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REVIEWS

Mitochondrial Respiration of the Photosynthesizing Cell

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Abstract—Current notions on respiration of photosynthesizing cells are reviewed. Over the past three decades, the modern methods based on isotope techniques and reverse and molecular genetics provided convincing evidence that mitochondrial respiration is functional in the light and contributes to the creation of optimal conditions for photosynthesis and for protection of cells from photodegradation. Novel data are presented on the substrates that are used for respiration in the light. Individual respiration steps are considered in the context of their possible role in photosynthesizing cells. The mechanisms and carriers mediating the export of reducing equivalents from chloroplasts for their subsequent oxidation in the mitochondrial electron-transport chain are discussed. The regulation of nonphosphorylating (unrelated to energy generation) electron transport pathways mediated by alternative oxidase and alternative type II NADPH-dehydrogenases, as well as the role of uncoupling proteins in plant mitochondria, are analyzed. These components were shown to play a significant role in NAD(P)H oxidation for maintaining the redox balance in mitochondria and whole green cells. A generalized scheme of biochemical interactions between organelles—chloroplasts, mitochondria, and peroxisomes—is presented. The directions for future research are outlined.

Keywords: plants, photosynthesis, respiration in the light, mitochondria, chloroplasts, respiratory substrates, tricarboxylic acid cycle (TCA), photorespiration, alternative oxidase, type II NAD(P)H dehydrogenases, nonphosphorylating pathways

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INTRODUCTION

Photosynthesis and respiration provide the substrates and energy for plant life. The light and dark reactions of photosynthesis perform CO_2 reduction to carbohydrates and oxidation of water to O_2. Carbohydrates participate in catabolic and anabolic reactions of metabolism, with respiration occupying the central position. In general terms, photosynthesis supplies building materials (reduced carbon), while respiration delivers intermediates and energy required for cell growth and functioning.

The relationships between photosynthesis and respiration are still a matter of debate. Until the mid 20th century, there was a paradigm that respiration is suppressed in the light during photosynthesis and that the respiratory component is a negative quantity in calculating the plant productivity. Over the past three decades, ample evidence has accumulated on functional relationships between photosynthesis and respiration and on the close interactions of chloroplasts and mitochondria [1–9].

Respiration is a multistep compartmentalized process (Fig. 1). The first stage of respiration, glycolysis, occurs in the cytoplasm; it accounts for the anaerobic breakdown of glucose to pyruvic acid (pyruvate). Then, pyruvate penetrates into the mitochondria, where it undergoes oxidative decarboxylation in the tricarboxylic acid cycle (TCA cycle). The reactions of the TCA cycle produce reducing equivalents, NADH and $FADH_2$. At the final stage, these compounds are oxidized in the electron transport chain of the mitochondrial inner membrane (mETC) with the generation of energy in the form of ATP (Fig. 2). This sequence of events is typical of the respiration occurring in darkness (dark respiration). When photosynthesis is activated in the light, the cell metabolism undergoes changes involving the respiratory system.

Analysis of dark respiration in the light has always been a complicated problem, because photosynthesis, as a quantitatively dominant process, masks the respiratory gas exchange by reassimilating CO_2 formed during respiration [1, 3, 10]. Russian scientists contributed considerably to the development of ideas on

Abbreviations: 2OG—2-oxoglutarate (α-ketoglutarate); 3PG—3-phosphoglyceric acid; AOX—alternative oxidase; PEP—phosphoenolpyruvate; GDC—glycine decarboxylase complex; mETC—mitochondrial electron-transport chain; mMDH, chMDH, cMDH—mitochondrial NAD-dependent malate dehydrogenase, chloroplast NADP-dependent MDH, and cytosolic NADH-dependent MDH, respectively; PDC—pyruvate dehydrogenase complex; PEP—phosphoenolpyruvate; PEPC—PEP carboxylase; type II NAD(P)H-DH—alternative NAD(P)H dehydrogenases; SHMT—serine hydroxymethyltransferase; TCA—tricarboxylic acid cycle; TPT—triose phosphate translocator; UCP—uncoupling proteins.

the relationship between photosynthesis and respiration. In the laboratory of photosynthesis of Botanical Institute (Academy of Sciences of the Soviet Union), a group of researchers guided by Zalenskii applied isotope techniques to quantify the incorporation and partitioning of photosynthetically assimilated ^{14}C into various compounds of the photosynthetic and respiratory metabolism [1, 3, 11]. Owing to these works, the occurrence of dark respiration during photosynthesis was proven, the features of respiratory metabolism in illuminated plants were revealed, and relationships between photosynthesis and respiration at the cell and whole plant levels were revisited. In the Institute of Plant Physiology (Academy of Sciences of the Soviet Union), Murray et al. [2, 12, 13] studied the kinetics of CO_2 release by whole plants after interrupting the steady-state light metabolism by the transition to darkness. This approach allowed the authors to assess the dark respiration component persistent in the light, propose a model for the formation and use of assimilates, and outline the quantitative organization of photosynthesis and respiration in the whole plant. Chmora et al. [4, 14] analyzed the kinetics of CO_2 and O_2 exchange upon light–dark transitions, examined the relations of respiration and photosynthesis to assimilate transport, and considered the role of above factors in the source leaf ontogeny.

Recent advances in the studies of relationships between respiration and photosynthesis were largely due to the methods of reverse and molecular genetics and analysis of respiratory fluxes of ^{13}C-labeled metabolites in combination with the methods of isotopic fractionation [5–9]. A convenient model to examine the regulation of respiration in the light is the process of de-etiolation, during which the photosynthetic function emerges in parallel with changes in cellular respiration [15–17].

