



The Significance of Chloroplast NAD(P)H Dehydrogenase Complex and Its Dependent Cyclic Electron Transport in Photosynthesis

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Chloroplast NAD(P)H dehydrogenase (NDH) complex, a multiple-subunit complex in the thylakoid membranes mediating cyclic electron transport, is one of the most important alternative electron transport pathways. It was identified to be essential for plant growth and development during stress periods in recent years. The NDH-mediated cyclic electron transport can restore the over-reduction in stroma, maintaining the balance of the redox system in the electron transfer chain and providing the extra ATP needed for the other biochemical reactions. In this review, we discuss the research history and the subunit composition of NDH. Specifically, the formation and significance of NDH-mediated cyclic electron transport are discussed from the perspective of plant evolution and physiological functionality of NDH facilitating plants' adaptation to environmental stress. A better understanding of the NDH-mediated cyclic electron transport during photosynthesis may offer new approaches to improving crop yield.

Keywords: chloroplast, NAD(P)H, dehydrogenase complex, photosynthesis, cyclic electron transport

INTRODUCTION

Regulation of photosynthetic electron transport in the thylakoid membrane of chloroplasts is fundamental for the maximum photosynthetic yield and plant growth. The light reactions in photosynthesis convert light energy into chemical energy in the forms of ATP and NADPH. The reactions involve two types of electron transport in the thylakoid membrane. While linear electron transport generates both ATP and NADPH, cyclic electron transport around photosystem I (PSI) is exclusively involved in ATP synthesis without the accumulation of NADPH (Johnson, 2011; Yamori et al., 2015). The cyclic electron transport (CET) around PSI includes two distinct and partially redundant pathways in plant chloroplasts. One, i.e., antimycin A-insensitive pathway, is mediated by chloroplast NADH dehydrogenase (NDH) complex (Peltier et al., 2016; Shikanai and Yamamoto, 2017). The other is mediated by PROTON GRADIENT REGULATION5 (PGR5) and PGR5-like Photosynthetic Phenotype1 (PGRL1) protein complex which is sensitive to antimycin A

(Munekage et al., 2002, 2004; Dalcorso et al., 2008). Some results have shown that NDH-dependent CET is also involved in plant response to various environmental stresses, such as drought (Munné-Bosch et al., 2005), high temperature (Wang et al., 2006), low temperature (Li et al., 2004; Leonid et al., 2011; Yamori et al., 2011; Wang et al., 2020), low light (Ishikawa et al., 2016a), and phosphorus deficiency (Carstensen et al., 2018; Shi et al., 2019). This review examines the background underlying the research of NDH. The significance of the NDH-mediated cyclic electron transport is discussed from the perspective of plant evolution and physiological functionality of NDH to understand how plants adapt to environmental stress by fine tuning their NDH-mediated cyclic electron transport.

DISCOVERY OF THE NDH COMPLEX

Arnon et al. (1954) discovered CET in spinach chloroplasts *in vitro*, but this did not accelerate the understanding of the NDH complex. It was not until 1986 that scientists discovered the NDH complex in the chloroplast genome sequencing of tobacco and liverwort (*Marchantia polymorpha*) (Ohyama et al., 1986; Shinozaki et al., 1986). There were 11 genes (*NdhA~NdhK*) in their chloroplast genome that were highly homologous to the genes encoding the human mitochondrial respiratory chain NADH dehydrogenase complex (Matsubayashi et al., 1987). With these genomic similarities, the NADH dehydrogenase complex in chloroplasts was aptly named as the NAD(P)H dehydrogenase-like complex or commonly referred to as the NDH complex (Yamamoto et al., 2011).

