The chloroplast NAD(P)H dehydrogenase (NDH) complex is involved in photosystem I (PSI) cyclic and chlororespiratory electron transport in higher plants. Although biochemical and genetic evidence for its subunit composition has accumulated, it is not enough to explain the complexes putative activity of NAD(P)H-dependent plastoquinone reduction. We analyzed the NDH complex by using blue native PAGE and found that it interacts with PSI to form a novel supercomplex. Mutants lacking NdhL and NdhM accumulated a pigment-protein complex with a slightly lower molecular mass than that of the NDH-PSI supercomplex in vivo. Although they lacked plastids, it interacted with PSI for up to 48 h during chloroplast development.

This article has been withdrawn at the request of the authors. The authors and the journal conclude that Figure 3 images in ndhl/PsaA panel are not correct due to artificial modification of some bands and Figure 3 ndhl/PsaD panel was flipped horizontally. The withdrawing authors stand by the overall conclusions of the study.

Modification of its subunit composition allows the cyanobacterial NDH-1 complex to be involved in multiple functions: respiration, PSI cyclic electron transport, and CO2 uptake (8, 9). Consistent with functional genomic analysis, proteome analyses revealed three distinct NDH-1 complexes in cyanobacteria. According to their molecular masses, these complexes are designated NDH-1L (large), NDH-1M (medium), and NDH-1S (small), with molecular masses of ~460, 350, and 200 kDa, respectively (19–23). The NDH-1L complex consists of a membrane-embedded arm (NdhA–C, E, G, I) and a hydrophilic connecting domain (NdhH–K, M–O). It is believed to be a basic subcomplex present in all cyanobacterial NDH-1 complexes (20–22). The NDH-1L complex contains NdhD1 and NdhF1 in addition to the components of the NDH-1M complex. It is involved in respiration and cyclic electron flow around PSI. NDH-1S associates with NDH-1M to form the NDH-1MS complex, of about 490 kDa (23). Expression of NDH-1MS can be induced under low CO2 conditions; it is considered to be involved in CO2 uptake (21, 23). The NDH-1S complex consists of four subunits: NdhD3, NdhF3, CupA, and CupS. Alternatively, NdhD4, NdhF4, and CupB
Supercomplex of NDH and PSI

form another NDH-1S complex, which is also associated with NDH-1M (8, 20).

Six ndhD and three ndhf genes are present in the genome of Synechocystis sp. PCC 6803, whereas the chloroplast genome contains only a single copy of each, which correspond, respectively, to ndhD1/D2 and ndhF1 of cyanobacteria (3, 8, 9). This fact suggests that the chloroplast NDH complex is similar to cyanobacterial NDH-1L that functions in respiratory and also probably PSI cyclic electron transport (2, 3, 8, 9). Chromatography was used to show that the NDH complex purified from pea chloroplasts has a molecular mass of about 550 kDa (23). An NDH complex with a similar molecular mass was detected by native PAGE in thylakoids isolated from tobacco (25), oat (26), and barley etioplasts (27). More recently, monomeric (~550 kDa) and dimeric (1000–1100 kDa) NDH complexes were detected in Zea mays mesophyll and bundle sheath chloroplasts by blue native (BN)-PAGE combined with mass spectrometry (28). Larger NDH complexes have been reported also in Arabidopsis (13, 29). During isolation and analysis, the NDH monomer usually splits into 300- and 250-kDa subcomplexes because of its fragile nature (25, 29). It seems that a low concentration of detergent is essential for detecting the intact NDH complex that is likely to be present in vivo (12).

