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SHORT REVIEW

Respiration and Photosynthesis in Energy-Transducing Membranes of Cyanobacteria[1]

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Abstract

Cyanobacteria are photolithotrophic organisms exhibiting oxygenic photosynthesis. In the dark they satisfy their need for energy with respiration. These reactions occur in the same compartment and probably on the same energy-transducing membranes. The characterization of the electron transport chain in the light and in the dark, photophosphorylation and oxidative phosphorylation, as well as possible common pathways in photosynthesis and respiration, are discussed.

Key Words: Respiration; photosynthesis; cyanobacteria; thylakoids; energy-transducing membranes.

Introduction

This review concentrates on light-driven and oxidative events and their relationship in energy-transducing membranes of cyanobacteria. So far the vast majority of investigations have been carried out with the photosynthetic system, and there exist a number of excellent reviews to which I will refer. On the other hand, very little work has been done on respiration although recently there is a rapidly growing interest in this subject.

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[1]Abbreviations: DCMU, 3-(3,4-dicholrophenyl)-1,1-dimethylurea; LDAO, lauryldimethylamine oxide; SDS-PAGE, Na-dodecyl sulfate polyacrylamide gel electrophoresis; DBMIB, 2,5-dibromo-3-methyl-6-isopropyl-*p*-benzoquinone; TTFA, 5-thenoxyltrifluoroacetone; *m*-CLAM, *m*-chlorobenzhydroxamic acid; DCCD, *N,N'*-dicyclohexylcarbodiimide. Systematical Notes: *Plectonema boryanum* = *Phormidium luridum; Anacystis nidulans* = *Synechococcus sp.; Mastigocladus laminosus* = *Fischerella sp.*

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Cyanobacteria, formerly called cyanophytae or blue green algae, are a distinct type of photosynthetic organism: they are the only prokaryotes with oxygenic photosynthesis of the higher plant type. Cyanobacteria are physiologically and structurally a heterogeneous group of organisms. A revised classification has been published by Rippka *et al.* (1979). This diversity has to be considered when experiments done with different species are compared.

Since cyanobacteria are prokaryotes, the energy-transducing membranes are not located in mitochondria nor chloroplasts as in higher plants. Instead cyanobacterial cells contain a densely packed membrane system (thylakoids) in the cytoplasm. In addition, the plasmalemma can serve as an energy-transducing membrane system like in other bacteria.

There is a fair amount of evidence today that chloroplasts of higher plants with their cyanobacterial-like genome structure and photosynthesis are endosymbiotic ancient prokaryotes (Gray and Doolittle, 1982). There are two recent reviews on the evolution of cyanobacteria and their relation to other photosynthetic organisms (Whatley *et al.*, 1979; Krogmann, 1981). Another report describes more generally the evolution of energy-transducing membranes and their functions (Wilson and Lin, 1980). Books about cytology, physiology, and biochemistry of cyanobacteria have been published by Carr and Whitton (1973) and by Fogg *et al.* (1973).

Structure of the Membranes

Thylakoid membranes of cyanobacteria are similar to those of chloroplasts of higher plants. Neverthelss there are two obvious structural differences: the lack of phycobilisomes in chloroplast thylakoids of higher plants and the absence of the typical chloroplast grana stacks in cyanobacteria. The prokaryotic origin of cyanobacteria is suggested by the rather high content of saturated or mono-unsaturated fatty acids in many lipids.

Whether the cell membrane (plasmalemma) is linked to the thylakoids is still a subject of controversy (Bisalputra, 1974). On electron micrographs the plasmalemma appears smoother than thylakoid membranes and does not have attached phycobilisomes (Holt and Edwards, 1972). Furthermore, cells deprived of carbon dioxide (Miller and Holt, 1977) or photobleached under extreme conditions (Schmetterer and Peschek, 1981) lose their thylakoids while the plasmalemma remains intact and the cells turn colorless. These results indicate that in general the plasmalemma does not possess photosynthetic activities. Cell envelopes with attached plasmalemma have been separated from thylakoids of *Anacystis nidulans* (Murata *et al.*, 1981), but functions of the cell envelopes have not been determined; thus the activities of the plasmalemma alone are not known yet.