Structure of the NDH-1 Complex in Cyanobacteria

The type I NADH dehydrogenase (NDH-1) is a multisubunit complex located in the thylakoid membrane (Ohkawa et al., 2000), which is widely found in bacteria, cyanobacteria, higher plants, and animals (Friedrich et al., 1995; Yagi et al., 1998; Friedrich and Scheide, 2000; Brandt et al., 2003; Miller et al., 2021). Previous studies have reported that NDH-2 exists widely in bacteria, some in fungi, plants, and protozoa (protist), but it is not involved in respiration and photosynthetic electron transport (Howitt et al., 1999). There are about 26 NDH subunits in cyanobacteria (Laughlin et al., 2020). Proteomic methods and cryoelectron microscopic (cryo-EM) have been used to study the different types of NDH-1 complexes in cyanobacteria, including NDH-1L, NDH1L', NDH-1MS, and NDH-1MS' (Figure 1; Peltier et al., 2016; Zhang et al., 2020). The NDH-1L and NDH-1L' are involved in respiration and the cyclic electron transfer around PSI. In addition, the NDH-1MS and NDH-1MS' are involved in the absorption of CO₂ and the cyclic electron transfer around PSI (Ogawa, 1991; Ohkawa et al., 2000). In addition to the NDH-1M component, NDH-1L has two specific subunits NdhD1 and NdhF1. Nowaczyk et al. (2011) found two new subunits: NdhP and NdhQ of NDH-1L in thermophilic cyanobacteria by mass spectrometry, which are located on the membrane arm and play a major role in the stability of NDH-1L (Wulfhorst et al., 2014; Zhao et al., 2015), in which NdhP subunits are unique to NDH-1L

(Wulfhorst et al., 2014). The small molecular hydrophilic subunit NdhS and NdhV subunit which can stabilize the binding of NdhS to ferredoxin (Fd) were found in *Synechocystis* sp. (Yamamoto et al., 2011; Zhao et al., 2014). Recently, some researchers reported the cryo-EM structure of the entire NDH-1L complex with all 19 subunits (including NdhV, a transiently associated subunit of NDH-1) and revealed the structure and arrangement of the principal oxygenic photosynthesis-specific (OPS) subunits in the NDH complex (Laughlin et al., 2019; Zhang et al., 2020). The NDH-1L' complex contains NdhD2 subunit but not NdhD1. The expression level of the complex generally increases under the condition of carbon deficiency (Wang et al., 2004). The subunits of NDH-1MS are CupA, CupS, NdhF3, and NdhD3 (Ohkawa et al., 1998), and the complex has a high affinity for CO₂, while the specific subunits of NDH-1MS' are NdhF4, NdhD4, and CupB (Wulfhorst et al., 2014).