According to [3, 7, 8, 11, 18] the major glycolytic route occurring in the cytoplasm of photosynthesizing cells is constrained under light, and the TCA cycle in the mitochondrial matrix is modified. The terminal stage of respiration associated with the operation of mitochondrial ETC (mETC) remains active [5, 6, 19]. During photosynthesis, nonphosphorylating pathways in mETC (pathways unrelated to generation of electrochemical proton gradient for ATP synthesis) play an important role. By virtue of these pathways, the cell dissipates the excess reducing equivalents exported from the chloroplasts [5, 6]. The respiration in the light is thought to optimize conditions for photosynthesis. It participates in the formation of the end products of photosynthesis, controls the accumulation of cell reductants, protects the photosynthetic apparatus from photoinhibition, and is a general prerequisite for the functioning of green plants [5–9, 19, 20]. According to various estimates, the respiration rate in the light may constitute from 30 to 100% of the dark respiration, up to 40% of the rate of apparent photosynthesis [4, 21], and 25% of gross photosynthesis [13].

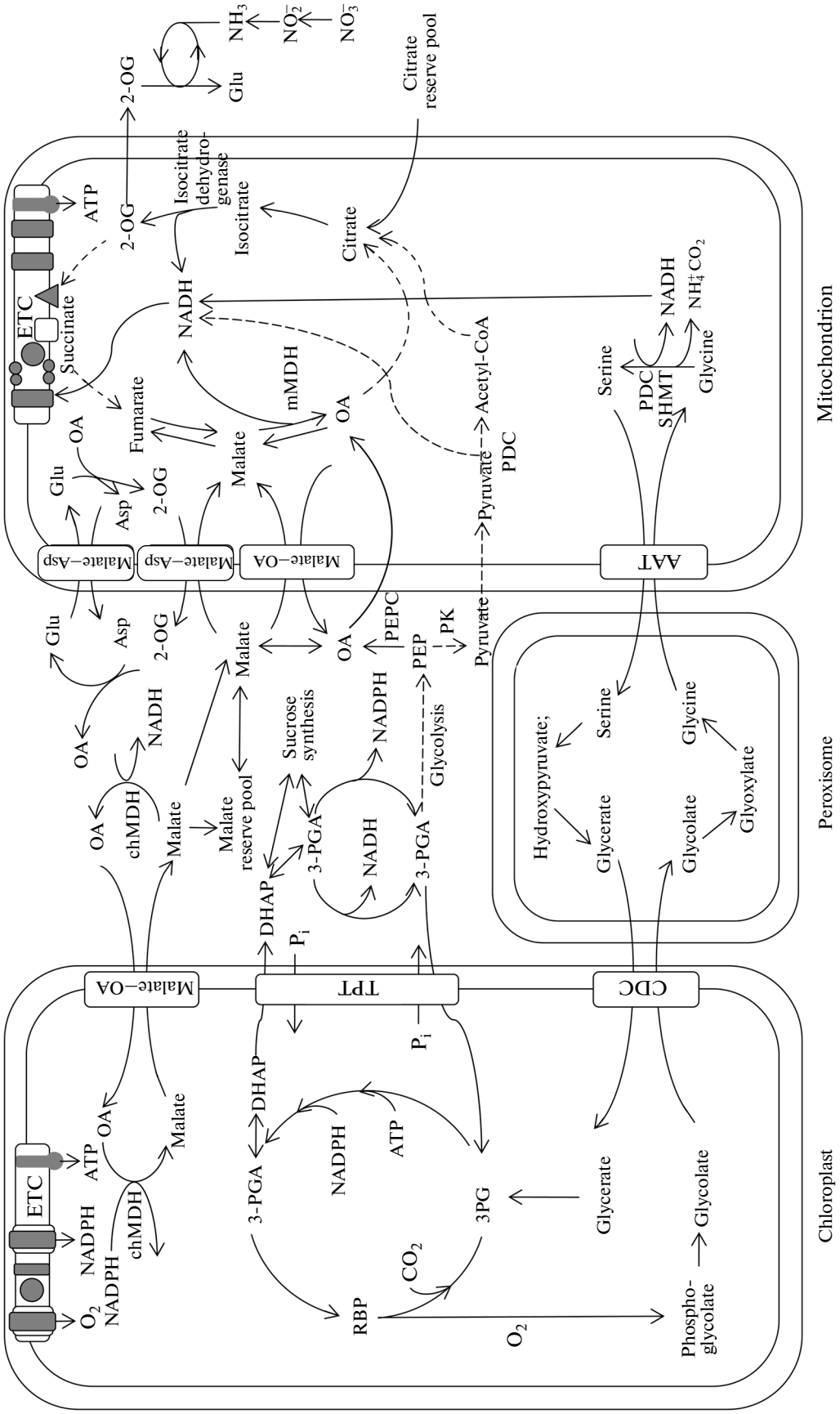
This review aims to analyze the current state of the problem and define the key issues for further research of respiration in the light. New information on the respiratory substrates supplied in the light is presented. Significance of individual respiration steps for photosynthesizing cells is outlined. The roles of nonphosphorylating pathways in the regulation of redox balance, as well as in functional and metabolic interactions between chloroplasts and mitochondria are considered. The review comprises original experimental data intended to clarify the mitochondrial ETC components involved in the development of leaf photosynthetic function during greening.

RESPIRATORY SUBSTRATES IN THE LIGHT

Isotopic labeling studies earlier showed that respiration consumes freshly formed primery photosynthates [3, 21, 22]. Later, it was found that respiration may dissipate not only the primary photosynthates, i.e., triose phosphates formed in the Calvin cycle, but also soluble carbohydrates (mainly disaccharides) hydrolyzable to monomers (glucose and fructose) [8, 22].