Methods for perparing active energy-transducing membranes have been reviewed by Spiller and Böger (1980). Although the authors only refer to photosynthetic activities, similar membrane preparations are also used for respiration studies. Good sources for stable membranes are thermophilic cyanobacteria such as *Synechococcus lividus* (Yamaoka *et al.*, 1978), *Mastigocladus laminosus* (Bohler and Binder, 1980), or *Phormidium laminosum* (Stewart and Bendall, 1980).

The broad temperature spectrum of cyanobacteria make them an ideal tool to investigate the influence of growth temperature on the phase-transition temperature of the membrane lipids, their composition, and the degree of saturation of their fatty acids. These works and their relation to photosynthesis have been reviewed by Ho and Krogmann (1982). The influence of growth temperature on respiratory electron transport has been measured in membranes of *Anacystis nidulans* (Peschek *et al.*, 1982).

Structures and Functions Typical for Photosynthesis

Cyanobacteria have an oxygenic photosynthesis with a mechanism which is very similar to that found in chloroplast thylakoids of eukaryotic cells (Trebst and Avron, 1977; San Pietro, 1980). Two extensive reviews on photosynthsis in cyanobacterial thylakoids cover the literature until 1979 (Krogmann, 1977; Ho and Krogmann, 1982).

The facultative anoxygenic photosynthesis which can be observed in many cyanobacteria involves photosystem I only and functions in two different ways. On the one hand, reducing power and ATP are formed in a photolithotrophic pathway using as electron donors either molecular hydrogen (Belkin and Padan, 1978; Eisbrenner and Bothe, 1979) or reduced sulfur compounds such as hydrogen sulfide (Padan, 1979). On the other hand, photosystem I in a photoorganotrophic pathway can either carry out cyclic photophosphorylation or it can mediate noncyclic phosphorylation with organic substrates acting as electron donors. In these reactions cyanobacteria are similar to the bacteria with obligate anoxygenic photosynthesis (Chlorobiaceae, Chromatiaceae, and Rhodospirillaceae). Yet these bacteria are considerably different from the cyanobacteria in their pigments, reaction centers, quinones, and cytochromes (Clayton and Sistrom, 1978). Crofts and Wood (1978) have published a comparison of the photosynthetic electron transport chains of plants and bacteria and their role as proton pumps.

Light-Harvesting Pigments

Cyanobacteria contain only chlorophyll *a* and no chlorophyll *b*. Several groups have separated chlorophyll proteins from higher plants and from

cyanobacteria by SDS-PAGE (reviewed by Thornber *et al.*, 1979). Four chlorophyll–protein complexes have been resolved in *Nostoc* sp. and compared with those of spinach chloroplasts (Rusckowski and Zilinskas, 1980), whereas in *Phormidium luridum* and *Anabaena cylindrica* (Reinmann and Thornber, 1979) as well as in *Phormidium laminosum* (Stewart, 1980) three chorophyll-containing peptides are described.

Holt and Krogmann (1981) have described the isolation of carotenoid protein complexes from a number of cyanobacteria. Carotenoids are mainly light-harvesting antenna pigments associated with photosystem II (reviewed by Ho and Krogmann, 1982). Raman spectroscopic evidence indicates that carotenoids may even be involved in the attachment of phycobilisomes to the membranes (Szalontai and Van de Ven, 1981).

The phycobiliproteins are water-soluble light-harvesting pigment proteins used mainly in photosystem II and are only found in cyanobacteria and red algae. Bryant *et al.* (1979) describe the isolation and structure of the hemidisocidal phycobilisomes of several cyanobacteria. Dissociation and reassociation of phycobilisomes have been carried out by Canaani *et al.* (1980) and Nies and Wehrmeyer (1981). The first complete sequences of C-phycocyanin and allophycocyanin have been reported from the thermophilic *Mastigocladus laminosus* (Frank *et al.*, 1978; Sidler *et al.*, 1981). From carbon and nitrogen starvation experiments (Miller and Holt, 1977; Ownby *et al.* 1979), it can be concluded that phycobiliproteins play an additional role as storage proteins. There exist three recent reviews on phycobiliproteins (Glazer, 1977; Gantt, 1980; Scheer, 1981).