Here we separated the Arabidopsis NDH complex by BN-PAGE and sucrose density gradient (SDG) after mild solubilization of thylakoids using a low concentration of n-dodecyl n-maltoside (DM). Inconsistent with the results from previous studies, the NDH complex was detected as a single form with a molecular mass of >1000 kDa. Further purification using NDH-deficient mutants indicated that this complex is composed of NDH and a large PSI-like supercomplex including PSI. We also investigated the formation of this supercomplex during the development of chloroplasts including PSI. We also investigated the formation of this supercomplex during the development of chloroplasts using NDH-deficient mutants indicated that this large protein complex is composed of NDH and a large PSI-like supercomplex including PSI.

EXPERIMENTAL PROCEDURES

Plant Materials and Growth Conditions—Arabidopsis thaliana (ecotype Columbia gl1 and Wassilewskija) and tobacco plants (Nicotiana tabacum cv. Xanthi) used in this work were grown in soil under growth chamber conditions (50 µmol photons m⁻² s⁻¹, 16-h photoperiod, 23 °C) for 3–4 weeks. An Arabidopsis mutant defective in the ndhM gene was obtained from the Salk T-DNA collection. The Arabidopsis sig4–10 mutant was kindly provided by Dr. Silva Lerbs-Mache. For light-induced greening studies, seeds were sterilized and sown on agar-solidified MS medium containing 3% sucrose (30). To ensure synchronized germination, the plates were kept in darkness at 4 °C for 2 days and then kept in the chamber with continuous light for the first 24 h. After growth in the dark for 1 week, seedlings were illuminated for 0, 24, or 48 h with continuous white light and then harvested.

Thylakoid Membrane Preparation, BN-PAGE, and Immunoblot Analysis—Chloroplasts were isolated as described (31) and osmotically ruptured in buffer containing 20 mM HEPES/KOH (pH 7.6), 5 mM MgCl₂, and 2.5 mM EDTA. Thylakoid membranes were pelleted by centrifugation (7700 × g for 3 min) and resuspended in the same buffer.

BN-PAGE was performed as described (32) with some minor modifications. The freshly isolated thylakoid membranes were gently washed twice with buffer containing 25 mM BisTris·HCl (pH 7.0), 20% glycerol, and solubilized in 25 mM BisTris·HCl (pH 7.0), 20% glycerol, 1% DM, at a final chlorophyll concentration of 1 mg ml⁻¹. After incubation on ice for 10 min and centrifugation at 12,000 × g for another 10 min, the supernatants were supplemented with 1/10 volume of BN sample buffer (100 mM BisTris·HCl, pH 7.0, 5% Serva blue G, 0.5 mM 6-aminohexanoic acid, 30% sucrose (w/v)). Thylakoid protein complexes were separated by 5–12% gradient BN-PAGE in 0.75-mm thick gels connected to a circulating cooler. For two-dimensional SDS-PAGE/Western blotting analysis, excised BN-PAGE lanes were soaked in SDS sample buffer (100 mM Tris·HCl, pH 6.8, 2% SDS, 15% glycerol) containing 2.5% β-mercaptoethanol for 30 min at room temperature, and then layered onto 1-mm thick 12.5% gels. After electrophoresis, the proteins were transferred to nitrocellulose membranes and probed with specific antibodies against NdhH1, NdhL1, PsAN, and CP47, respectively.

Total membranes were isolated from etiolated and greening seedlings as described (31). The leaves were ground with 1% DM, 50 µl of isolation buffer (5 mM MgCl₂, 0.1 mM NaCl, 0.06% DM, and 25 mM HEPES/KOH (pH 7.0), 20% glycerol, and solubilized in 25 mM BisTris·HCl, pH 6.8) and then centrifuged at 17,000 × g for 10 min on ice. The cleared supernatant (1 ml) was loaded on the top of a 15-ml linear sucrose gradient (5–40%) prepared with buffer containing 5 mM MgCl₂, 10 mM NaCl, 0.06% DM, and 25 mM MES/NaOH (pH 6.8). Thylakoid protein complexes were separated by ultracentrifuge for 24 h at 141,000 × g at 4 °C in an SW28 rotor (Beckman). The gradients were then fractionated from top to bottom into 48 fractions by an automatic density gradient fraction collector (Advantec model CHD255AA), and equal amounts of alternate fractions were used for further immunoblot analysis.