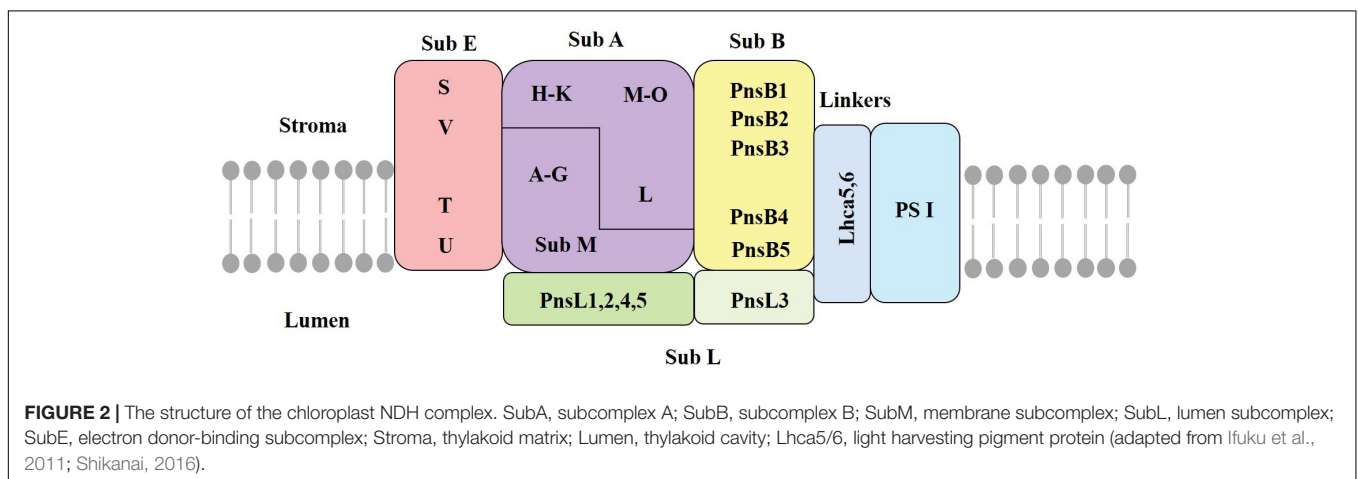
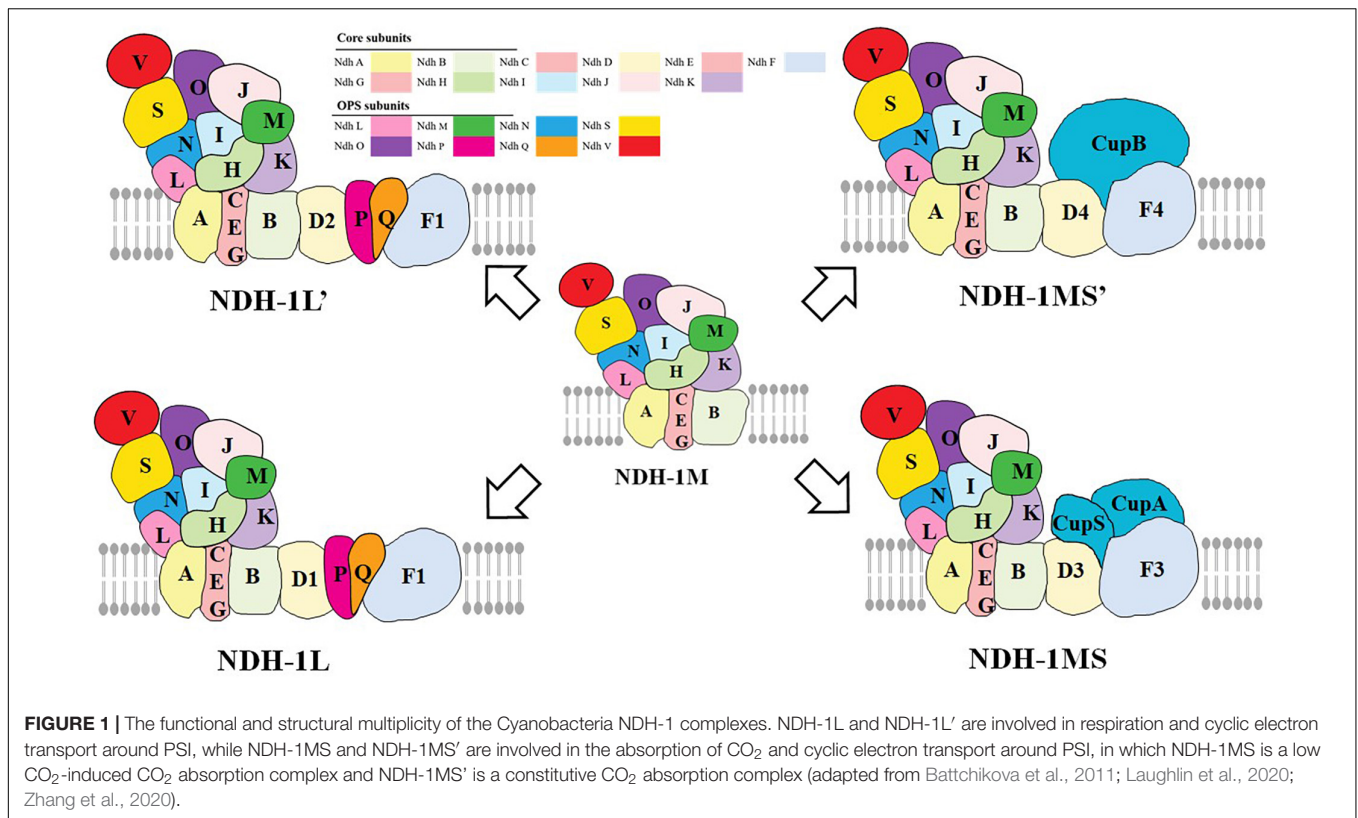
Structure of the Chloroplast NDH Complex

The chloroplast NDH complex, located in the thylakoid membrane, mediates CET and chloroplastic respiration (Laughlin et al., 2020). A recent work lists 35 subunits as the presently identified NDH subunits in chloroplasts, of which many have an unknown function. The chloroplast NDH complex is a large thylakoid protein complex composed of 11 chloroplast-encoded subunits (Ndh A~K) and another 24 nuclear-encoded subunits (Laughlin et al., 2020). These subunits are distributed in different subcomplexes (Sirpio et al., 2009). Previous studies have shown that the NDH complex consists of subcomplex A (SubA), subcomplex B (SubB), lumen subcomplex (SubL), membrane subcomplex (SubM), and electron donor-binding subcomplex (SubE) (Figure 2; Shikanai, 2016). The formation of this supercomplex helps to maintain the stability of the NDH complex under strong light conditions (Peng and Shikanai, 2011). Three subunits of NdhS, NdhT, and NdhU in SubE have been identified through proteomic analysis of NDH-PSI supercomplex (Yamamoto et al., 2011). Fan et al. (2015) identified NdhV as a new subunit of SubE, which is a thylakoid membrane peripheral protein located on the side of the stroma. SubE binds to SubA to form a ferredoxin-binding site; the key function is to bind ferredoxin and facilitating catalysis (Yamamoto et al., 2011).