A triose phosphate, 3-phosphoglyceraldehyde (3-PGA) formed in the Calvin cycle from 3-phosphoglyceric acid (3PG) is exported in the form of dihydroxyacetone phosphate by the shuttle mechanism termed triose phosphate translocator (TPT) and is used for synthesis of sucrose (Fig. 1). The lack of TPT in *Arabidopsis* mutants resulted in accumulation of starch in chloroplasts and retarded the rates of photosynthesis and growth [23]. In the cytosol, 3-PGA is oxidized by dehydrogenases to 3PG. It is supposed that 3PG is partly catabolized during glycolytic conversion of trioses, while the other part is reimported into the chloroplasts by means of TPT [24]. The percentage of primary photosynthates used for respiration ranges from 25 to 80% of the total pool of respiratory substrates [25].

Fig. 1. Biochemical interactions of organelles in the photosynthesizing cell (based on schemes presented in [5, 6, 8]). Dashed lines indicate metabolic fluxes whose activity can be reduced or completely suppressed in the light (see text for discussion). *Transmembrane transporters*: AAT—amino acid translocator; GGT—glycolate–glycerate translocator; Malate–Asp—malate–aspartate shuttle; Malate–OA—malate–oxaloacetate shuttle; TPT—triose phosphate translocator. *Enzyme systems*: GDC—glycine decarboxylase complex; IDH—isocitrate dehydrogenase; mMDH, chMDH, cMDH—mitochondrial, chloroplastic, and cytosolic malate dehydrogenases, respectively; PDC—pyruvate dehydrogenase complex; PK—pyruvate kinase; SHMT—serine hydroxymethyltransferase, PEPC—phosphoenolpyruvate carboxylase. *Metabolites*: DHAP—dihydroxyacetone phosphate; OA—oxaloacetate; 2-OG—2-oxoglutarate; PA—pyruvic acid (pyruvate), 3-PGA—3-phosphoglyceraldehyde; 3PG—3-phosphoglyceric acid; PEP—phosphoenolpyruvate.


Mitochondrion
Peroxisome
Chloroplast
ETC
ATP
2-OG
Isocitrate dehydro-genase
Isocitrate
Citrate
Citrate reserve pool
NADH
Succinate
Fumarate
mMDH
OA
Malate
Glu
Asp
2-OG
Pyruvate
Acetyl-CoA
PDC
Serine
PDC
SHMT
Glycine
NADH
NH_4^+ CO_2
Malate–Asp
Malate–Asp
Malate–OA
AAT
PEPC
PK
PEP
Sucrose synthesis
NADPH
Glycolysis
chMDH
Malate reserve pool
3-PGA
DHAP
P_i
Hydroxypyruvate;
Glycerate
Glycolate
Glyoxylate
Malate–OA
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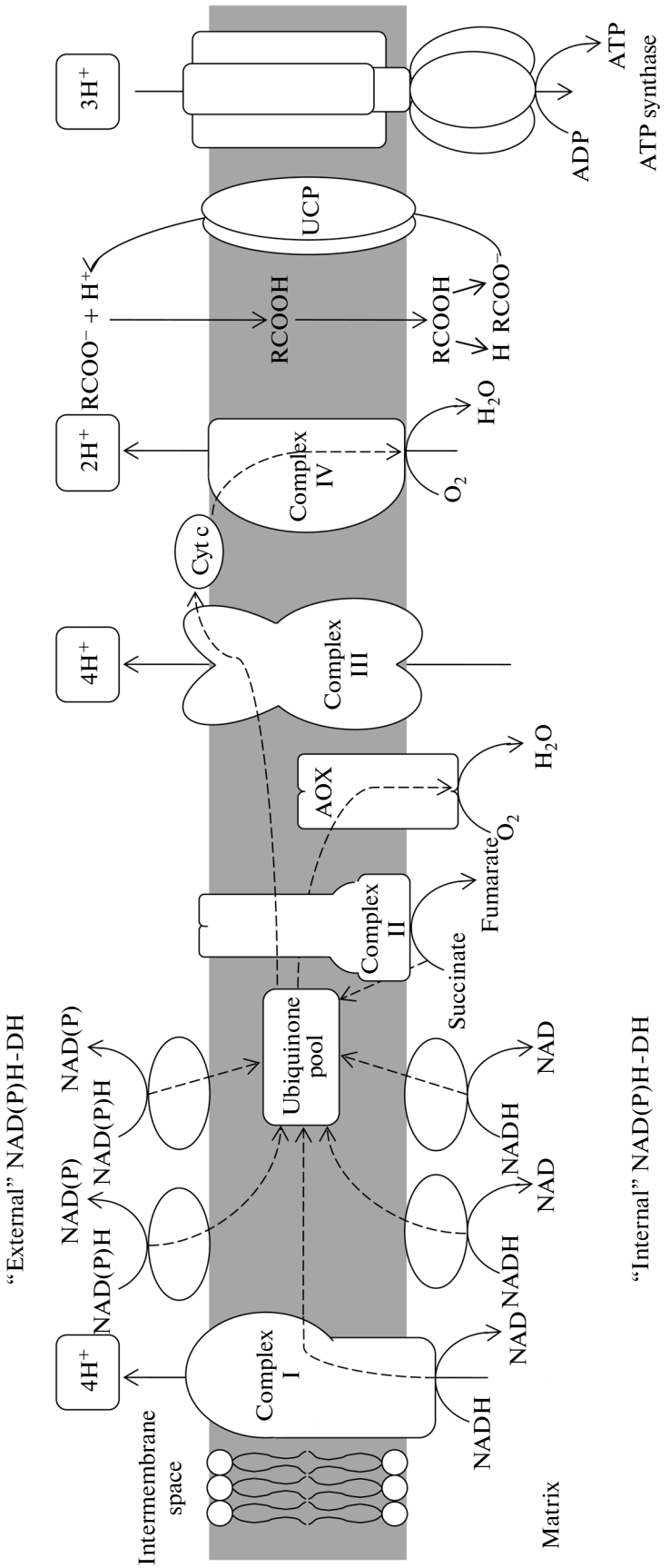

Fig. 2. Mitochondrial electron-transport chain (modified from [68]). AOX—alternative oxidase; "internal" and "external" NAD(P)H-DH—type II alternative NAD(P)H dehydrogenases; UCP—uncoupling protein.