Reaction Centers with Their Electron Donors and Acceptors

Highly active photosystem II particles, including the photosystem II reaction center P680 and the water-splitting enzyme system Y, have been prepared and purified from thermophilic cyanobacteria (Stewart and Bendall, 1981; G. Schatz, personal communication) and from a number of mesophilic species (England and Evans, 1981; Evans and Pullin, 1981). The primary electron acceptor of the photosystem II reaction center, a bound plastoquinone molecule (Q, C-550, X-320), known from plant chloroplasts, has also been identified in cyanobacteria (Fujita, 1976).

A number of publications describe the extraction and purification of the photosystem I reaction center complex P700 from cyanobacteria (for a review see Olson and Thornber, 1979; Shiozowa, 1980). Some of the publications also report the simultaneous preparation of photosystem I and II reaction centers (Newman and Sherman, 1978; Stewart and Bendall, 1979; Nakayama *et al.*, 1979; Reinmann and Thornber, 1979; Evans and Pullin, 1981). All the P700 preparations contain a large amount of light-harvesting chlorophyll in contrast to purple bacteria reaction centers which contain none (Olson and Thornber, 1979). The best preparations from cyanobacteria are reported to

have 40 chlorophyll *a* molecules per one P700 complex (Evans and Pullin, 1981; Newman and Sherman, 1978). In a comprehensive review by Olson and Thornber (1979), reaction centers of cyanobacteria and higher plants are compared with those of the purple and green bacteria.

The first electron acceptor of P700 is known to be a nonheme iron sulfur protein (P430, X, bound ferredoxin). EPR and Mössbauer spectra in different cyanobacteria have been reported by a number of groups (Cammack *et al.* 1979a, b; Evans *et al.* 1979; Hiyama and Fork, 1980). The cyanobacterial iron sulfur center itself or an unknown compound near to it is easily autooxidizable, i.e., it efficiently catalyzes the reduction of oxygen as shown in *Anabaena variabilis* (Honeycutt and Krogmann, 1970) and in *Phormidium luridum* (Binder *et al.*, 1976).

In higher plants and cyanobacteria, soluble ferredoxin is the electron acceptor of the bound iron sulfur centers. Under iron deficiency, cyanobacteria can replace ferredoxin with the flavoprotein flavodoxin (Fitzgerald *et al.*, 1977; Hutber *et al.*, 1978), a low-potential compound which is also found in *Clostridium, Rhodospirillum,* and others (Adman, 1979; Tollin and Edmondson, 1980).

The last enzyme in the electron transport from photosystem I to NADP is the membrane-bound flavoprotein, ferredoxin-NADP-oxidoreductase (reviewed by Zanetti and Curti, 1980).

Structures and Functions Typical for Respiration

Several cyanobacteria are known to grow in the dark with respiration. Heterotrophic growth and the carbon metabolism of cyanobacteria have been reviewed by Stanier (1975) and Stanier and Cohen-Bazire (1977).

The mitochondrial-like aerobic respiration is not the only possible heterotrophic dark metabolism in cyanobacteria. *Oscillatoria limnetica,* for example, can anaerobically break down intracellular glycogen in the dark (Oren and Shilo, 1979). In the absence of elemental sulfur, the organism carries out a fermentation to lactate, whereas in its presence anaerobic respiration occurs in which sulfur is reduced to sulfide.

In cyanobacteria dark growth is very slow and all the respiratory activities, including oxidative phosphorylation, are extremely low compared to the corresponding rates in the light. Thus, it seems that in most cases the purpose of respiration is the maintainance of a minimal energy metabolism in order to survive dark periods. The photosynthetic bacteria in the family of the Rhodospirillaceae, on the other hand, can actually adapt their energy metabolism to either anaerobic photosynthesis or aerobic respiration with good growth rates under both conditions (Baccarini-Melandri and Zannoni, 1978).

