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REVIEW

Identification, regulation and physiological functions of multiple NADPH dehydrogenase complexes in cyanobacteria

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Abstract Cyanobacteria possess multiple, functionally distinct NADPH dehydrogenase (NDH-1) complexes. In this mini-review, we describe the cyanobacterial NDH-1 complexes by focusing on their identification, regulatory properties, and multiple functions. The multiple functions can be divided into basic and extending functions, and the basic functions are compared with those in chloroplasts. Many questions related to cyanobacterial NDH-1 complexes remain unanswered and are briefly summarized here.

Keywords cell respiration, CO_2 uptake, cyanobacteria, cyclic electron transport around photosystem I, NADPH dehydrogenase complexes

1 Introduction

The cyanobacterial NADPH dehydrogenase (NDH-1) complex was discovered 16 years ago in *Synechocystis* sp. strain PCC 6803 (hereafter, *Synechocystis* 6803; Berger et al., 1991, 1993). This enzyme is confined to the thylakoid membrane (Ohkawa et al., 2001), where it accepts electrons from NADPH (Mi et al., 1995; Ma et al., 2006). NDH-1 comprises at least 15 subunits, NdhA, B, C, D1, E, F1, G, H, I, J, K, L, M, N, and O (Fig. 1; Nixon et al., 1989; Steinmüller et al., 1992; Herranen et al., 2004; Prommeenate et al., 2004; Zhang et al., 2004; Battchikova et al., 2005), which are encoded by genes homologous to the *ndh* genes in chloroplast and mitochondria (Ohyama et al., 1986, Kaneko et al., 1996). Three subunits (NuoE, F and G) that are involved in accepting electrons from NADH in *Eschericia coli*, however, are missing from the cyanobacterial NDH-1 complex (Fig. 1 see question marks; Friedrich and Scheide, 2000).

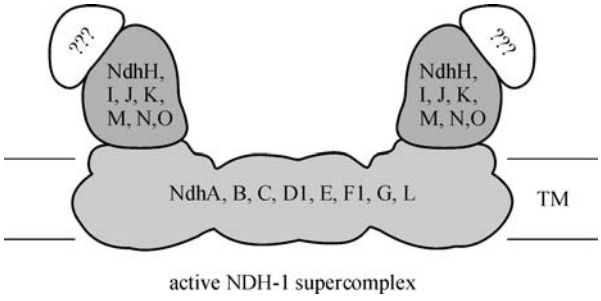

Fig. 1 A hypothetical scheme for the active NDH-1 supercomplex (Act-NDH-1Sup) in the cyanobacterium *Synechocystis* 6803. Act-NDH-1Sup is a highly active NDH-1 supercomplex, but the active domain in *Eschericia coli* (NuoE, F and G, indicated by question marks) is missing from the cyanobacterial NDH-1 supercomplex. TM: thylakoid membrane.

Recent studies using reverse genetics, proteomics and activity staining have revealed the presence of multiple, functionally distinct NDH-1 complexes in cyanobacterial cells (Matsuo et al., 1998; Ohkawa et al., 2000; Shibata et al., 2001; Maeda et al., 2002; Deng et al., 2003a, b; Herranen et al., 2004; Prommeenate et al., 2004; Zhang et al., 2004, 2005; Ma et al., 2006). This mini-review describes these complexes, with emphasis on their identification, regulation and multiple functions. The multiple functions are divided into basic and extending functions, and the basic functions of NDH-1 in cyanobacteria are compared with those in chloroplasts. Previous reviews are recommended for an overview of cyanobacterial NDH-1 complexes (Friedrich et al., 1995; Friedrich and Scheide, 2000; Ogawa and Kaplan, 2003; Battchikova and Aro, 2007; Ogawa and Mi, 2007).

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2 Identification

2.1 Two types of NDH-1 as identified by reverse genetics

From the analysis of the entire genomic sequence of *Synechocystis* 6803, it was found that at least 4 *ndhD* genes (*ndhD1–D4*) and 3 *ndhF* genes (*ndhF1*, *F3*, and *F4*) are present in this cyanobacterium, although most of the other *ndh* genes are present as single copies (Kaneko et al., 1996; http://www.kazusa.or.jp/cyano/). Reverse genetic studies using various Δ*ndhD* mutants showed that one double mutant, Δ*ndhD1*/*ndhD2*, was unable to survive under photoheterotrophic conditions, although it could take up CO_2 in the light and grow normally under air levels of CO_2; the other double mutant, Δ*ndhD3*/*ndhD4*, could grow under photoheterotrophic conditions but was unable to take up CO_2 and to grow in air at pH 7.0 (Ohkawa et al., 2000). The opposite phenotypes of the 2 Δ*ndhD* double mutants not only revealed the different effects of various NdhD subunits on the physiological functions of cyanobacterial NDH-1 complexes, but also first indicated the presence of two functionally distinct types of NDH-1 in *Synechocystis* 6803.

