REVIEW

Optimization of photosynthesis by multiple metabolic pathways involving interorganelle interactions: resource sharing and ROS maintenance as the bases

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Abstract The bioenergetic processes of photosynthesis and respiration are mutually beneficial. Their interaction extends to photorespiration, which is linked to optimize photosynthesis. The interplay of these three pathways is facilitated by two major phenomena: sharing of energy/metabolite resources and maintenance of optimal levels of reactive oxygen species (ROS). The resource sharing among different compartments of plant cells is based on the production/utilization of reducing equivalents (NADPH, NADH) and ATP as well as on the metabolite exchange. The responsibility of generating the cellular requirements of ATP and NAD(P)H is mostly by the chloroplasts and mitochondria. In turn, besides the chloroplasts, the mitochondria, cytosol and peroxisomes are common sinks for reduced equivalents. Transporters located in membranes ensure the coordinated movement of metabolites across the cellular compartments. The present review emphasizes the beneficial interactions among photosynthesis, dark respiration and photorespiration, in relation to metabolism of C, N and S. Since the bioenergetic reactions tend to generate ROS, the cells modulate chloroplast and mitochondrial reactions, so as to ensure that the ROS levels do not rise to toxic levels. The patterns of minimization of ROS production and scavenging of excess ROS in intracellular compartments are highlighted. Some of the emerging developments are pointed out, such as model plants, orientation/movement of organelles and metabolomics.

Abbreviations

2-OG	2-Oxoglutarate
3-PGA	3-Phosphoglycerate
AOX	Alternative oxidase
APX	Ascorbate peroxidase
ASC	Ascorbate
AT	Adenylate transporter
BPGA	Bisphosphoglycerate
CAT	Catalase
CET	Cyclic electron transport
DHAP	Dihydroxyacetone phosphate
DiT1/2	Plastidic 2-oxoglutarate-malate transporter/plastidic glutamate-malate transporter
DTC	Dicarboxylate/tricarboxylate carrier
Fd	Ferredoxin
FNR	Fd-NADP$^+$ reductase
GABA	γ-Aminobutyric acid
GAP	Glyceraldehyde 3-phosphate
GDC	Glycine decarboxylase
GO	Glycolate oxidase
GOGAT	Glutamine:oxoglutarate aminotransferase
GPx	Glutathione peroxidase
GS	Glutamine synthetase
GSH	Glutathione
MET	Mitochondrial electron transport
NiR	Nitrite reductase
NiTr	Nitrate transporter
NR	Nitrate reductase
OAA	Oxaloacetate
PC	Plastocyanin
PEP	Phosphoenolpyruvate

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PLGG1	Plastidic glycolate glycerate transporter
PQ	Plastoquinone
PrxR	Peroxiredoxins
PyrT	Pyruvate transporter
ROS	Reactive oxygen species
SOD	Superoxide dismutase
TPT	Triose phosphate/phosphate translocator
XO	Xanthine oxidase

Introduction

Photosynthesis and respiration are the most important primary metabolic processes, being involved in energy supply, besides assimilation/metabolism of carbon, nitrogen and even sulfur in plants. The first phase of photochemical reactions convert solar energy into ATP and NADPH (or reduced ferredoxin), while the second phase consists of biochemical reactions which utilize ATP/NADPH/reduced ferredoxin to reduce inorganic carbon or nitrogen or sulfur. The photochemical reactions, which involve the transfer of electrons and protons, operate at a much higher speed than the biochemical reactions. A balance of these processes is essential not only to optimize, but also to sustain photosynthesis under challenging environments, such as high light.

The importance of mitochondrial oxidative metabolism for the regulation of photosynthetic carbon assimilation has been emphasized in several reviews (Raghavendra and Padmasree 2003; Nunes-Nesi et al. 2011; Millar et al. 2011). The components of bioenergetic metabolism of mitochondria (which include oxidative phosphorylation, NAD(P)H dehydrogenases, cytochrome oxidase pathway, alternative oxidase (AOX) pathway, and uncoupling proteins) are all essential for efficient functioning of chloroplastic photosynthesis (Noguchi and Yoshida 2008; Nunes-Nesi et al. 2008). We present a comprehensive overview of the interactions between chloroplasts and mitochondria, extending to peroxisomes and cytoplasm. The interorganelle interactions are based on two major principles: (i) sharing of energy and metabolite resources, backed by transporters, and (ii) maintenance of cellular redox state at an optimal level. A few of the emerging trends are highlighted.

Sharing of energy and metabolite resources

Besides being the primary source of biological energy, photosynthesis facilitates the conversion of inorganic forms of C, N and S into organic substrates required for metabolic pathways located in different compartments of cell. ATP/NAD(P)H are required for several metabolic reactions, located in compartments, such as chloroplasts, cytosol, mitochondria and peroxisomes (Table 1). Dynamic interactions between organelles ensure the sharing of these energy resources and metabolite use. The result is the optimization of photosynthesis and sustenance at high rates, even under unfavorable conditions.