Electron Donors of the Respiratory Chain

NADPH, which is, in general, the better electron donor to the respiratory chain than NADH, is supplied from the oxidative pentose phosphate cycle. Whether NADH is formed through a transhydrogenase remains to be determined. Inhibitors of flavoproteins such as rotenone and TTFA are also inhibitors of the cyanobacterial dehydrogenase (Leach and Carr, 1970; Peschek, 1980a). In *Mastigocladus laminosus,* the NAD (P) H dehydrogenase activitiy is thermostable (Binder *et al.,* 1981). There is no information yet on the characteristics of the NAD (P) H dehydrogenase of cyanobacteria nor on the endogenous electron acceptor of the dehydrogenase, plastoquinone or vitamin K1.

Although there are several reports on the presence of succinate dehydrogenase in the respiratory chain of cyanobacteria (Leach and Carr, 1970; Peschek, 1980a; Binder *et al.,* 1981), the characteristics of this enzyme are not yet known.

Uptake hydrogenases have been characterized from different cyanobacteria by Eisbrenner *et al.* (1978). One of the functions described is the utilization of hydrogen in the respiratory chain to reduce oxygen in the Knallgas reaction. Eisbrenner and Bothe (1979), using whole cells of *Anabaena cylindrica,* and Peschek (1980a), using a membrane preparation of *Anacystis nidulans,* have shown that hydrogen oxidation in the dark operates through a respiratory electron transport chain without the participation of flavoproteins and pyridine nucleotides. Whether the hydrogenase directly reduces the quinone pool is uncertain. The same Knallgas reaction is also found in the respiration of hydrogen bacteria (Probst, 1980). Several eukaryotic algae have retained the ability to use hydrogen as an electron donor for photosynthesis under anaerobic conditions (Ben Amotz, 1979).

Cytochrome Oxidase

Several groups have described cytochrome oxidase activities in various cyanobacteria showing different inhibition characteristics toward cyanide, azide, and carbon monoxide (Biggins, 1969; Leach and Carr, 1970; Tang and Krogmann, 1972; Peschek, 1980a). Although these data are rather inconsistent, they show that at least some cyanobacteria have a cytochrome *aa*3 type oxidase. This has been confirmed by the spectral identification of cytochrome *aa*3 in *Anacystis nidulans* (Peschek, 1981a) and in *Nostoc* sp. (Peschek, 1981b). The reaction of cytochrome *aa*3 from *Anacystis nidulans* with various soluble c-type cytochromes has been described by Peschek *et al.* (1981b).

The partial insensitivity of the cyanobacterial cytochrome oxidase activity toward the classic heme *aa*3 inhibitors indicates a branched end oxidation with alternate oxidases as has been found in many bacteria and higher plants.

The inhibition by *m*-CLAM (Peschek, 1980a) points to a cyanide-resistant oxidase which is also found in higher plants (Solomos, 1977). Other alternatives would be the cytochrome *o* type oxidase found in *Vitreoscilla* (Webster and Hackett, 1966; Dietrich and Biggins, 1971) and many other bacteria (Jurtshuk and Yang, 1980) or the cytochrome *b* type oxidases typical for Rhodospirillaceae (Zannoni and Baccarini-Melandri, 1980).

Common Structures and Functions in Respiration and Photosynthesis

The occurrence of cyanobacterial respiration and photosynthesis in the same compartment indicates a close relation of these two activities. During dark heterotrophic growth, cells of several species remain pigmented for years and resume photoautotrophic growth immediately when placed in the light (Rippka, 1972; White and Shilo, 1975). However, cells of *Plectonema boryanum* and *Anacytstis nidulans* become chlorotic when grown in the dark (Pan, 1972; Shanmugasundaram and Lakshmanan, 1979). Phycocyanin is retained during dark growth in *Plectonema boryanum* (Raboy *et al.*, 1976) but is lost in *Chlorogloea fritschii* (Lex *et al.*, 1974). In the latter organism it has in fact been shown that photosystem I activities are retained during growth in the dark whereas photosystem II is lost (Evans *et al.*, 1978). The authors have also observed that following transition to light, photosystem II and carbon dioxide fixation recover in a fast and a slow phase.