2.2 Multiple NDH-1 complexes as identified by proteomics

Recently, proteomic studies first revealed the presence of several functionally distinct NDH-1 complexes, NDH-1L (large size, 460 kDa), NDH-1M (middle size, 330 kDa), and NDH-1S (small size, 190 kDa), in the thylakoid membrane of *Synechocystis* 6803 (Herranen et al., 2004). In addition, NDH-1MS (490 kDa), NDH-1L and NDH-1S were identified in *Thermosynechococcus elongatus* BP-1 (hereafter, *T. elongatus*; Zhang et al., 2005). Further, single particle electron microscopic analysis of thylakoid proteins from *T. elongatus* enabled visualization of the L-shaped NDH-1L and NDH-1M, and the U-shaped NDH-1MS (Arteni et al., 2006; Folea et al., 2008). The NDH-1L complex contains NdhD1 and NdhF1 in addition to NdhA, NdhB, NdhC, NdhE, NdhG, NdhH, NdhI, NdhJ, and NdhK as well as the newly identified subunits, NdhL, NdhM, NdhN, and NdhO (Zhang et al., 2004; Battchikova et al., 2005), and appears to be identical to NDH-1A as reported by Prommeenate et al. (2004). All these subunits, except NdhD1 and NdhF1, are present in NDH-1M. NDH-1S comprises the NdhD3, NdhF3, CupA, and CupS subunits (Herranen et al., 2004; Ogawa and Mi, 2007). Recently, CupB was identified in an NDH-1 complex of approximately 450 kDa but was absent in the Δ*ndhD4* and Δ*ndhF4* mutants (Xu et al., 2008). This implies that CupB is associated with NdhD4 and NdhF4 to form NDH-1S', a homologue of NDH-1S, and present as a complex of NDH-1MS' (Battchikova and Aro, 2007; Ogawa and Mi, 2007). However, a complex such as NDH-1MS' has not been detected either by 2D-gel electrophoresis or single particle electron microscopic analysis. Also, none of these purified and/or otherwise identified cyanobacterial NDH-1 complexes mentioned above show NADH/NADPH dehydrogenase activity.

2.3 Two active NDH-1 complexes as identified by activity staining

The purification and identification of active cyanobacterial NDH-1 complexes is an important step toward studying their functional properties and better understanding the bioenergetics of the thylakoid membrane. Thus, many efforts have been made in order to purify and identify the active cyanobacterial NDH-1 complexes since 1993, and the main progress is summarized as follows: (1) Berger et al. (1993) first described an isolation of the NDH-1 subcomplex consisting of several peripheral subunits, but the complex was functionally inactive; (2) Matsuo et al. (1998) purified an active NDH-1 subcomplex of 376 kDa, but 2 membrane subunits (NdhA and NdhB) were not detected in this complex; (3) Deng et al. (2003b) isolated 2 active NDH-1 subcomplexes of about 200–250 kDa including the hydrophobic NdhA subunit.

Recently, the activity of NDH-1 was found to be strongly affected by the growth phase of cells, and was the highest in cells in the logarithmic phase of growth (Ma and Mi, 2005). Thus, cyanobacterial cells in the logarithmic phase were utilized and success was achieved in identifying active NDH-1 complexes. Analysis of staining of native gels for NADPH-nitroblue tetrazolium (NBT) oxidoreductase activity after electrophoresis of *n*-dodecyl-β-maltoside (DM)-treated membranes of wild-type (WT) *Synechocystis* 6803 and its specific *ndh* gene knockout mutants Δ*ndhB* (M55) and Δ*ndhD1/D2* (D1/D2), and immunoblotting of these active bands using various antibodies of NDH-1 membrane and peripheral subunits demonstrated the presence of two major active NDH-1 complexes in the unicellular cyanobacterium (Ma et al., 2006). Based on the size, the two active NDH-1 complexes were named as Act-NDH-1Sup (active supercomplex; approximately 1000 kDa; Fig. 1) and Act-NDH-1M (active mediumcomplex; approximately 380 kDa). Act-NDH-1Sup is a newly identified supercomplex and its protein activity is much higher than that of Act-NDH-1M (Ma et al., 2006). In contrast, Act-NDH-1M is similar to complexes previously identified by Matsuo et al. (1998) and Deng et al. (2003a).