Cellular requirements of ATP/NAD(P)H: integrated view

The ATP and/or NADPH generated during the photosynthetic electron transport are used in a variety of metabolic processes in the chloroplasts, including the assimilation of CO_2, nitrate and sulfate (Table 1). ATP and NADPH are required also for the biosynthesis of lipids, nucleic acids and pigments (Kramer and Evans 2011). Besides chloroplasts, mitochondria through their oxidative metabolism also provide significant amounts of ATP required for metabolic processes. Role of cytosolic glycolysis in plant cells cannot be ignored even in the light, as triose-P continues to be metabolized to phosphoenolpyruvate (PEP) and pyruvate. ATP produced in glycolytic reactions is an important source of energy for cellular metabolism (Givan 1999).

Under sub-optimal or supra-optimal environmental conditions, there is usually an imbalance in the generation and use of reductants in photosynthesis during illumination. It is essential to dissipate excess redox equivalents to prevent over-reduction of electron transport and thereby to avoid damage to thylakoid membranes (Foyer et al. 2012; Harbinson 2012). Cyclic electron transport by generation of ATP can help balance the requirement for ATP/NADPH, and the Mehler reaction can consume NADPH in thylakoids, but these processes are not sufficient. The excess reducing equivalents are transported from chloroplasts (in the form of DHAP and malate) to the cytosol and can be used to generate NADH. In parallel, the reduction of nitrite to ammonia and oxoglutarate to glutamate within the chloroplasts facilitates the consumption of not only ammonia but also the reduced ferredoxin. Similarly, the mitochondria are capable of either directly oxidizing external NADH and NADPH or indirectly through the shuttles of related metabolites (described in "Metabolite transporters"). Another site of NADH consumption is peroxisomes, wherein hydroxypyruvate reduction is supported by the supply of malate from either mitochondria or chloroplasts.

Metabolite exchange during primary metabolism

Many metabolic processes in plant tissues, such as the assimilation of carbon as well as nitrogen or sulfur, are stimulated by light, due to elevated supply of ATP and NADPH from thylakoid electron transport. These assimilatory pathways are integrated through cross-talks between organelles, to optimize the utilization of energy and

Table 1 Major processes which produce or consume ATP, NADPH, reduced Fd, NADH and their location in different compartments

Compound	Production		Consumption	
	Process	Compartment	Process	Compartment
ATP	Photophosphorylation	Chloroplast	C/N/S assimilation & glycolate to PGA	Chloroplast
	Oxidative phosphorylation	Mitochondria	GSH formation	Chloroplast & Cytoplasm
	Glycolysis	Cytoplasm	G6P to sucrose	Cytoplasm
NADPH	Electron transport	Chloroplast	Calvin cycle, sulfate reduction & NADP-MDH	Chloroplast
	Oxidative pentose phosphate pathway	Cytoplasm	Nitrate reductase	Cytoplasm
	Isocitrate dehydrogenase	Mitochondria		
Reduced ferredoxin (Fd)	Electron transport chain	Chloroplast	NH_4 assimilation & sulfite reduction	Chloroplast
NADH	TCA cycle	Mitochondria	Hydroxypyruvate reduction	Peroxisomes
	NAD-MDH	Cytoplasm	Oxidative electron transport	Mitochondria
			Nitrate reductase	Cytoplasm
Reactive oxygen species (ROS)	Photosynthetic electron transport	Chloroplast	Water–water cycle	Chloroplast
			Catalase	Peroxisomes
	Respiratory electron transport	Mitochondria	Ascorbate peroxidase (APX) & superoxide dismutase (SOD)	Cytoplasm, chloroplast, mitochondria, peroxisomes
	Glycolate oxidase, xanthine oxidase & fatty acid oxidation	Peroxisomes	Glutathione peroxidase (GPX)	Cytoplasm, Chloroplast, mitochondria
Ascorbate (ASC)	Biosynthesis	Cytoplasm & mitochondria	Ascorbate peroxidase (APX)	Chloroplast, mitochondria, peroxisomes & cytoplasm
GSH	Biosynthesis	Chloroplast	Sulfate reduction	Chloroplast & cytoplasm
	Biosynthesis	Cytoplasm	GSH conjugate formation	Cytoplasm & vacuole
			Glutathione peroxidase (GPX)	Chloroplast, mitochondria & cytoplasm

The details for ROS, ASC and GSH also are shown. The scheme of ROS production/scavenging is represented in Fig. 3

metabolite resources (Figs. 1, 2). Such optimization involves shuttling of carbon, nitrogen and sulfur compounds between the organelles of chloroplasts, mitochondria, peroxisomes and cytoplasm (Takahashi et al. 2011; Foyer et al. 2011; Taniguchi and Miyake 2012).

Carbon

Carbon compounds produced from photosynthesis are essential for providing carbon skeletons for whole plant metabolism, growth and development (Stitt 2012). The major end products of carbon assimilation in chloroplasts are triose phosphates (GAP and DHAP, together termed triose-P) and starch (Fig. 1). Triose-P is exported from the chloroplast stroma to the cytosol, and converted into sucrose, to be exported to different sink tissues. A part of carbon from the synthesis of P-glycolate by RuBP oxygenase activity is recovered through the glycolate pathway in the form of glycerate, which enters chloroplasts, is converted to phosphoglycerate and fed into the Calvin cycle.