NDH-CET IN PLANT EVOLUTION

Phycophyta

While examining the NDH-CET from the perspective of plant evolution, we uncovered some salient observations in some phylogenetically primitive organisms. Mi et al. (1992) found inactivated NDH in which the electron transport chain (ETC) from the reduction product produced by the respiratory stroma and the reduction side of PSI to P700⁺ were completely lost in the cyanobacteria mutants. Conversely, in cyanobacterial mutants with partial inactivation of NDH, this ETC was partially inhibited. The CET in cyanobacteria (and not PGR5-CET) occurs mainly *via* the NDH-1 complex (Mi et al., 1995; Yermenko et al., 2005). Meanwhile, it was found that plant PGR5 suffices



to reestablish cyanobacterial cyclic electron transport, albeit less efficiently than the cyanobacterial PGR5 or the plant PGR5 and PGRL1 proteins together (Dann and Leister, 2019; Margulis et al., 2020). Despite the lack of *ndhA~K* gene (encoded by chloroplasts) in *Chlamydomonas reinhardtii*, it still has the ability for CET (Martin et al., 2004). It is plausible that there might be another CET pathways operating in these primitive protists. However, recent data suggest that *Chlamydomonas reinhardtii* performs CET also through the PGR5-PGL1 pathway (Jokel et al., 2018; Yadav et al., 2020). It was proposed that in the process of CET transmission within *Chlamydomonas reinhardtii*, the reduction of plastoquinone (PQ) was facilitated by the NADH:

PQ oxidoreductase (a type II NADH: PQ oxidoreductase, Nda2) (Desplats et al., 2009). The structure of Nda2 was considered to be simple, and the catalytic reaction was faster than that of NDH-CET (Kramer and Evans, 2011).

Plants With C₃ Mode of Photosynthesis

In *Arabidopsis*, NDH-1 forms a supercomplex with photosystem I and light-harvesting complex I proteins Lhca5 and Lhca6 (Peng et al., 2009; Yadav et al., 2017). Furthermore, the NDH-1-PSI supercomplex has also been identified in barley (Kouřil et al., 2014). Under normal growth conditions, the content of NDH complex in C₃ plants was lower than that of the thylakoid

membrane protein complexes such as PSI, PSII, cytochrome b_6f (Cyt b_6f), and ATP synthase (Pribil et al., 2014), accounting for only 1.5% of the PSII content (Burrows et al., 1998). The involvement of NDH complex in the CET process was demonstrated using chlorophyll fluorescence parameter kinetics and inhibitor blocking analysis in tobacco *ndh* mutants (Joët et al., 2001). Interestingly, it has been shown that damage of NDH-CET in rice causes a reduction in the electron transport rate through PSI at the low light intensity with a concomitant reduction in CO₂ assimilation rate (Yamori et al., 2015). Therefore, NDH-CET plays an essential role in normal growth and yield under low light (Rantala et al., 2020).

Plants With C₄ Mode of Photosynthesis

During the evolution of plants from C₃ to C₄, the expression of NDH increased significantly (Nakamura et al., 2013). The content of NDH in C₄ plants was higher than that in C₃ plants, indicating that NDH-CET have a vital role in C₄ plants (Berger et al., 1993; Ishikawa et al., 2016b). Takabayashi et al. (2005) found that the content of NDH in vascular bundle sheath is 1.6 times higher than that in mesophyll cells of *Scutellaria barbata*. In *Flaveria bidentis*, the content of NDH protein in vascular bundle sheath was three times higher than that in mesophyll cells (Nakamura et al., 2013). In the NADP-ME-type of C₄ plants, their vascular bundle sheath cells contained more NDH indicating a requirement for more ATP (Friso et al., 2010; Ishikawa et al., 2016b). Darie et al. (2010) not only detected the expression of a new gene (*ndhE*) in maize mesophyll (MS), bundle sheath (BS), and etioplast (ET) plastids but also found that the NDH complex was divided into 300 kDa subcomplex (corresponding to membrane subcomplex, detected by the NDHE antibody) and 250 kDa subcomplex (detected by the NDHH, -J, and -K antibodies) (Darie et al., 2010). Interestingly, in NAD-ME-type C₄ plants, the mesophyll cells contained an abundance of NDH protein (Kanai and Edwards, 1999). Besides, chloroplast NDH-1 contains at least 13 additional OPS subunits compared with cyanobacteria, although the current structure of the NDH-1 complex reveals the role of conserved OPS subunits (Laughlin et al., 2019, 2020; Zhang et al., 2020).