3 Regulation

Recent studies using functional proteomics showed that the expression levels of the NDH-1M and/or NDH-1S complexes were considerably stimulated by low CO_2, while that of the NDH-1L complex was markedly decreased (Zhang et al., 2004). Furthermore, our research

showed that the various properties of the two active NDH-1 complexes responded differently to environmental signals and nutrition levels. The main findings are summarized herein: (1) Ma et al. (2006) demonstrated that low CO_2 markedly suppressed the activity of Act-NDH-1Sup, while significantly stimulating that of Act-NDH-1M; (2) both redox changes in the plastoquinone (PQ) pool and exogenous glucose levels regulated the expression and activity of Act-NDH-1Sup, but not Act-NDH-1M (Ma et al., 2008a, b). Taken together, these findings revealed an important role of the NDH-1 complexes, especially Act-NDH-1Sup, in the adaptation of cyanobacterial cells to changing environmental conditions.

4 Multiple physiological functions

4.1 Basic functions

4.1.1 CO_2 uptake

The isolation of *Synechocystis* 6803 mutants (RKa and RKb) defective in CO_2 uptake, and the identification of *ndhB* and *ndhL* as the genes impaired in the mutants, demonstrated the essential role of NDH-1 in CO_2 uptake (Ogawa, 1990, 1991a, b, 1992). Although the mechanism of CO_2 uptake is not yet known, it is postulated that CO_2 enters the cells by diffusion and is converted to HCO_3^- by NDH-1 complexes (Kaplan and Reinhold, 1999; Tchernov et al., 2001) localized on the thylakoid membrane (Ohkawa et al., 2001; Zhang et al., 2004). Recently, studies using reverse genetics showed the presence of two CO_2-uptake systems in cyanobacterial cells, one dependent on *ndhD3*, *ndhF3*, and *cupA*, and the other dependent on *ndhD4*, *ndhF4* and *cupB*. Further research indicated that the former showed high affinity to CO_2 and was induced by low CO_2, and the latter showed low affinity to CO_2 and was constitutively expressed (Shibata et al., 2001). Analysis of the physiological properties of various cyanobacterial mutants with mutations in components of the multiple NDH-1 complexes indicates that both NDH-1MS and Act-NDH-1M participate in high affinity CO_2 uptake in cyanobacteria (Ohkawa et al., 2000; Zhang et al., 2004; Ma et al., 2006).

4.1.2 Cyclic electron transport around photosystem I

Extensive studies using various inhibitors of electron transport and inactivating mutations in specific *ndh* genes revealed an essential role of cyanobacterial NDH-1 in cyclic electron transport around photosystem I (cyclic PSI; Mi et al., 1992a, b). Recently, by analysis of the characteristics of NDH-1 complex mutants, both NDH-1M and Act-NDH-1M were found to be involved in cyclic PSI in cyanobacteria (Ohkawa et al., 2000; Zhang et al., 2004; Ma et al., 2008a).

4.1.3 Cell respiration

In 1992, Mi et al. (1992b) demonstrated that cyanobacterial NDH-1 functions in cellular respiration. Subsequent analysis of various mutants in the multiple NDH-1 complexes indicated that both NDH-1L and Act-NDH-1Sup participate in cellular respiration in cyanobacteria (Ohkawa et al., 2000; Zhang et al., 2004; Ma et al., 2008a).

4.2 Extending functions

Recently, the response to heat stress of electron transport mediated by active NDH-1 complexes was investigated in cyanobacteria. The findings showed that Act-NDH-1Sup and Act-NDH-1M are essential for alleviating the heat-induced inhibition of the electron transport rate driven by photosystem II (PSII), and for accelerating the heat-induced stimulation of the electron transport rate driven by PSI. Furthermore, it appears that these effects are most likely brought about by electron transport that is mediated by the two active NDH-1 complexes (Ma et al., 2008c).

The transition of cyanobacterial cells to state 2 was strongly inhibited in the M55 mutant (Schreiber et al., 1995), indicating the important function of cyanobacterial NDH-1 complexes in state transitions. Whether the inhibition was a result of low cell respiration activity mediated by Act-NDH-1Sup and NDH-1L, or resulted from the absence of cyclic PSI mediated by Act-NDH-1M and NDH-1M, remains to be clarified. In addition, the absence of cyclic PSI mediated by the NDH-1 complexes might be the cause of high NaCl sensitivity in the M55 mutant, although the mechanism of this phenotype was also unclear (Tanaka et al., 1997).