The role of mitochondrial ATP to sustain the conversion of triose-P into sucrose is now well documented (Raghavendra and Padmasree 2003). Mitochondrial respiration can also be a significant source of internal CO_2 for photosynthetic carbon fixation (Riazunnisa et al. 2006; Busch et al. 2013). In illuminated plant cells, the substrates for mitochondrial oxidation include malate and glycine, being supplied from recently assimilated carbon from chloroplasts. In turn, mitochondria provide C skeletons for amino acid biosynthesis. For example, mitochondria operate a modified TCA cycle in the light and export isocitrate to the cytosol, which is converted to oxoglutarate and sent to chloroplasts, to support glutamate biosynthesis (Hanning and Heldt 1993; Sweetlove et al. 2010; Foyer et al. 2011). Cytosolic reactions in glycolysis (particularly PEP carboxylase and pyruvate kinase) provide carbon skeletons needed for mitochondrial respiration and amino acid biosynthesis, involving also chloroplasts.

Nitrogen

Plant growth and development are dependent on C and N, as well as on the interactions between them. A deficiency of N decreases C assimilation, while C starvation reduces
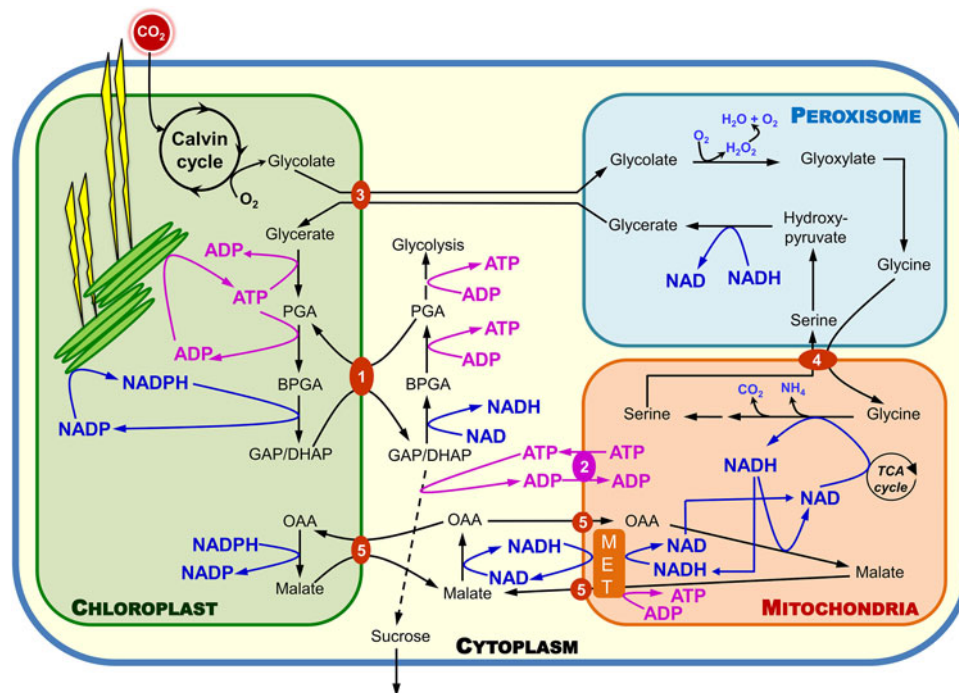
Fig. 1 The assimilatory metabolism of carbon in plant cells involving exchange of metabolites across different organelles. The transporters in the inner envelope membranes of chloroplasts or mitochondria facilitate the metabolite movement (indicated by *arrows*). In Calvin cycle, 3-PGA is converted to triose-P (GAP/DHAP), utilizing ATP and NADPH generated from photochemical reactions. Triose-P is exported out to cytosol through Pi transporter, TPT (*1*). A part of triose-P is metabolized to sucrose, utilizing mitochondrial respiratory ATP, exported to cytosol by adenylate translocator, AT (*2*). Within chloroplasts, ATP is required to convert glycerate coming in from peroxisomes, by plastidial glycolate/ glycerate transporter, PLGG1 (*3*) into PGA. Glycolate from Rubisco oxygenase reaction is metabolized to glycine in peroxisomes, which moves into mitochondria by glycine/serine translocator (*4*). Glycine is decarboxylated in mitochondria to yield serine and NH_3, the latter

moving into chloroplasts, where it is reduced by the synthesis of glutamate. The reductants in chloroplasts can be moved into cytosol also in the form of malate, via a dicarboxylate translocator, DiT (*5*). The exchange of reductants between cytosol and mitochondria is facilitated by DTC. Mitochondrial oxidative electron transport (MET) generates ATP, accepting NADH on both sides of the inner membrane. Photorespiration is an internal source of CO_2, which may be partially refixed by the Calvin cycle. The reactions involving ATP and NADPH are indicated with specific colors of *pink* and *blue*, respectively. Further details are described in Raghavendra and Padmasree (2003), Linka and Weber (2010) and Weber and Bräutigam (2013). *BPGA* bisphosphoglycerate, *DTC* dicarboxylate/ tricarboxylate transporter, *GAP* glyceraldehyde-3-phosphate, *OAA* oxaloacetate, *PGA* phosphoglycerate

N utilization in plants. Thus, C and N metabolism are tightly coordinated and are modulated by the signals from C, N and C/N ratio (Nunes-Nesi et al. 2010). The mutual dependence of plants on carbon and nitrogen assimilation is observed even under elevated CO_2 conditions (Kant et al. 2012).