THE PHYSIOLOGICAL FUNCTIONALITY OF THE NDH COMPLEX

Providing ATP for Efficient Carbon Assimilation

Theoretically, the NADPH/ATP produced by the linear electron transport is deficient for the assimilation of CO₂ at different growth stages; the CET pathway, which only produces ATP, but not NADPH, can effectively compensate for this deficiency (Shikanai, 2007; Walker et al., 2016; Nakano et al., 2019). With no NDH activity, the cyanobacteria mutants of *ndhB* (Ogawa, 1990), *ndhH*, *ndhJ*, *ndhN*, and *ndhM* (He et al., 2015), could not survive in normal air CO₂ concentration; other mutants with partial NDH activity grew slowly in normal air CO₂ concentration (He and Mi, 2016). The non-functional NDH-CET pathway

was attributed to the loss of *ndhB* in plants (Mi et al., 1995). Ogawa (1992) proposed that the NDH-CET pathway provided energy for CO₂ assimilation and inorganic carbon transport in cyanobacteria. Similarly, the NDH-CET pathway is likely to contribute to the proton motive force (*pmf*) and ATP in chloroplasts of higher plants (Strand et al., 2017). In *Arabidopsis* NDH complex defective mutants, the reduction of *pmf* across the thylakoid membrane led to low availability of ATP. Moreover, the *pmf* produced by NDH-CET was higher than that produced by PGR5/PGRL1-CET (Wang et al., 2015). It was observed that the ATP produced by NDH-CET could effectively compensate for CO₂ assimilation in a changing environment (Xu et al., 2014; Pan et al., 2020). It was found that the carbon assimilation efficiency of rice mutants (with no NDH activity caused by the lack of CRR6 assembly factor of subcomplex A) is lower than normal rice plants when grown under low light, resulting in a significant decrease in biomass (Yamori et al., 2015). Meanwhile, NDH-CET is also promoted under corresponding stress conditions to adapt to the needs of ATP and ΔpH during changing environment to ensure an effective photosynthetic carbon fixation process (Quiles, 2006).

Mitigating Oxidative Stress and Stroma Overreduction

It was found that the concentration of NADPH was higher, and more H₂O₂ was produced on the acceptor side of PSI, when measuring the NADPH fluorescence kinetics of cyanobacteria NDH mutant (Mi et al., 2000). These observations indicated that NDH-CET plays a key role in the process of antioxidation. Specifically, the NDH-CET initiates photoprotection *via* downregulating electron transport in the Cyt b_6f complex to acidify the thylakoid lumen (Munekage et al., 2004) and induces energy-dependent quenching (qE) component of non-photochemical quenching (NPQ) in PSII to dissipate the absorbed excess light energy. Thus, the oxidative stress of chloroplast can be alleviated and the overreduction of stroma can be prevented (Li et al., 2002). The role of NDH-CET in the process of antioxidation in higher plants principally stems from the study of *ndh* gene knockout in tobacco plastids. Endo et al. (1999) repeatedly irradiated tobacco *ndhB* mutant leaves with strong light and found that the PSII in mutants produced serious photoinhibition. When tobacco leaves were subjected to anaerobic condition, the activity of NDH-CET increased significantly, indicating that it was regulated by the redox state of intersystem electron transporters (Joët et al., 2002). Wang et al. (2006) found that tobacco *ndhC-J-K* mutants accumulated reactive oxygen species more easily than wild types when growing under low- (4°C) or high-temperature (42°C) stress. Chloroplast NDH was able to alleviate oxidative stress in rice under fluctuating light conditions (Yamori et al., 2016), and hydrogen peroxide could be used as a signaling compound to activate NDH-CET (Strand et al., 2015). Moreover, it was shown that the NDH-1-PSI supercomplex consumed electrons for CET as quickly as possible, limiting the space required by Fd_{red} diffusion and stabilizing PSI (Gao et al., 2016; Zhao et al., 2018). This accelerated electron consumption is thought to be

an antioxidant mechanism, especially when stresses such as high light leads to increased Fd reduction (Miller et al., 2021). These studies suggested that the NDH complex get involved in alleviating the effects of photooxidative stress. Wu et al. (2011) found that a low concentration of NaHSO₃ promoted NDH-CET in tobacco under a dark-light transition episode, which slowed down the damage of photooxidation while improving plant photosynthesis. These findings revealed that the NDH complex is involved in alleviating the effects of photooxidative stress.

