evidence indicates that a reduced photorespiratory capacity, results in significant oxidative stress. A homozygous barley mutant deficient in GDC complex showed no obvious phenotypic difference to wild-type plants, but these plants had enhanced chloroplastic ATP/ADP and NADP/NADPH ratios under photorespiratory conditions (Igamberdiev *et al.* 2001). This indicates that deficiency in GDC lead to over-reduction of chloroplasts accompanied by increased respiration and a reduction in glyoxylate. Thus, photorespiration can serve as an efficient redox transfer mechanism in plants (Igamberdiev *et al.* 2001). In another study with *Arabidopsis*, the T-DNA insertional mutation of both genes coding for GDC-P protein resulted in a lethal phenotype, where plants only survived for a few weeks under non-photorespiratory conditions (Engel *et al.* 2007). Similarly, deficiency in mitochondrial uncoupling protein (UCP1) results in decreased glycine decarboxylation, indicating a down-regulation of photorespiration; these plants also suffer localised oxidative stress (Sweetlove *et al.* 2006).

OUR CONCEPT AND CONCLUDING REMARKS

Our concept of photorespiration as an important mechanism to meet the challenge of excess reducing equivalents and concomitant formation of ROS as common upon stress impact is based on multiple lines of evidence. Plants exposed to mild or severe stress adapt to abiotic stress, utilising multiple mechanisms to dissipate energy and prevent ROS generation/accumulation (Strodtkötter *et al.* 2009; Hebbelmann *et al.* 2012). The present review emphasises the role of photorespiration as an important component of such flexible systems to optimise photosynthesis while protecting against oxidative stress. Photorespiration integrates the functions of chloroplasts, peroxisomes, mitochondria and the cytoplasm. It is therefore necessary to identify the actual redox signals that connect photosynthesis and photorespiration operating across the cellular compartments. While the signals appear to be mainly ROS (in particular, H_2O_2), the targets related to induction of photorespiration need to be identified. Different types of stress require specific adaptations and cooperation among different systems. It is therefore of great importance to carefully design future experiments to uncover more molecular and functional details of such a flexible network. The study of double and triple mutants will reveal the importance of such an integrating network that allows adjustment to different types of stress, occurring either alone or in combination.

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