In *Anacystis nidulans* and *Anabaena variabilis* the inhibition of respiratory oxygen uptake during illumination (absorbed by chlorophyll *a*) is due to the competition of photosystem I for electrons (Jones and Myers, 1963; Imafuku and Katoh, 1976; Rubin *et al.*, 1977). Light dim enough not to allow any photoautotrophic metabolism but sufficient to drive cyclic photophosphorylation in photosystem I stimulates heterotrophic growth of a *Nostoc* strain (Bottomley and Van Baalen, 1978). In a theoretical treatise, Broda and Peschek (1979) discuss the common origin of respiration and photosynthesis in evolution. In addition to dark respiration and photosynthesis, one should mention that photorespiration, a reaction catalyzed by ribulose bisphosphate carboxylase-oxygenase found in chloroplasts and photosynthetic bacteria, has also been reported in cyanobacteria (reviewed by Stanier and Cohen-Bazire, 1977; Wolk, 1980).

Electron Transport

It is striking that in all the respiratory and photosynthetic membranes (bacteria, mitochondria, and chloroplasts) the electron transport chains between the dehydogenases and cytochrome oxidase and between the two photosystems respectively have basically the same compounds with similar

structures: quinone pool, cytochrome *b/c* or cytochrome *b/f* complex, and soluble cytochrome *c* or plastocyanin. In cyanobacteria the thylakoids are known to be the site of the photosynthetic electron transport whereas the localization of the respiratory chain is still controversial. Basically two models are discussed.

1. The respiratory chain is only located in the plasmalemma and is separated from the photosynthetic one. This model is supported by experiments which show different uncoupling effects of ammonium ions in photophosphorylation versus oxidative phosphorylation (Almon and Böhme, 1982).

2. Respiration is not only located on the plasmalemma but also on the thylakoid membranes sharing a common electron transport chain with the photosynthetic system (Fig. 1). Many observations support this model and make it the more likely one. It has also been proposed that the two chains may be located in different areas of the thylakoids (Scherer *et al.*, 1981) coupled via mobile carriers (quinone, cytochrome *c*, or plastocyanin). A similar model was proposed by Anderson (1981) for the spatial separation of photosystems II and I in chloroplast thylakoids.

Respiration in the thylakoids of *Nostoc sphericum* has been visualized with specific cytochemical markers in electron micrographs (Bisalputra *et al.*, 1969). With the same cytochemical markers, Peschek *et al.* (1981a) have found respiration in cells of *Anacystis nidulans* both in the thylakoids and in the plamalemma. In addition, with photobleached cells it has been confirmed that the plasmalemma, as well as the thylakoids, can, in fact, be a site for respiration (Schmetterer and Peschek, 1981).

In membranes of cells grown photolithotrophically and in the presence of DCMU, organic acids or NAD (P) H can serve as electron donors for photosystem I through the respiratory oxidases (Murai and Katoh, 1975; Binder *et al.*, 1981). The same activity has been reported for the green alga *Chlamydomonas reinhardii,* which is possibly a relic from the respiratory chain of an ancient cyanobacterium (Godde and Trebst, 1980). Furthermore, photosystem I competes with the respiratory cytochrome oxidase for electrons from the common electron transport chain (Jones and Myers, 1963; Imafuku and Katoh, 1976). More evidence for a common pathway is given below.

Quinone Pool. The plastoquinone pool in cyanobacteria participates in photosynthetic electron transport as in chloroplasts (Lightbody and Krogmann, 1966). The absence of ubiquinone raises the question of which quinone is functioning in cyanobacterial respiration. The plastoquinone pool in *Synechococcus lividus* is not only involved in the photosynthetic but also in the respiratory electron transport chain, thereby forming a link betwen the two systems (Hirano *et al.*, 1980). Furthermore, reactions with molecular hydrogen in the dark and in the light have shown that plastoquinone is indeed a