The use of starch as a respiratory substrate in the light is completely or partially inhibited [22]. The utilization of reserve assimilates in starch-accumulating plants (arabidopsis, tobacco, potato, and sunflower), was shown to be severalfold lower in the light than in the dark [22, 25]. Cereals represent a plant group where respiratory substrates accumulate in the form of soluble carbohydrates [22]. We observed the accumulation of starch grains in leaf mesophyll cells of 5-day-old etiolated wheat seedlings [17]; starch was possibly synthesized in etioplasts [26]. The transfer of plants to continuous light was followed by disappearance of starch by the sixth hour of light exposure, when the rate of net photosynthesis became a positive quantity [17]. We supposed that respiratory decarboxylation in the light can dissipate part of the starch. According to some reports, starch degradation may proceed when photosynthetic rate is below a certain threshold [27].

Utilization of glucose as a respiratory substrate in the light implies the operation of glycolysis, having its distinct features in photosynthesizing cells. It is known that plant cells possess two glycolytic pathways that differ at the stage where fructose-6-phosphate (a glucose phosphorylation product) is phosphorylated to fructose-1,6-bisphosphate [28]. In the main glycolytic pathway operating in darkness, this reaction is mediated by ATP-dependent phosphofructokinase. In the light, pyrophosphate-dependent phosphofructokinase is activated; this enzyme catalyzes the reaction in an ATP-independent manner and is needed for synthesis of sugars from trioses during gluconeogenesis. Hence, the second ("adaptive") glycolytic pathway, unlike the main one, is not under the adenylate control and is independent of ATP, whose relative content increases in the light. It is assumed that both glycolytic pathways are active in growing leaves, when the adenylate control is relieved at high rates of metabolic exchange [29, 30]. In mature cells that have ceased growing, illumination suppressed glycolysis by 40–50%, because of the inhibition of the main glycolytic pathway. Some authors believe that glycolysis ceases almost completely in the light; the lack of inhibition of respiration in the light is likely due to the direct flow of malate from chloroplasts to mitochondria, where malate enters directly into the TCA cycle [31].

FUNCTIONING OF THE KREBS CYCLE IN THE LIGHT

In darkness, phosphoenolpyruvate (PEP) produced in glycolysis from 3PG is converted by pyruvate kinase to pyruvate (Fig. 1). However, the activity of pyruvate kinase in the light is lower than that of PEP carboxylase (PEPC) that converts PEP to oxaloacetate [32]. It is known that PEPC is activated by glycine, while pyruvate kinase is inhibited by NH_4^+, both compounds being the products of photorespiration [33]. Oxaloacetate can be converted into malate by cytosolic NADH-dependent malate dehydrogenase (cMDH). Both metabolites—oxaloacetate and malate—can enter the mitochondria via specialized carrier proteins and participate in the TCA cycle [6, 8]. Their entry is regulated through a feedback control loop: the excess oxaloacetate in mitochondria inhibits the activity mMDH that converts malate to oxaloacetate. At the same time, oxaloacetate can be exported to the cytosol in exchange for malate; in mitochondria, oxaloacetate can be converted into malate in the backward reaction catalyzed by mMDH. The formation of oxaloacetate catalyzed by PEPC is thought to quickly replenish the malate and fumarate pools [34]; the role of these pools will be considered later.

The functioning of TCA cycle in the light still attracts the increased attention of phytophysiologists [7, 8]. Using ^{14}C-labeled substrates, Mamushina et al. [11, 30] showed that the TCA cycle does not undergo significant changes in the light under natural concentration of CO_2; only a slight inhibition, not exceeding 10–20% was noted. Studies on mutant plants deficient in TCA-cycle enzymes also confirmed an important role of TCA cycle in photosynthesis [18]. A detailed study on metabolic conversions (decarboxylation) of ^{13}C-labeled glucose or pyruvate in combination with the methods of isotope $^{16}O/^{18}O$ fractionation and NMR-based analysis of metabolite fluxes led to the conclusion that the TCA cycle continues to function in the light, although with significant modifications [8, 34].

In darkened mitochondria, the operation of TCA cycle starts with the decarboxylation of pyruvate by pyruvate dehydrogenase complex (PDC) resulting in acetyl-CoA and NADH (Fig. 1). According to various estimates, the PDC activity can drop in the light by at least 30% [31] or can be completely inhibited by high levels of NADH and NH_4^+, the products of photorespiration [35]. The latter assumption is supported by the absence of light-dependent induction of E1 gene coding for the alpha 2 subunit of PDC [36, 37]. The high relative content of NADH is the major limiting factor not only for PDC but also for some dehydrogenases located in the mitochondrial matrix and involved in the TCA cycle [38].

An important advance in clarifying the performance of TCA cycle in the light was the discovery by French physiologists of the "noncyclic" nature of TCA operation in the light [8, 31, 34]. The authors found that the cycle can operate both in forward and reverse directions (Fig. 1). In the forward reaction, citrate is converted to α-ketoglutarate (also known as 2-oxoglutarate, 2-OG) by means of aconitase and NAD-dependent isocitrate dehydrogenase, which is followed by the release of 2-OG into the cytosol and by the formation of glutamate (Glu) in the amination reaction [8]. Apparently, the substrate (citrate) enters from the cytosolic reserve pool, rather than originates from oxaloacetate by means of citrate synthase, because the products of this enzyme, acetyl-CoA and NADH might inhibit PDC in a feedback manner [19, 35].