5 Comparison of the basic functions of NDH-1 complexes in cyanobacteria with those in chloroplasts

The basic functions of cyanobacterial NDH-1 complexes are compared with those of chloroplastic NDH-1 complexes (Table 1). Phylogenic analysis has indicated that the cyanobacterial *ndhD1/ndhD2* and *ndhF1* genes are highly homologous to the chloroplastic *ndhD* and *ndhF* genes, respectively (Shibata et al., 2001). The *ndhD3*/*ndhD4* and *ndhF3*/*ndhF4* genes are absent in chloroplast genomes, however, suggesting that the CO_2 uptake systems dependent on these genes are present only in cyanobacteria, and that the function of CO_2 uptake is specific to cyanobacteria but not chloroplasts.

NDH-1 in cyanobacteria is essential for cyclic PSI and cell respiration, which are two common physiological

Table 1 Comparison of basic functions mediated by cyanobacterial NDH-1 complexes and chloroplast NDH-1 complexes

basic functions	cyanobacterial NDH-1 complexes	chloroplastic NDH-1 complexes
CO_2 uptake	yes	no
cyclic PSI	high	low
respiration	high	low

NDH-1: NADPH dehydrogenase; PSI: photosystem I.

functions also associated with chloroplast NDH-1 (Ogawa 1991a; Mi et al., 1992b; Burrows et al., 1998; Casano et al., 2000; Shikanai and Endo, 2000; Joët et al., 2002; Peltier and Cournac, 2002; Munekage et al., 2004; Braun and Zabaleta, 2007). The main routes of cyclic PSI in chloroplasts are dependent on *pgr5* (Munekage et al., 2002), and the contribution of NDH-1-mediated cyclic PSI is relatively small, although it plays an especially important role under stress conditions (Munekage et al., 2004). The *pgr5* homolog is present in cyanobacteria, and is involved in antimycinA-sensitive cyclic PSI (Yeremenko et al., 2005), but in cyanobacteria, the contribution of *pgr5*-dependent cyclic PSI is minor compared to that of NDH-1.

In 1982, Bennoun first proposed the concept of chlororespiration in the chloroplast. Furthermore, the discovery in higher-plant chloroplasts of a plastid-encoded NDH-1 complex homologous to the bacterial complex I, and of a nuclear-encoded plastid terminal oxidase (PTOX) homologous to the plant mitochondrial alternative oxidase, brought molecular support to the concept of chlororespiration (Carol et al., 1999; Josse et al., 2000; Joët et al., 2002). Chlororespiration in the thylakoids of mature chloroplasts appears to be a relatively minor pathway, although it might play an important role in the regulation of photosynthesis by modulating the activity of cyclic PSI. In cyanobacteria, however, cell respiration is a relatively major electron transport pathway.

In conclusion, the comparisons described above unambiguously demonstrate that the physiological functions of cyanobacterial NDH-1 complexes to overall cyanobacterial function are more significant than those of chloroplastic NDH-1 complexes to chloroplasts (Table 1).

6 Future perspectives

In the past few years, much progress has been made toward revealing the multiplicity, regulatory properties and physiological functions of NDH-1 complexes in cyanobacteria. In order to better characterize the cyanobacterial NDH-1 complexes, many questions must be answered in the future, the major points of which are as follows: First, although multiple NDH-1 complexes have been identified, might there be other, still unidentified NDH-1 complexes in cyanobacterial cells? Second, the identified NDH-1 complexes are important for cyanobacterial cells to adapt to the changing environment, but what is the regulatory mechanism for this process? Third, the three basic functions of cyanobacterial NDH-1 complexes have been widely characterized, but knowledge about their extending functions is still lacking. Also, the correlative molecular mechanisms are unclear. Fourth, the absence of homologous genes for the active NuoE, NuoF, and NuoG subunits of *Eschericia coli* in cyanobacterial NDH-1 complexes gives rise to the most important question: why do the catalytically active subunits of cyanobacterial NDH-1 complexes differ so remarkably from the corresponding proteins that perform the diaphorase function in the NDH-1 complexes of *Eschericia coli*? The identification of these subunits in cyanobacteria would be a significant step forward in understanding the bioenergetics of the thylakoid membrane. Conversely, if these subunits do not exist in cyanobacterial NDH-1 complexes, what is the reaction mechanism and how are electrons donated to the NDH-1 complex? Finally, the hydrophilic domain of the respiratory complex from *Thermus thermophilus* was recently purified and its crystal structure solved at 3.3 Å resolution (Sazanov and Hinchliffe, 2006). The purification of intact and homogeneous cyanobacterial NDH-1 complexes remains elusive, however. Thus, one of the most important future tasks is to develop a technique to purify the active NDH-1 complexes in order to study their enzymatic properties, subunit compositions and 3-D structures, and to verify the results of reverse genetic studies at the protein level.

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