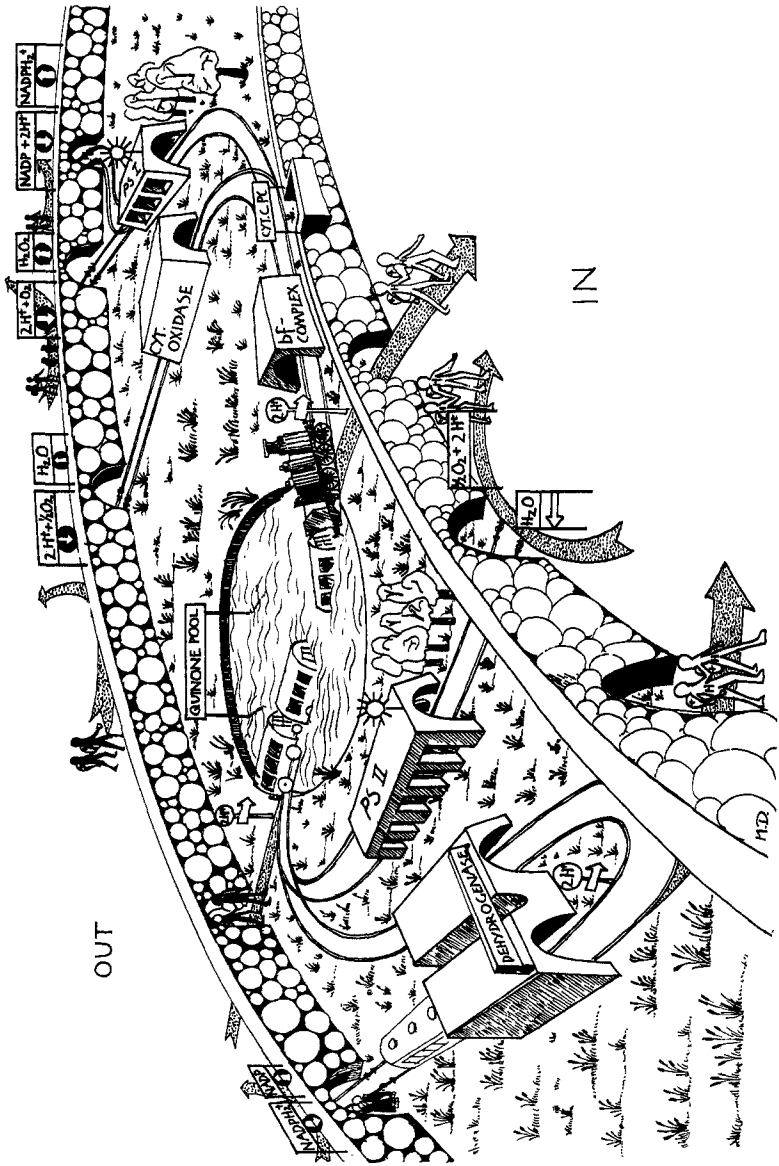

Fig. 1. Possible arrangement of respiratory and photosynthetic electron transport in cyanobacterial thylakoid membranes.

common electron carrier (Eisbrenner and Bothe, 1979; Antarikanonda *et al.*, 1980). Hence, cyanobacteria would be the only example of organisms using plastoquinone in respiration. In reconstitution experiments, Peschek (1980b) has demonstrated, however, that phylloquinone, which is about 20 times less abundant than plastoquinone, might be the respiratory quinone in *Anacystis nidulans*.

*Cytochrome b*559. Cytochrome *b*559 is known to be closely associated with photosystem II. This has indirectly been confirmed by the absence of cytochrome *b*559 in the heterocysts of *Nostoc muscorum* (Almon and Böhme, 1980). Although different functions of cytochrome *b*559 have been proposed, such as cyclic electron transport in photosystem II or involvement in the water splitting reaction, the exact role remains unclear. Cytochrome *b*559 has been dealt with in more detail in the review on photosynthetic cytochromes by Cramer and Whitmarsh (1977).