The uptake and assimilation of inorganic N depends on the supply of C skeletons from chloroplasts and mitochondria. Further, the process of nitrogen assimilation is highly energy dependent and requires reduced compounds, such as NADH, NADPH, reduced ferredoxin and ATP (Fig. 2). These energy-rich compounds are provided by either photosynthesis or mitochondrial oxidative metabolism or even the cytosolic reactions. Significant supply of reductants can also come from mitochondrial photorespiratory reactions through glycine decarboxylase (Szal and Podgorska 2012). A striking dependence of N assimilation

on mitochondrial oxidative electron transport has been demonstrated in *Nicotiana sylvestris* CMSII mutant, deficient in complex I. The enhanced availability of NADH in these mutants upregulates their AOX pathway and N assimilation into amino acids (Dutilleul et al. 2005). Thus, the reactions of N assimilation form a dynamic link among chloroplasts, mitochondria, peroxisomes and cytosol (Nunes-Nesi et al. 2010; Foyer et al. 2011). The novel role of photorespiration as an adaptive mechanism against abiotic stress, by virtue of forming a sink for N metabolism, has been emphasized (Voss et al. 2013).

Sulfur

Sulfur, an essential element for plants, has a variety of functions. The uptake, reductive assimilation of sulfate, and integration into cysteine and methionine constitute the
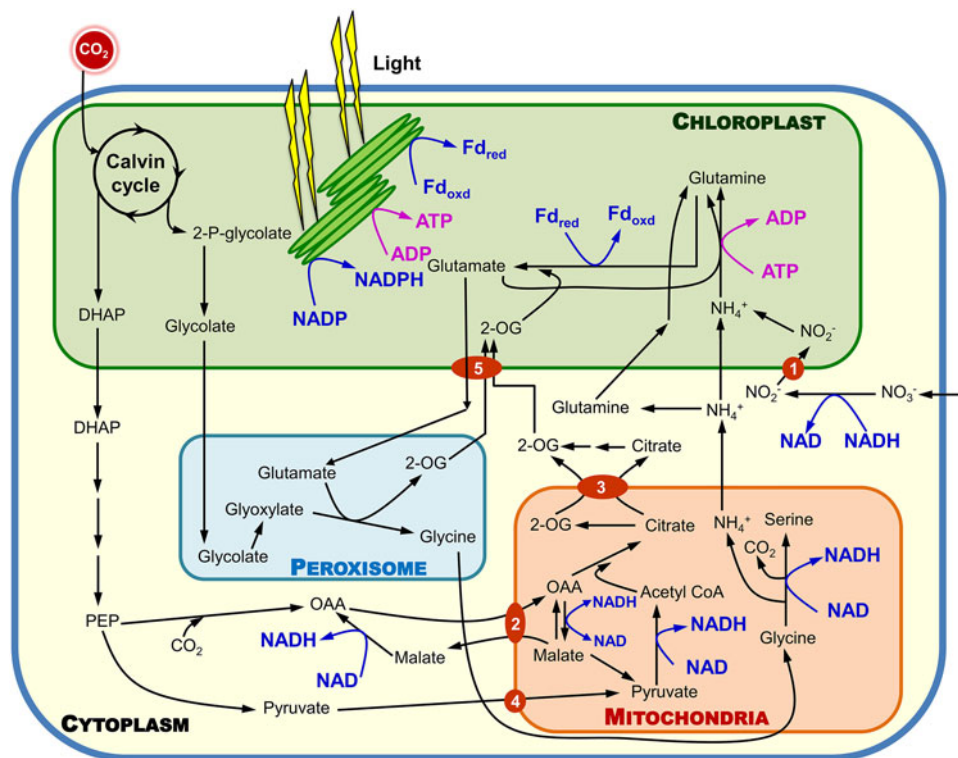
Fig. 2 Nitrogen metabolism involving integrated functioning of chloroplasts, mitochondria, peroxisomes and cytosol. The reactions of N assimilation require ATP and reduced equivalents (in the form of NAD(P)H or reduced ferredoxin), and are facilitated by transporters. Nitrate is reduced to nitrite, by nitrate reductase (NR) localized in the cytosol. Nitrite enters chloroplasts, via a nitrite transporter, NiTr (*1*), and converted to ammonium by nitrite reductase (NiR). Glycine synthesized in the glycolate pathway, moves from peroxisomes into mitochondria, though a glycine/serine translocator. Ammonium is assimilated into glutamine/glutamate and other amino acids by GS and GOGAT, utilizing reduced ferredoxin or NAD(P)H and ATP, generated in photosynthetic metabolism. 2-OG required for GS–GOGAT in chloroplasts can come from either mitochondria, through a modified TCA cycle or peroxisomes. The exchange of 2-OG and glutamate, between chloroplasts and cytosol, is facilitated by DiT1/2 (*2*), while the movement of 2-OG and citrate between mitochondria and cytosol occurs via DTC (*3*). Mitochondria import pyruvate and OAA/malate by DTC (*3*) and PyrT (*4*), respectively. The reactions involving ATP and NADPH are indicated with specific colors of *pink* and *blue*, respectively. Further details are in the reviews of Palmieri et al. (2009), Foyer et al. (2011) and Taniguchi and Miyake (2012). *DHAP* dihydroxyacetone phosphate, *DiT1/2* plastidic 2-oxoglutarate-malate transporter/glutamate-malate transporter, *DTC* mitochondrial dicarboxylate/tricarboxylate carrier, *Fd* ferredoxin, *GOGAT* glutamate synthase, *GS* glutamine synthetase, *OAA* oxaloacetate, *2-OG* 2-oxoglutarate, *PEP* phosphoenol pyruvate, *PyrT* pyruvate transporter

conversion of inorganic form of sulfur into organic form. The reactions of sulfur assimilation/metabolism take place in chloroplasts, mitochondria, cytoplasm and even in the vacuole. Sulfate is utilized to form cysteine in chloroplasts, methionine in mitochondria and cytosol, but their oxidation is restricted to peroxisomes (Takahashi et al. 2011).