When the reaction runs in the reverse direction, it converts oxaloacetate into malate with the subsequent formation of fumarate, since all partial reactions are reversible [8]. The transition from light to darkness was shown to induce decarboxylation of the pools of these metabolites [39, 40]. This is one of the reasons for the postillumination burst of CO_2 release, a phenomenon known as light-enhanced dark respiration (LEDR). The LEDR can last up to 30 min and even longer [35]; it indicates the involvement of malate and fumarate in biochemical control of respiration after changes in light conditions [8, 39, 40]. Furthermore, malate and fumarate can serve as counterions in regulation of intracellular pH during nitrogen metabolism [41]. It is also assumed that the cell can employ the interactions between various malate pools (chloroplastic, vacuolar, mitochondrial, glyoxysomal, and apoplastic) to regulate the photosynthetic rate through the changes in NADH level [7].

Modifications of TCA cycle in the light may result from inhibition of succinate dehydrogenase [42]. Under natural CO_2 concentration, the release of $^{14}CO_2$ during oxidation of ^{14}C-succinate was shown to be lower in the light than in the dark [11]. In our experiments, we also observed the decreased activity of succinate oxidation by mitochondria isolated from greening wheat leaves [43].

Thus, the conversion of citrate to 2-OG with the subsequent formation of Glu proceeds separately from the malate metabolism; i.e., it occurs irrespective of the production of oxaloacetate that refills the mitochondrial pools of malate and fumarate. "Noncyclic" functioning of the Krebs cycle might be useful, since it "reflects a compromise" between two opposing processes: on the one hand, it relieves NADH- and ATP-related control that limits the activity of TCA-cycle enzymes, on the other hand, it provides the cell with organic acids as buffer components and with carbon skeletons (intermediates of the TCA cycle are used as precursors for the formation of amino acids and lipids and in other biosynthetic pathways) [8]. This ensures fast readjustments of the respiratory metabolism in response to diurnal changes in light conditions and, in general, facilitates the maintenance of energy metabolism in photosynthesizing cells [8, 34].

PHOTORESPIRATION

Photorespiration is a light-stimulated process associated with the release of CO_2 and uptake of O_2. This cyclic process interconnects three types of cell organelles: chloroplasts, peroxisomes, and mitochondria. Photorespiration begins in chloroplasts: Rubisco exhibits oxygenase activity, thus oxidizing ribulose bisphosphate (RBP) by oxygen to form phosphoglycolate (Fig. 1). Phosphoglycolate is converted into glycolic acid (glycolate), which is then transported via the glycolate–glycerate translocator into peroxisomes. In these organelles, glycolate is oxidized to glyoxylate. The resulting hydrogen peroxide is eliminated by peroxisomal catalase. Next, the amination reaction results in the formation of glycine, with Glu as an amino group donor for this reaction. Glycine moves into the mitochondria, where two of its molecules condense to form serine and CO_2 in the reaction catalyzed by glycine decarboxylase complex (GDC) and serine hydroxymethyl transferase. Serine enters the cytosol, where it is used for protein synthesis or returns to the peroxisomes (by means of the amino acid translocator), and is converted to glycerate, which is transported into the chloroplast and participates in the Calvin cycle. It is known that light absorbed by the phytochrome system directly regulates the expression of genes for enzymes involved in the formation of photorespiratory peroxisomes and in photorespiration, including GDC and serine hydroxymethyltransferase [36, 44, 45].

Under natural CO_2 concentration in the atmosphere, the portion of photorespiration in the photosynthetic gas exchange equals to 25–30% and sharply rises with the increase in O_2 concentration or with the decrease in CO_2 content [35, 46]. One approach to detecting photorespiration is to monitor the postillumination burst of CO_2 release lasting for the first 3–4 min after darkening [3, 46]. After switching off the light, photosynthetic uptake of CO_2 ceases immediately, while the production and metabolic conversions of glycolate remain running in the dark. Therefore, the conversion of glycine to serine, taking place for some time in darkness, results in the CO_2 release, provided the photosynthetically produced RBP is present. During greening of etiolated wheat seedlings, the postillumination burst of CO_2 was observed after 24 h of de-etiolation [43], when the photosynthetic apparatus, including PSI and PSII, was completely formed [17, 47].

Since photorespiration is not accompanied by energy accumulation, the role of this process in photosynthesizing cells has been a matter of long-term discussions. It is known that plants with the C_4 type carbon metabolism are characterized by low photorespiration and comparatively high productivity. Analysis of C_3 plants under conditions of diminished photorespiration confirmed that the light-dependent oxidative processes are indispensable for covering energy demands and providing optimal conditions for the photosynthetic organ (leaf) and the whole plant [14]. Moreover, the energy efficiency of photosynthesis and the respiratory component in the apparent photosynthesis were equal for C_3 and C_4 plants under comparable conditions [12]. Currently, there are reasons to believe that photorespiration is an integral part of not only photosynthesis but also of the production process [46, 48, 49]. Photorespiration enables synthesis of amino acids and prevents the accumulation of intermediary toxic products (phosphoglycolate, glyoxylate). Photorespiration disposes excessive amounts of NADPH and ATP formed at the light stage of photo-

synthesis (if the capacity of the Calvin cycle is insufficient), thus preventing overreduction of the chloroplast [48]. The functioning of GDC in mitochondria produces a large amount of NADH that can be used in the photorespiration itself and can be exported to the cytosol and oxidized in the respiratory chain [48]. Thus, photorespiration plays an important role in regulation of the redox balance in photosynthesizing cells [48, 49].