Cytochrome b/f Complex. The cytochrome *b/c* complex of mitochondria (complex III) contains cytochrome *b*, cytochrome *c*, the Rieske Fe-S center, and possibly bound quinone (Trumpower and Katki, 1979). In chloroplasts this cytochrome *b6/f* complex extracted with cholate and octylglucoside contains five subunits and shows plastoquinol-plastocyanin-oxidoreductase activity (Hurt and Hauska, 1981). Recently a similar complex has been isolated with the same detergents from the cyanobacterium *Anabaena variabilis* (W. Lockau and G. Hauska, personal communication). It is feasible that the complex in cyanobacteria is involved in the common pathway of the respiratory and photosynthetic electron transport chain, but no data are available so far. Besides acting in the linear electron transport, the complex is also involved in cyclic electron flow in photosystem I (Bouges-Bocquet, 1980). If the scheme for mitochondria applies (Trumpower and Katki, 1979), the mechanism of electron transfer within the complex is probably from cytochrome *b*6 to the iron sulfur center to cytochrome *f*.

Cytochrome *b*6 (−*b*563) has been observed in *Nostoc muscorum* (Knaff, 1977) and it seems to be oxidized and reduced by photosystem I, suggesting a role in a cyclic pathway. In the eukaryotic alga *Bumilleriopsis filiformis*, cytochrome *b*563 is a component of both cyclic and noncyclic electron transport chains (Böhme and Kunert, 1980). The possible involvement of cytochrome *b*6 in the respiratory chain is described by Metzler (1980).

Cytochrome *f* from the cytochrome *b/f* complex has been isolated and characterized from different cyanobacteria (Ho *et al.*, 1979; Böhme *et al.*, 1980). Sequence analysis of the *N*-terminus has shown that cytochrome *f* of *Spirulina maxima* and *Aphanizomenon flos-aquae* are identical and are similar to spinach cytochrome *f* (Ho and Krogmann, 1980). In *Anabaena variabilis*, organic acids such as malate and succinate can donate electrons to photosystem I via cytochrome *f* (Murai and Katoh, 1975), which is evi-

dence for cytochrome *f* being in the common pathway for respiration and photosynthesis.

*Cytochrome c*553 *and Plastocyanin.* Higher plants contain plastocyanin as the only P700 reductant, whereas in cyanobacteria and in a number of primitive eukaryotic algae cytorchrome *c*553 is more common. Exchange of plastocyanin and cytochrome *c*553, induced by copper, has been reported in the green alga *Chlamydomonas reinhardii* (Wood, 1978) and in the cyanobacteria *Anabaena vairabilis* and *Plectonema boryanum* (Sandmann and Böger, 1980). An extensive review on the relationship between plastocyanin and cytochrome *c* has been written by Crofts and Wood (1978).

Several cytochrome *c*533 species and plastocyanins acting as electron donors to photosystem I have been investigated (Davis *et al.,* 1980). These data indicate that basic cytochromes in more primitive cyanobacteria have evolved to acidic cytochromes in more recent species and eukaryotic algae (Krogmann, 1981). The structure and function of the cyanobacterial cytochrome *c*553 and plastocyanins have been reviewed in detail by Ho and Krogmann (1982).

Cyanobacterial cytochrome *c* 553 which donates electrons either to the cytochrome oxidase or to the reaction center is homologous to cytochrome *c* of mitochondria and respiratory bacteria as well as to cytochrome *c*2 of photosynthetic bacteria (reviewed by Salemme, 1977). A comparision of plastocyanin with azurin, a bacterial copper protein very similar to plastocyanin which reacts with cytochrome *c*, has been published by Adman (1979).

Evidence for a dual role of cytochrome *c*553 and plastocyanin in photosynthesis and respiration of cyanobacteria comes from the work of Lockau (1981). He has shown that soluble cytochrome *c* types from *Anabaena variabilis,* horse heart mitochondria, and, to a small extent, from two Rhodospirillaceae are able to stimulate photosystem I activity in the light as well as respiratory electron transport in the dark. Similar results have been obtained for *Mastigocladus laminosus* (A. Binder, unpublished data).