The process of sulfate assimilation into cysteine is heavily dependent on the supply of ATP and reducing power in chloroplasts and thus forms an important sink for energy produced in the chloroplasts. The activity of mitochondrial electron transport as well as other proteins is modulated by cysteine (Juszczuk and Ostaszewska 2011), mitochondrial AOX, being a good example. Cysteine is a precursor of methionine, which can be synthesized in chloroplasts as well as cytoplasm (Wirtz and Droux 2005). Further, cysteine and methionine are incorporated into glutathione (GSH), another sulfur containing metabolite, which is an integral part of antioxidant components in plant cells. The synthesis and metabolism of GSH occur in chloroplasts and cytosol. Further details of the role of GSH as antioxidant are described in the following sections.

Photorespiration

Photorespiration is intimately connected with C as well as N metabolism and involves high metabolite flux (Bauwe et al. 2012). The biochemical reactions, participating enzymes and the carbon flux through photorespiration have been studied extensively (Stitt 2012; Bauwe et al. 2012). The carbon from 2-phosphoglycolate, a toxic product of RuBP oxygenase activity, is recycled back into chloroplasts to form PGA and enter the Calvin cycle. When CO_2 is limiting, the utilization of ATP, NADH and reduced ferredoxin in photorespiration helps preventing the over-excitation of electron transport. Photorespiratory reactions protect photosynthesis against glycolate toxicity and even

recover part of carbon from glycolate as glycerate (Figs. 1, 2). Although it was once considered to be an unavoidable process, photorespiration may be an adaptation to oxygenic atmosphere. Photorespiration is beneficial under CO_2 limiting conditions, by preventing the accumulation of toxic products and allowing photochemistry to function (Voss et al. 2013). Photorespiration can help also to minimize the intracellular reactive oxygen species (ROS) levels in multiple ways: providing intracellular CO_2 for chloroplasts (Fig. 1), promotion of AOX pathway in mitochondria by NADH generated from glycine decarboxylase and upregulation of cyclic electron transport in chloroplasts.

Metabolite transporters

The rapid exchange of metabolites among chloroplasts, cytosol, peroxisomes and mitochondria is essential for interorganelle communication and maintenance of metabolic equilibrium, as the redox-rich compounds such as NAD(P)H or ATP are not freely permeable. Metabolite translocators mediate a dynamic and coordinated metabolite flux between chloroplasts and other cellular compartments, facilitating the movement of metabolites as well as movement of NAD(P)H/ATP-related compounds (Figs. 1, 2). There are excellent reviews on the transporters located in the inner envelope membranes of chloroplasts and mitochondria (Palmieri et al. 2009; Linka and Weber 2010; Weber and Linka 2011). Recent articles indicate the operation of transport proteins in peroxisomal membranes to facilitate metabolite movement (Eisenhut et al. 2012; Linka and Esser 2012).

The triose phosphate translocator (TPT) located in the inner chloroplast membrane facilitates the simultaneous exchange of triose-P generated in the chloroplast into cytoplasm and import of cytosolic Pi (Fig. 1). The triose-P in cytoplasm is metabolized to sucrose. Glycerate, an important product of photorespiration in peroxisomes, is moved into chloroplasts by glycolate/glycerate transporter (PLGG1) (Pick et al. 2013). The dicarboxylate transporter displays a high affinity for OAA, can function also as a malate-valve and is quite effective in balancing redox equivalents between the cytosol and the stroma (Scheibe et al. 2005; Kinoshita et al. 2011). The chloroplastic redox shuttle systems, based on dicarboxylate and Pi translocators, help in the optimization of C/N assimilation and balance the stromal ATP/NADPH ratio (Taniguchi and Miyake 2012).

Mitochondrial oxidative phosphorylation is an important source of energy for sucrose biosynthesis as well as other reactions (Raghavendra and Padmasree 2003). Mitochondrial AT transporter transports ATP into cytoplasm in exchange for ADP (Fig. 1). The TCA cycle provides reducing equivalents for oxidative electron transport and carbon skeletons, with the help of metabolite transporters in the inner mitochondrial membrane (Linka and Weber 2010). A typical example of

mitochondrial transporter is dicarboxylate/tricarboxylate carrier (DTC), which mediates the transport of both dicarboxylates (such as oxoglutarate, malate or oxaloacetate) and tricarboxylate (such as citrate). Recent reports indicate the operation of NAD carrier proteins (Palmieri et al. 2009).