RESULTS

Separation of NDH Complex by BN-PAGE—For characterization of the structure of the NDH complex, we solubilized freshly isolated thylakoids from WT Arabidopsis plants in 1% DM and separated protein complexes by BN-PAGE. After the first-dimensional separation in the presence of Coomassie Brilliant Blue G 250 dye, several major bands were clearly separated, including PSII supercomplexes, PSI + PSII dimer, PSII monomer, CP43-less PSII, and light-harvesting complex II (LHCII) trimmer (Fig. 1A). Notably, one higher molecular mass green band (Band I) also appeared at the top of the gel (Fig. 1A).

To assign the position of the NDH1 complex in the BN-PAGE, we performed second-dimension SDS-PAGE and subsequent
immunoblot analysis using specific antibodies against NdhH and NdhL. Both were present at the same high molecular mass position, co-localized with NDH subunits in the BN gel. In addition, a major spot corresponding to the PSI monomer, a subunit of PSI, occurred in a putative supercomplex at the high molecular mass position, co-localized with NDH subunits in the BN gel.

**NDH Complex Interacts with PSI**—Recently, we characterized an Arabidopsis crr23 (chlororespiratory reduction 23)/ndhl mutant defective in the ndhl gene and showed that the NDH complex almost completely disappeared (12). BN-PAGE found no major differences in the major complex bands between WT and ndhl (Fig. 2, A and C). However, the higher molecular mass green band (Band I of WT) shifted to a position with a slightly lower molecular mass (Band II) in the mutant; this difference was clearer after staining with Coomassie Brilliant Blue (Fig. 2, A and C). The most straightforward interpretation is that the complex corresponding to Band II interacts with the NDH complex to form a supercomplex (Band I) in WT plants.

To further investigate the components of Bands I and II, we excised them from the BN gels and immunoblotted them (Fig. 2, A and B). Band III, corresponding to the PSII supercomplex, and Band IV, corresponding to the PSI monomer and the PSII dimer excised from the WT lane, were also included in the analysis. Western blot results clearly show that Band I includes subunits NdhH and NdhL, which were not detected in the other bands and the ndhl mutant (Fig. 2B). We also performed immunoblot assays using antibodies against the subunits of PSI. Both PsaA and PsaD were detected in both Bands I and II. A subunit of LHCI, Lhca3, was also present in both bands, but no D1 or cytochrome f was detected in either band (Fig. 2B). These results indicate that NDH and PSI co-localize in the BN gel, forming Band I, which does not contain PSI or the cytochrome b6/f complex. On the other hand, Band II does not contain NdhH and NdhL and only PSI subunits could be detected in Band II, suggesting this may be an intermediate supercomplex including PSI. The intermediate is stable even in the absence of NdhH and NdhL and was specifically detected in ndhl, suggesting that it forms a supercomplex with NDH in WT. All results imply that NDH and PSI form a supercomplex, present as Band I in the BN gel.

A previous report (1) indicated that NDH and PSI reside on the stroma lamellae. To remove the dominant PSII supercom-
plexes and allow better incorporation of the large NDH-PSI supercomplex into the gel, we first separated the stroma and grana lamellae and then analyzed the supercomplex by BN-PAGE. Our results (supplemental Fig. S1) showed that the NDH-PSI supercomplex (Band I) and intermediate (Band II) were specifically detected in stroma lamellae of the WT and ndhl, respectively. The PSIi and LHCII complexes are mainly detected in the grana lamellae fraction (supplemental Fig. S1). The reproducibility of the gel with different isolation methods suggests that the NDH-PSI supercomplex and the intermediate stably exist in vivo.