SUPPLY OF REDUCING EQUIVALENTS TO MITOCHONDRIAL ETC IN THE LIGHT

The final stage of respiration, most important for energy metabolism, is associated with the operation of mETC, where reducing equivalents are oxidized to produce energy in the form of ATP (Fig. 2).

There is evidence that mitochondria of photosynthesizing cells can produce NADH in the TCA cycle (in the reactions catalyzed by isocitrate dehydrogenase and mitochondrial NAD-dependent malate dehydrogenase oxidizing malate to oxaloacetate) [8], as well as in photorespiration (reaction of serine formation catalyzed by GDC) [48] (Fig. 1).

An important aspect of mitochondrial function in photosynthesizing cells is the ability of mETC to oxidize reducing equivalents produced in the chloroplasts. The reducing equivalents can be exported from chloroplasts into the cytosol and then to mitochondria by means of various shuttle mechanisms [6]. Since the inner membrane of the organelle is impermeable to NADH molecules, there exist special mechanisms (shuttle systems) that take hydrogen atoms from NADH in one cell compartment and transfer them to another compartment. The best known shuttle mechanisms are malate–oxaloacetate shuttle (Malate–OA) and malate–aspartate shuttle (Malate–Asp) [6].

The Malate–OA-shuttle mechanism is localized on the inner membrane of chloroplasts and mitochondria and is considered the most important system for the exchange of reducing equivalents among these organelles. The Malate–OA–shuttle mediates the transport of malate from chloroplasts into the cytosol, where the cytoplasmic MDH (cMDH) can convert malate to oxaloacetate in association with reduction of NAD to NADH (Fig. 1). The formation of malate in the chloroplast stroma is catalyzed by NADPH-dependent MDH (chMDH). It is known that chMDH plays a major role in NADPH recycling (turnover), especially upon the excess formation of reducing agents needed for photosynthetic fixation of CO_2 [50]. Malate, produced from the recycled oxaloacetate and the cytosolic NAD(P)H, is transferred to mitochondria in exchange for oxaloacetate, thus entering the TCA cycle [8]. In mitochondria, malate is oxidized by mMDH to form NADH and oxaloacetate. Oxaloacetate returns to the cytosol to repeat the cycle.

The Malate–Asp–shuttle is localized in the inner mitochondrial membrane and ensures simultaneous operation of the two transporters [6, 51]. The cytosolic malate is transported in exchange for mitochondrial 2-OG. In mitochondria, oxaloacetate is converted into malate by mMDH with the concurrent production of NADH. Oxaloacetate is transformed into aspartate by means of aspartate aminotransferase that transfers an amino group from Glu. The deamination of Glu to 2-OG is catalyzed by the same enzyme. The antiporter exchanges aspartate for glutamate, and the cycle repeats.

It is also important to note the operation of TPT, a shuttle mechanism localized in the chloroplast envelope membrane, which is not directly related to the transport of reducing equivalents. TPT belongs to the family of phosphate translocators; it exports triose phosphate (particularly, dihydroxyacetone phosphate) from chloroplasts in exchange for cytosolic phosphate [52, 53]. Dihydroxyacetone phosphate enters the cytosol and is used for synthesis of sucrose. The import of phosphate into the chloroplast is needed for ATP formation. Remarkably, triose phosphate is oxidized in the cytosol by two forms of cytosolic dehydrogenases (NAD-dependent phosphorylating dehydrogenase and nonphosphorylating NADP-dependent dehydrogenase); this reaction produces 3PG, NADH, and NADPH [24]. Further, the reducing equivalents can enter the mitochondria via the shuttles located in the inner membrane of the respiratory organelles.

Currently, ample evidence has accumulated that functioning of the shuttle mechanisms, especially malate–oxaloacetate shuttle, ensures the removal of excess reductants from the chloroplasts, thus maintaining the optimal ATP/ADP and NADH/NAD ratios in the cell, while mETC oxidizes the reducing equivalents exported from chloroplasts [5, 6, 20].

FUNCTIONING OF ETC IN PLANT MITOCHONDRIA IN THE LIGHT

Plant mitochondria differ from animal ones in composition of ETC carriers (Fig. 2). Apart from the main cytochrome pathway, mETC contains nonphosphorylating alternative pathways. Electron transport along the nonphosphorylating pathways is not associated with the generation of the proton gradient required for ATP synthesis. The main electron carriers in the nonphosphorylating pathways are alternative oxidase (AOX) [54] and alternative "external" and "internal" type II NAD(P)H dehydrogenases (type II NAD(P)H-DH) [55]. Uncoupling proteins (UCP) of the inner mitochondrial membrane are the systems capable of dissipating the proton gradient [56]. Owing to activation of nonphosphorylating pathways, mETC dissipates the excess reductants, including those exported from chloroplasts. Over the last decade, a great deal of information has accumulated on functioning of mETC in the light; the main results are summarized in several reviews [5–9, 57]. However, the mechanisms that regulate activities of individual mETC components in the light are still insufficiently understood.