Maintenance of optimal ROS levels within the cell

The metabolic pathways in plant organelles tend to produce ROS, which can be toxic at high concentrations. However, low levels of ROS act as key signaling molecules during the regulation of many metabolic and growth/development processes in plants. Such dual role of ROS depends on their concentration as well as on the status of the environment (Mullineaux and Baker 2010). The major forms of ROS are hydrogen peroxide (H_2O_2), singlet oxygen ($^1O_2$), superoxide radical (O_2^-) and hydroxy radical ($OH^.$); they are produced mainly in chloroplasts, mitochondria and peroxisomes, along with the production of ROS via NADPH oxidases located in the plasma membrane (Mittler et al. 2011; Suzuki et al. 2012). Increased accumulation of ROS can induce oxidative stress, leading to oxidation of cellular components, hindering metabolic activities and affecting organelle integrity (Mittler et al. 2004). Since the molecules are diffusible, ROS can disturb multiple compartments, irrespective of the site of production. It is therefore not surprising that all the cellular organelles have means of controlling, to some extent, the levels of ROS. This can be done by either minimizing ROS production or elevating scavenging systems, or both (Fig. 3).

Minimization of ROS production

The production and scavenging of ROS in mitochondria and chloroplasts are interlinked. Electron transport in both chloroplasts and mitochondria tend to generate ROS (Fig. 3). Under normal conditions, when electron acceptors (Fd and NADP in chloroplasts and O_2 in mitochondria) are insufficient, the generation of ROS increases (Mubarakshina et al. 2010). High amounts of ROS in the form of H_2O_2 are generated during glycolate oxidation in peroxisomes, but are scavenged by catalase. Noncyclic PS II-mediated electron transport has the potential to generate high amounts of ROS (acceptance of electrons from PS I by O_2, resulting in the formation of O_2^- and H_2O_2). Therefore, chloroplasts employ water–water cycle and cyclic electron transport to keep the ROS levels low (Miyake 2010). During illumination, the difference in redox potential between chloroplast stroma and cytosol is high (Nunes-Nesi et al. 2007), posing a risk of oxidative damage to thylakoid membranes and other cellular components.
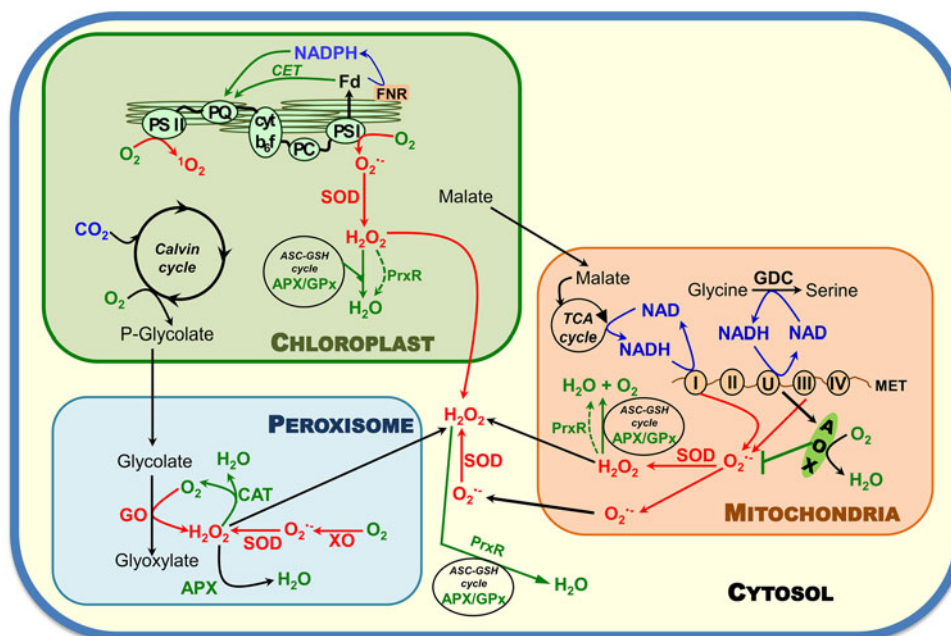
Fig. 3 The sites of generation and scavenging of reactive oxygen species (ROS) in plants. Majority of the ROS is generated during either the electron transport in chloroplasts/mitochondria, or conversion of glycolate to glyoxylate in peroxisomes. Plasma membrane-bound NADPH oxidases also produce ROS (not shown in figure for convenience). When in excess, ROS are scavenged by antioxidant systems in chloroplasts, mitochondria, peroxisomes and cytosol. Cyclic electron transport (CET) minimizes the ROS production in chloroplasts by transferring electrons from Fd to PQ. In mitochondria, two major sources of NADH are TCA cycle and glycine decarboxylation. High amounts of ROS are produced in peroxisomes, during glycolate oxidation, but are scavenged by CAT. Peroxisomes contain also xanthine oxidase (XO), which produces ROS. The reactions of ROS production are indicated in *red*, while those minimizing or scavenging are indicated in *green*. More details can be found in the reviews of Mittler et al. (2004) and Mhamdi et al. (2010). *AOX* alternate oxidase pathway, *ASC-GSH cycle* ascorbate–glutathione cycle, *APX* ascorbate peroxidase, *CAT* catalase, *Fd* ferredoxin, *FNR* *Fd-NADP*$^+$ reductase, *GDC* glycine decarboxylase, *GO* glycolate oxidase, *GPX* glutathione peroxidase, *MET* mitochondrial electron transport, *PC* plastocyanin, *PQ* plastoquinone, *PrxR* peroxiredoxins, *SOD* superoxide dismutase, *TCA* cycle tricarboxylic acid cycle