Like ndhl, the ndhm mutant also lacks the intermediate NDH-PSI supercomplex because of the absence of the NdhM subunit (ndhm), and two additional mutants, crr6-1 and crr7-1, impaired the accumulation of the NDH complex (15, 16), in further analysis to test the possibility of the interaction of NDH with PSI, we performed SDG analysis, which facilitates the separation of protein complexes under milder conditions. After centrifugation, 48 equal fractions were divided up and alternate fractions were immunoblotted using specific antibodies. With Coomassie Brilliant Blue (right), B, thylakoid membrane complexes separated by BN-PAGE in A were further subjected to 12.5% SDS-PAGE, and the proteins were immunodetected with specific antibodies against PsaA and CP47. C, thylakoid membrane complexes isolated from WT and mutants defective in NDH (ndhl, ndhm, crr6-1, and crr7-1) were separated by BN-PAGE (top panel) and stained with Coomassie Brilliant Blue (bottom panel). WS indicates wild-type samples. The top part of the gel is closed up.
SDS-PAGE also confirmed that the high molecular complex containing PSI corresponding to Band II was missing in ΔndhB (Fig. 4B).

Although the lack of NdhM or NdhL subunits only destabilizes the complex corresponding to Band I in Arabidopsis (Fig. 2), both Bands I and II were missing in ΔndhB in tobacco (Fig. 4A and B). To study the possibility that the discrepancy is due to the difference in plant materials, we also analyzed Arabidopsis crr2-2 defective in the ndhB expression (36), crr4-3 defective in the ndhD expression (37), and the sig4–10 mutant defective in the ndhF expression (38). Consistent with the results using ΔndhB (Figs. 4A and B), both Bands I and II were missing in these lines (Fig. 4C). The trace level of band I detected in crr2-2 is probably ascribed to the leaky accumulation of the NDH complex in this mutant (36) and the same story is probably true to sig4–10. We conclude that the membrane-embedded subunits of NdhB, NdhD, and NdhF are essential for accumulating both Band I and Band II complexes. In contrast, NdhL and a soluble subunit of NdhM are required for stabilizing the Band I complex, and Band II complex is stable in the absence of these subunits. Most probably, Band I contains all the subunits of NDH and PSI, whereas Band II contains PSI and some of NDH subunits including NdhB, NdhD, and NdhF. Indeed, proteomics analysis of Band II showed that it includes PSI subunits and some NDH subunits including NdhB, NdhD, and NdhF.4

Formation of the Supercomplex during Chloroplast Development—Previous reports showed that the NDH-PSI supercomplex is already present in etioplasts (27, 39). Here, we focused on the assembly of PSI is light-dependent, and the PSI monomer is stably assembled only in the chloroplast membranes at least 24 h after exposure to light (39). For this reason, we investigated the time course of PSI accumulation during chloroplast development. Membranes of etiolated and greening leaves were separated by BN-PAGE and protein complexes were separated by SDS-PAGE. Gel strips were subjected to two-dimensional SDS-PAGE, and immunoblot analysis was performed using antibodies against NdhL (Fig. 5A) and PsaA (Fig. 5B). The NDH complex was present as a 550-kDa complex in etiolated seedlings and co-migrated with the PSI monomer, which appeared in greened leaves with 24- or 48-h illumination (Fig. 5). Accumulating information (24–28) suggests that this complex should be NDH monomer. After 24 h illumination, NDH complex occurred mainly as a monomer, and a small quantity was shifted to the high molecular weight side in the BN gel. Because the spot was also detected by an antibody against PsaA, it corresponds to the NDH-PSI supercomplex (Fig. 5). The NDH-PSI supercomplex was fully assembled after 48 h of illumination during chloroplast development. These results strongly suggest that the NDH complex is present as the monomer in etioplasts and interacts with PSI in chloroplasts. Taking together all these results, we conclude that the NDH complex interacts with PSI in chloroplasts.