Data on functioning of the cytochrome path in the light are controversial. It was shown that transcription rate of mitochondrial genes changed accordingly to diurnal rhythm, while the relative abundance of transcripts was stable during light and dark periods [58]. The lack of apparent light dependency was shown for gene expression and nuclear-encoded proteins of complex I subunits (76 kDa and NAD9) in potato leaves [59] and *Arabidopsis* [60], as well as for mitochondrial-encoded subunits of cytochrome *c* oxidase (*COX2*) in leaves of *Arabidopsis* [61], and wheat [43]. At the same time, analysis of genome expression in *phyA/phyB* phytochrome mutants of *Arabidopsis thaliana* revealed light-dependent expression for eight genes encoding protein complexes of the cytochrome pathway [36, 37]. Studies of the mitochondrial mutants deficient in respiratory complexes of the cytochrome pathway revealed the reduction in some photosynthetic parameters, which indicates a significant role of the main respiratory phosphorylating path in photosynthesizing cells [62, 63]. The activation of the cytochrome path in the light is presumably determined by the content of photosynthetic metabolites, carbohydrates in particular [57]. Expression of nuclear genes coding for cytochrome *c* and the subunits of complex IV (cytochrome *c* oxidase) depended primarily on the carbohydrate content rather than on illumination conditions [61, 64]. A positive linear correlation was found between the cytochrome route activity and the content of soluble sugars in greening wheat leaves [65].

It should be noted that the electron transport along the cytochrome path is constrained by the adenylate control, the control being enhanced in photosynthesizing cells. The main pathway of respiratory ETC comprises four multienzyme complexes composed of a large number of subunits. According to some authors [6], these features might restrict the response time of the cytochrome pathway to changes in illumination conditions.

Alternative Oxidase

The ETC of plant mitochondria is distinguished by its ability to transport electrons directly from the ubiquinone pool to O_2 through AOX [54, 66–68]. Since this path is resistant to cyanide, it was termed cyanide-resistant (alternative) pathway. The ubiquinol–oxygen oxidoreductase, AOX, is a low-molecular-weight protein (32–34 kDa) composed of one polypeptide. The synthesis of this protein is encoded by the family of nuclear genes [69]. The functional form of AOX in the membrane of plant mitochondria is a dimer [70]. The enzyme is largely inactive when its subunits are covalently linked by a disulfide bridge. The enzyme is activated upon the reduction of the disulfide bond. Electron transport along the alternative path bypasses two complexes III and IV, the two sites associated with the generation of membrane potential; therefore, this electron transport pathway is low efficient in terms of energy conservation. Nevertheless, alternative respiration plays an important role in the plant cell functioning. Electron transport along the alternative pathway is not limited by adenylate control, which is important for maintaining cell activity under restricted operation of the main pathway. The alternative respiration stabilizes the redox balance in mETC because it "rapidly" oxidizes NADH and prevents excessive ROS generation [67, 71].

The last decade has brought sufficient evidence that the alternative respiratory path is an important means to optimize photosynthesis and protect the cell from photoinhibition [5, 6, 19, 20]. In the light, the alternative respiration participates in oxidation of reducing equivalents delivered from chloroplasts to mitochondria via the Malate–OA-shuttle, which facilitates the "unloading" of photosynthetic ETC in chloroplasts [5]. Light induces the expression of AOX genes through the photoreceptors or the mechanisms associated with activation of photosynthetic metabolism and changes in the carbohydrate pool [6, 9, 57]. The increased activity of the alternative (cyanide-resistant) respiratory pathway and its involvement in the metabolism was demonstrated in greening leaves [15–17] and in plants exposed to high irradiance [16, 72, 73].

The light induction of AOX genes may involve phytochromes *A* and *B*, as evidenced by genome expression profiles in *phyA/phyB* phytochrome mutants of *A. thaliana* at various stages of seedling de-etiolation [36, 37]. Expression of *AOX1a* in leaves of *Arabidopsis* [16, 36, 37, 60] and *AOX2* in soybean cotyledons [74] was light-dependent. In experiments with greening wheat seedlings, expression of *AOX1a* was clearly light-dependent and concurrent in dynamics with the activity of alternative respiration [43]. Expression in wheat leaves of the second identified AOX-encoding gene, *AOX1c* [75], was not induced by illumination and was complementary to *AOX1a* expression. Hence, it is evident that not all AOX genes are light-inducible.

Changes in the pool of organic carbon (carbohydrates, amino acids) and the intracellular redox state during photosynthesis can also affect the expression of genes and AOX activity [57]. According to some authors, the enhancement of alternative respiration in plants exposed to high irradiance could be due to the increase in carbohydrate content and to the substrate regulation of AOX activity [73, 76–78]. However, the described stimulation was not found in some plant species [76, 77]. Apparently, the influence of carbohydrates on alternative respiration differs in sun and shade plants and depends on the capacity for growth.

Our studies demonstrated complex relationships between the alternative respiration and dynamics of carbohydrate reserves during greening of wheat seedlings [65] and the lack of correlation between the *AOX1a* expression and the content of AOX protein [43]. For example, *AOX1a* expression and the fractional contribution of alternative path to leaf total respiration

decreased after 24-h de-etiolation, whereas the content of AOX protein remained largely unchanged. Our analysis of the substrate regulation of AOX recruitment revealed that suppression of alternative respiration on the background of constant AOX protein content during this period could be due to limited availability of soluble carbohydrates as a substrate [65]. This circumstance could affect the posttranslational protein modification. The limited availability of the substrate might retard the decomposition of sucrose to pyruvate, a compound known to activate AOX and to increase AOX affinity to ubiquinone [79].

The lack of a clear relation between the activity of alternative respiration and the content of AOX protein under variable light conditions was also noted by other authors [15, 73]. This indicates the existence in cells of additional mechanisms for regulating the enzyme activity. It is assumed that AOX activity depends on the NADPH/NADP ratio in the mitochondrial matrix, which is higher in illuminated than in darkened leaves [38] and might be controlled by $NADP^+$–thioredoxin-dependent system [6]. Experiments with *Alocasia odora* leaves revealed that high irradiance promoted the conversion of AOX protein to the active reduced form [80]. The mechanisms of AOX activity regulation in photosynthesizing cells are intriguing and warrant further research.