Regulating the Photosynthetic Apparatus

Generally, PSI is more stable than PSII and less vulnerable to light damage (Sonoike, 2011). *Arabidopsis* (Kono and Terashima, 2016) and rice (Yamori et al., 2016) cannot grow well under fluctuating light due to photoinhibition (Kono et al., 2014); the *pgr5* mutants of *Arabidopsis thaliana* die at the seedling stage under fluctuating light, indicating that the CET pathway has a protective effect on PSI (Suorsa et al., 2016). The relative electron transport rate (ETR) and CO₂ assimilation rate of rice NDH complex-deleted mutant decreased under long-term low-light and low-temperature conditions (Peng et al., 2009; Peng and Shikanai, 2011; Kono and Terashima, 2016). Conversely, the CET had little regulation on the ratio of ATP/NADPH under high light (Yamori et al., 2015). However, Walker et al. (2014) held an opposite view that CET plays a major role during high light, such as increasing the ATP requirements. In this regard, Huang et al. (2015) deemed that the effect of CET alters in tandem and coinciding with any changes in light intensity. When subjected to subsaturated light intensity, CET is conducive for the formation of proton dynamic potential across the thylakoid membrane, activating ATP synthase to synthesize ATP, while maintaining an optimal ATP/NADPH. Under saturated light, CET provides an important photoprotective role for the activity of oxygen evolution complex (OEC) by forming the proton gradient across the thylakoid membrane (pH) (Huang et al., 2016b), and *pmf* to protect PSI and PSII *via* the acidification of thylakoid lumen (Golding et al., 2004; Basso et al., 2020). Chilling leads to photoinhibition in cold-sensitive plants like tobacco, peanut, and cucumber which is mainly related to CET activity (Huang et al., 2016a; Liu, 2020; Song et al., 2020; Wu et al., 2020). At 4°C, CET plays a photoprotective role in PSI primarily through the acidification of thylakoid lumen (Huang et al., 2017b). The protective mechanism of CET would alter in accordance with the different growth status of the heliophyte leaves. Under strong light, immature leaves protect the photosystems mainly through the acidification of thylakoid lumen. For the mature leaves, they achieve high light protection through the formation of cross-thylakoid membrane proton gradient, activation of ATP

enzyme, and lumen acidification (Huang et al., 2017a). However, Rantala et al. (2020) indicated that PGR5 and NDH-1 systems do not function as protective electron acceptors but mitigate the consequences of PSI inhibition. There is no consensus that the PGR5/PGRL1 compose a true cyclic electron pathway (i.e., acting as electron transporters) mainly due to the lack of solid molecular evidence, although PGR5/PGRL1 seems to be involved in CET at least indirectly (Nawrocki et al., 2019; Rantala et al., 2020).

FUTURE OUTLOOK

Although the energy provided by NDH-CET is lower than that of LET, it still plays a principal role in fine-tuning energy availability in plants. Besides, it plays a significant role in maintaining photosynthetic carbon fixation of algae and higher plants when encountering abiotic stress events. At present, there are several unanswered questions about NDH-CET: namely, the regulation of NDH pathway which affects the efficient operation of photosynthetic apparatus; the activation of its regulatory mechanism under abiotic stress; the electron transfer processes of NDH; and how they might influence the CO₂ concentrating mechanism in algae and higher plants. Moving forward, in-depth studies about the NDH-CET pathway are required to improve the light energy utilization efficiency of plants and to further elucidate the mechanism associated with photoprotection. With the availability of newer technology, harnessing these novel and sensitive tools would improve our understanding of the NDH-CET pathway and ultimately help us to improve crop yield and quality.

AUTHOR CONTRIBUTIONS

YL, MM, and JY are responsible for the general overview of the opinions stated in the manuscript. YL, CB, and JY wrote and modified the manuscript. All authors reviewed and approved the final version of the submitted manuscript.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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