4 L. Peng, H. Shimizu, and T. Shikanai, unpublished result.
by the additional PsbH subunit close to PsbL (47). It is still likely, however, that Band II corresponds to the PSI trimer, because it was detected specifically in mutants lacking the NDH complex (Fig. 2).

Unexpectedly, however, Band II was unstable in the mutants lacking NdhB, NdhD, and NdhF. We consider that Band II is an intermediate for the supercomplex including PSI subunits and also at least NdhB, NdhD, and NdhF. It is possible that other membrane-embedded subunits like NdhA, NdhE, and NdhG are also included in Band II. Although NdhL also contains transmembrane domains, it is not essential for stabilizing Band II and thus unlikely to be included in Band II. The idea is consistent with the phenotype of the cyanobacterial ndhI mutant defective in NDH activity but not in the accumulation of the complex (22). It is likely that the position of NdhL is different in the complex from that of the other membrane-embedded subunits. Although we are not sure of the function of CRR6 and CRR7 (15, 16), they are likely to be required for stabilizing the soluble subcomplex of NDH, because Band II was detected in the mutant backgrounds.

Burrows et al. (25) showed a stoichiometry of approximately one NDH complex per 50–100 PSI complexes in tobacco. If we assume the PSI/PSII ratio of about 1:1 in normal conditions, then NDH is present at ~1–2% of the PSI on a molar basis. Our BN-PAGE and two-dimensional/immunoblot showed that PsaA in the supercomplex, estimated from the immunoblot signal, was 0.5–5% of the total PsaA in Arabidopsis thaliana (Figs. 1, 4, and 5). Although it is difficult to draw exact conclusions about stoichiometry, the ~1% molecular mass PSI complex is comparable to the NDH complex.

BN-PAGE analysis also revealed only a NDH monomer in etioplasts, and that the accumulation of Band II is independent of light (Fig. 5). Consistently, the 34 kDa NDH complex with NADH dehydrogenase activity from etioplast membranes of barley was recognized as a monomeric subunit of the NDH complex could be detected in Band II as judged by immunoblot analysis, yet it was not found in the stained two-dimensional BN/SDS-PAGE gels (39). These results indicate that the NDH complex is not a dominant protein complex in etioplasts, just as it is not dominant in chloroplasts (25). Rumeau et al. (5) concluded that the NDH complex may act as a proton pump in etioplasts to energize the plastid membrane and/or to favor the biogenesis of photosynthetic complexes. Even in the absence of the NDH complex, however, greening is not affected, a fact that does not support this idea (5). According to our finding (Fig. 5), it is necessary to reconsider the function of NDH in etioplasts in which its PSI partner is not yet present. The NDH complex may switch its function from chlororespiration to PSI cyclic electron transport during chloroplast development. It is also possible that monomeric NDH does not have activity in vivo in etioplasts and is waiting for the assembly of PSI to form an active supercomplex.

Recently, Ma et al. (48) reported a supercomplex of about 1000 kDa with high NADPH dehydrogenase activity in Synechocystis sp. PCC 6803. This supercomplex, composed of several NDH subunits, is absent in the ΔndhD1ΔndhD2 double mutant and the M55 mutant defective in ndhB. The authors concluded that it represented an NDH-1L dimer. High similarity in structure and function between the cyanobacterial and chloroplast NDH complexes suggests that NDH-1L interacts with PSI also in cyanobacteria. The most straightforward demonstration of the interaction between NDH and PSI is co-immunoprecipitation using antibodies against their subunits. Although our trial was unsuccessful, possibly because of a low abundance of the complex in chloroplasts, the strategy may be possible using cyanobacteria, which accumulate more NDH in cells than chloroplasts.

Acknowledgments—We thank S. Asazuma and K. Sugimoto for help in the SDS analysis. T. Endo, G. Peltier, and A. Makino are acknowledged for their gifts of antibodies.

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DECEMBER 12, 2008 • VOLUME 283 • NUMBER 50
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