Alternative Type II NAD(P)H Dehydrogenases

The inner mitochondrial membrane contains "internal" and "external" type II NAD(P)H dehydrogenases that are encoded by a family of nuclear genes and are insensitive to rotenone, an inhibitor of complex I [55] (Fig. 2). These dehydrogenases oxidize endogenous and exogenous NAD(P)H by transferring electrons to ubiquinone via the bypass around the first energy-coupling site of ETC. Unlike the "internal" NAD(P)H dehydrgenases, the activity of "external" dehydrogenases depends on the concentration of intracellular Ca^{2+} known to increase under stress conditions [55].

Isolated plant leaf mitochondria are characterized by relatively high activity of type II NAD(P)H dehydrogenase [81]. Polymerase chain reaction (PCR) analysis revealed the light-induced expression of certain genes coding for "internal" and "external" NAD(P)H dehydrogenases [59, 60, 82]. In leaves of *A. thaliana*, expression of only two genes coding for "internal" and "external" NAD(P)H dehydrogenases, i.e., *NDA1* and *NDB2*, respectively, exhibited the diurnal dynamics and was intensified during the daytime [82, 83]. Experiments with photoreceptor mutants revealed that the expression of the above genes is directly controlled by phytochromes *A, B* and cryptochrome 1. The light-sensitive core element of *NDA1* gene is located in the region of 99-bp promoter containing a cluster of *cis*-regulatory elements of genes of photosynthetic proteins [60, 84].

It is commonly supposed that the "internal" Type II NAD(P)H dehydrogenases are involved in oxidation of photorespiratory reductants, while "external" dehydrogenases oxidize the cytosolic NADH [9, 24]. Simultaneous photoactivation of "internal" NAD(P)H dehydrogenases and AOX on the background of the increasing pool of photorespiratory NADH was noted by many authors [59, 60]. It was found that *NDA1* gene is located in the cluster shared with the gene encoding the P-subunit of GDC, a photorespiratory enzyme [83].

The concerted action of AOX and Type II NAD(P)H dehydrogenase in oxidizing the reductants of mitochondrial and extramitochondrial origin was also shown in experiments with deetiolated wheat seedlings [43]. The highest rates of O_2 consumption by mitochondria during oxidation of exogenous NADH by "external" NAD(P)H dehydrogenases were observed 6 h from the onset of de-etiolation, at the period concurrent with the increased activity of alternative respiration. After this period, the chloroplast structure was stabilized and elevated rates of net photosynthesis were noted. The rate of glycine oxidation, an indicator for the activity of "internal" NAD(P)H dehydrogenases, and the AOX involvement in the presence of this substrate were found to increase after 24 h of greening. These changes correlated with the development of photorespiratory activity.

Uncoupling Proteins

Uncoupling proteins (UCP) are mitochondrial proteins involved in thermogenesis; they were discovered in adipocytes of brown adipose tissue [85]. They are now found in mitochondria of both animal and plant cells [56, 85]. The UCP are highly homologous and belong to the family of mitochondrial anion transporters. In the presence of fatty acids acting as cyclic protonophores, UCP1 transports protons across the inner mitochondrial membrane into the matrix (Fig. 2). As a result, the electrochemical potential energy generated by the respiratory chain is dissipated as heat. Thus, the uncoupling of respiration and phosphorylation takes place [85–87].

Uncoupling proteins are nuclear-encoded proteins with mol wt ~32 kD. In *A. thaliana*, six genes encoding UCP were identified [56]. The plant UCP account for heat generation in thermogenic tissues [88], for the climacteric rise in fruit respiration, and for the protection against oxidative stress; they are also activated under hypothermia [56, 89, 90]. In photosynthesizing cells, the activation of UCP is presumably associated with the additional demand for NADH oxidation, especially at high irradiance; the activation enhances the turnover rate of TCA cycle [91]. The exposure of *Arabidopsis* plants to the photon flux density of 400 μmol/(m^2 s) promoted the expression of *UCP1* and *UCP5* [92]. The lack of *UCP1* gene in leaves of *Arabidopsis* mutant retarded the photorespiratory glycine oxidation and inhibited photosynthesis [93]. How-

ever, under normal irradiance, the expression *UCP1* and *UCP2* genes in deetiolating leaves of *Arabidopsis* [60] and wheat [94] showed no light dependency.

CONCLUSIONS

Recent development and application of modern physicochemical and molecular–genetic techniques brought new knowledge on functioning of respiration during photosynthesis and on cooperation of these two processes in the photosynthesizing cell. It becomes obvious that mitochondrial respiration not only persists under light but also optimizes the conditions for photosynthesis and protects the cells from photodestruction. At the same time, new questions and interesting perspectives have appeared. Photosynthesis and respiration are the main energy-generating processes; therefore, the extent and direction of metabolic fluxes, as well as the controlled involvement of respiratory pathways are largely determined by cell demands for energy and metabolites. It is reasonable to assume that the impact of light on respiration and mitochondria–chloroplast interactions may vary depending on plant preferences for high or low irradiance, on plant functional condition and growth potential, as well as on the duration and strength of stresses and plant resistance to stress factors. All these issues require further study.

The insufficiently explored topics include the signal transduction mechanisms underlying mobilization of respiratory pathways and their coordinated functioning in photosynthesizing cells, the posttranslational regulation of the respiratory enzymes and electron transport carriers in the nonphosphorylating pathways, and the control and interactions of energy-dissipating pathways in chloroplasts and mitochondria. We believe that research in these promising areas will clarify direct and indirect mechanisms of light-regulated respiration and broaden our understanding of interorganellar signaling in the plant cell. Keen attention to the problem of light-modulated mitochondrial respiration would help to create an integrated model of regulated energy metabolism and synthetic processes in the photosynthesizing cell as a unique source of life on Earth. This may possibly facilitate the future development of artificial energy-generating biosystems.

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