When there is limitation on the utilization of ATP produced by the cytochrome pathway, the AOX pathway can be induced, preventing the donation of electrons to O_2 from other parts of the pathway to form O_2^-. The predominance of AOX pathway in mitochondrial respiration helps dissipate excess of photosynthetic reducing power and minimizing ROS production (Noguchi and Yoshida 2008; Dinakar et al. 2010). Photorespiratory glycine decarboxylation generates considerable NADH, which can upregulate not only AOX pathway, but also chloroplastic cyclic electron transport (Voss et al. 2013). In turn, ROS can be signals to coordinate and co-regulate multiple compartments (Mittler et al. 2011).

Scavenging ROS: antioxidants

Ascorbate (ASC) and GSH are among the most important antioxidants in plant cells. Besides its antioxidant function, ASC is a key component of interorganelle cross-talk between mitochondria and chloroplasts (Talla et al. 2011; Szarka et al. 2013). The biosynthesis of ascorbate occurs mostly in cytoplasm, with the terminal step in mitochondria. Yet, ASC biosynthesis appears to be dependent on photosynthetic electron transport (Yabuta et al. 2007). The levels and oxidized/reduced status of ascorbate can influence the overall photosynthetic performance and photoinhibition (Chen et al. 2003; Talla et al. 2011). The ascorbate synthesis is shown to be coupled with mitochondrial electron transport at complex IV and also influences the activity of AOX (Bartoli et al. 2006). Thus, changes in either mitochondria or chloroplasts can influence each other, through ascorbate (Szarka et al. 2013). Similarly, GSH is mostly synthesized in chloroplasts, but is required for redox balancing reactions in mitochondria and cytoplasm, besides chloroplasts themselves (Noctor et al. 2012). The GSH-based redox state operating in different organelles becomes an essential part of optimization of photosynthesis, respiration and even N metabolism (Szalai et al. 2009).

Emerging trends and concluding remarks

Model plants and mutants

Arabidopsis has evolved to be the best model plant for elucidating not only photosynthesis but also different

metabolic pathways and their interactions (Stitt et al. 2010; Koornneef and Meinke 2010). Availability of a wide spectrum of mutants/transgenics of *Arabidopsis*, as well as established protocols for isolation of protoplasts, transient gene expression analysis and metabolite analysis using *Arabidopsis* offer a wide scope for diverse experiments in photosynthesis research (Riazunnisa et al. 2007; Yoo et al. 2007). There have been extensive reports on the modulation of photosynthesis and mitochondrial respiration in *Arabidopsis* mutants, deficient in specific components of chloroplasts and mitochondria, for example, NADP-MDH in chloroplasts (Hebbelmann et al. 2012) and AOX in mitochondria (Yoshida et al. 2011). Besides *Arabidopsis*, other important experimental models that have been used widely are: spinach, pea and green algae (*Chlamydomonas* and *Synechocystis*) (Harris 2001; Sunil et al. 2008; Nogales et al. 2012). It is essential to identify and exploit the use of other model plants. For example, maize has a high potential, in view of the availability of mutants and C_4 photosynthesis. Similarly, *Setaria viridis* is being considered as model of C_4 grass, *Cleome* as a C_4 dicot and *Brachypodium* as a model C_3 grass (Brown et al. 2005; Brutnell et al. 2010; Brkljacic et al. 2012).

Organelle proximity and movement

The strong biochemical interactions between the organelles in plant cells depend on dynamic metabolite exchange, which can be quite effective, where there is physical proximity between them. The importance of the close association of chloroplasts, mitochondria and peroxisomes is being considered as an important component of functional anatomy of leaf photosynthesis (Terashima et al. 2011). Chloroplasts are known to reorient within the cell, either horizontally or vertically, depending on the intensity of incident light. The reorientation and movement of chloroplasts as well as mitochondria is mediated by phototropins and facilitated by cytoskeleton (Kong and Wada 2011). Similar movement of mitochondria and even peroxisomes has also been reported (Islam et al. 2009; Mano et al. 2002). The reorientation of chloroplasts and mitochondria can modulate the intercellular conductance of CO_2, increase light use efficiency and may improve the chance of refixation of CO_2 by Rubisco (Terashima et al. 2011). The significance and consequences of such organellar movement on the cross-talk between chloroplasts and other organelles are highly interesting and need validation.

Role of proline and GABA

Plants are known to accumulate compatible solutes (e.g., proline, polyols, glycine betaine, trehalose), which seem to serve a dual purpose of stabilizing cellular proteins/nucleic acids and even scavenging ROS, which can protect photosynthesis and other processes. These osmolytes can also provide a source of carbon, nitrogen and energy, when the stress is relieved. Among these osmolytes, proline and γ-aminobutyric acid (GABA), may have a role in redox-state mechanisms. Proline is considered as a potent non-enzymatic antioxidant that can mitigate the adverse effects of ROS (Verslues and Sharma 2010). Similarly, GABA, which has until now been treated as a plant metabolite, may provide signaling to modulate metabolic activities in response to stress and carbon/nitrogen metabolism.