Proton-Motive Force

As predicted by Mitchell's chemiosmotic theory (Mitchell, 1968), the main characteristic of energy-transducing membranes is the electrochemical gradient of protons across the membrane. There is general agreement that the pH, more acidic inside the vesicle, is the driving force of photophosphorylation in the cyanobacterial thylakoids and that the electrical potential is practically nil. This has been observed in *Anacystis nidulans* (Falkner *et al.,* 1976), in *Plectonema boryanum* (Masamoto and Nishimura, 1977; Padan and Schuldiner, 1978; Barsky *et al.,* 1981), in *Anabaena variabilis* (Wax and Lockau,

1980), in *Mastigocladus laminosus* (Bohler and Binder, 1980) and in *Nostoc muscorum* (Almon and Böhme, 1982). It can be concluded that energy transduction in cyanobacterial thylakoids is similar to that in chloroplast thylakoids.

Upon energization of spheroplasts or whole cells by oxygen or by light, protons are extruded into the medium as in other prokaryotic cells (Scholes *et al.*, 1969; Masamoto and Nishimura, 1977; Barsky *et al.*, 1981). A proton-motive force has been shown to be necessary for active transport of glucose through the plasmalemma (Raboy and Padan, 1978). These results show that the plasmalemma indeed represents an energy–transducing membrane (for a model see Padan and Schuldiner, 1978).

ATP Synthesis

The coupling factor (F0–F1), bound to all energy-transducing membranes, is able to utilize the proton-motive force to synthesize ATP from ADP and phosphate (oxidative phosphorylation and photophosphorylation). In various cyanobacteria species, phosphorylation induced by light-driven electron transport has been observed with P/O ratios up to 1 and higher for the electron transport through both photosystems (Padan and Schuldiner, 1978; Ono and Murata, 1978; Binder *et al.*, 1976; Wax and Lockau, 1980; Spiller, 1980; Bohler and Binder, 1980).

Indirect evidence for the occurrence of oxidative phosphorylation in whole cells of cyanobacteria has been reported by several groups (Biggins, 1969; Imafuku and Katoh, 1976; Nitschmann and Peschek, 1982). Oxidative phosphorylation has been directly measured in spheroplasts and heterocysts (Almon and Böhme, 1982). Although respiration in isolated membranes of cyanobacteria is established, there has been only one report in the literature of oxidative phosphorylation in isolated membranes of *Anabaena variabilis* (Leach and Carr, 1970). Recently it has been possible to measure oxidative phosphorylation also in membranes of *Mastigocladus laminosus* (Binder *et al.*, 1981).

The first report of an isolated cyanobacterial coupling factor (AF1) for the thermophilic *Mastigocladus laminosus* (Binder and Bachofen, 1979) showed that the structure and function of this coupling factor is simlar to the CF1 of chloroplasts. Heat stability and dependence of the structure of the cyanobacterial coupling factor on growth conditions of the cells has been reported by Wolf *et al.* (1981). Reconstitution experiments have been carried out with AF1 and depleted membranes (Binder *et al.*, 1980; Bohler *et al.*, 1982) as well as with a crude coupling factor extract from *Spirulina platensis* (Owners-Narhi *et al.*, 1979). It remains to be proven whether the same coupling factor catalyzes both oxidative phosphorylation and photophosphorylation.

The coupling factor complex F0–F1 with ATP–P_i exchange activities has been extracted with cholate and octylglucoside from membranes of *Mastigocladus laminosus* (Binder *et al.*, 1980). The proton channel of the F0 part of this complex, the DCCD binding protein, has been sequenced and was shown to be very similar to the DCCD binding protein of the chloroplast coupling factor (W. Sebald, personal communication). This demonstrates again the close evolutionary relationship between chloroplasts and cyanobacteria.

Conclusion

Cyanobacteria are ubiquitous and adapted to a broad spectrum of environmental conditions. They satisfy their need for energy with oxygenic photosynthesis through photolithotrophic growth, but they may also be photoorganotrophic and many of them are even chemoorganotrophic. Thus energy-transducing membranes of this wide variety of cyanobacteria offer a unique tool to investigate the relationship between respiration and photosynthesis.

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