Two key enzymes involved in the biosynthesis of proline—Δ1-pyrroline-5-carboxylate synthase (P5CS or P5C synthase) and P5C reductase (P5CR)—are localized in cytosol and chloroplast, whereas two key catabolic enzymes—proline dehydrogenase (PDH) and P5C dehydrogenase (P5CDH)—are located in mitochondria. Such distribution of biosynthetic reactions in chloroplasts and degrading components in mitochondria and cytoplasm makes proline a relevant case for interorganelle interactions. Accumulation of P5CS and P5CR transcripts in chloroplasts (Szekely et al. 2008; Szabados and Savoure 2009) suggests that, under adverse conditions, photosynthesis-derived glutamate could increase proline biosynthesis in plastids. Proline catabolism in the mitochondria is connected to oxidative respiration that provides energy, as the oxidation of one molecule of proline can yield as much as 30 ATPs (Kishor et al. 2005). Proline oxidation can also regulate mitochondrial ROS levels.

GABA, a four-carbon non-protein amino acid and a key player in "GABA-shunt", is linked to stress and signaling in plants. GABA is derived from glutamate, which is converted to SSA (succinic semialdehyde) and then to succinate, to enter the tricarboxylic acid cycle. These three successive reactions are catalyzed by glutamate decarboxylase (GAD), pyruvate- and 2-oxoglutarate-dependent GABA transaminase (GABA-T) and SSA dehydrogenase (SSADH), respectively. GAD is localized in the cytosol, while GABA-T and SSADH are located in mitochondria (Shelp et al. 2012), implicating the transport of GABA across the mitochondrial membranes. Clark et al. (2009) suggested that photorespiration can interact with GABA metabolism.

GABA and proline could quench the production of $O_2^{\cdot-}$, H_2O_2, and $^1O_2$ in an in vitro system. GABA had a stronger scavenging capacity than proline (Liu et al. 2011). Such quenching capacity can be the basis for the accumulation of these osmolytes in plants. Further experiments are needed to understand the inter-relations of biosynthesis/degradation of proline or GABA by photosynthetic carbon assimilation and mitochondrial respiration.

Retrograde signaling

The ROS-mediated cross-talk between chloroplasts and mitochondria to optimize the function of photosynthesis is reflected also at the level of gene expression in different plant cell compartments (Suzuki et al. 2012). The concept of retrograde signaling in terms of control of nuclear gene expression by mainly chloroplasts in plant cells has long been known. In the last few years, the concept is extended to regulation of nuclear gene expression by mitochondria as well (Leister 2012). The purpose of such dynamic regulation of gene expression in multiple compartments seems to be the need for dynamic coordination of metabolic components in different compartments. The expression of several genes in chloroplasts, mitochondria and the nucleus are highly coordinated, and respond to the energy state of the cell as well as environmental stresses (Leister 2012; Schwarzlander and Finkemeier 2012; Berry et al. 2013).

The exact signal(s) originating from chloroplasts or mitochondria has been a matter of debate. A favored view point is that retrograde signaling is redox-related. For example, the regulations of transcripts encoding components of the photosynthetic and respiratory electron transport chains are regulated by hydrogen peroxide, ascorbate and GSH (Queval and Foyer 2012). The photosynthetic function of chloroplasts is expected to sense and direct intracellular adjustments (Pfannschmidt et al. 2009), but the exact sensor molecule needs to be identified clearly.

Metabolomics

The interactions of chloroplasts with other organelles is a dynamic process and results in marked changes in relative levels of metabolites and their intracellular distribution. Plant metabolomics provide a comprehensive and quantitative analysis of primary and secondary metabolites in plants. Metabolomics, therefore, is a powerful tool to understand the biochemical basis of such metabolic network regulation. The analytical techniques of plant metabolomics are based broadly on either nuclear magnetic resonance (NMR) spectroscopy or mass spectroscopy (MS) or in combination. The combined analysis involving gas chromatography-mass spectrometry (GC–MS) and liquid chromatography (LC–MS) has been the most popular. The use of metabolomics has been helpful in studying the specific roles of selected enzyme/protein components of chloroplasts (NADP-MDH, Hebbelmann et al. 2012), mitochondria (AOX, Strodtkötter et al. 2009) and cytosol (Oliver et al. 2008). The integration of plant metabolomics with conventional information on enzyme activities, metabolite fluxes and modeling is quite promising to understand the synthetic and systems biology of photosynthesis (Arnold and Nikoloski 2011). The plant metabolomics and modeling should be exploited to understand and predict the components of interorganelle cross-talk.

Several reactions of secondary metabolism operate in chloroplasts, as their biosynthesis requires NAD(P)H and ATP, but parts of these metabolic pathways are located also in mitochondria and cytosol. Selmar and Kleinwächter (2013) suggested that biosynthesis of several secondary metabolites may serve to dissipate oxidative stress in plant cells. Some of the secondary metabolites (e.g., isoprenoids) from plastids may serve as signaling molecules in upregulation of mitochondrial transcripts (Hsieh et al. 2008). Further work is warranted on the role of secondary metabolism in integrating the function of chloroplasts with other organelles. Again, metabolomics should be able to reveal the roles of the key secondary metabolites in such interactions.

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