PHOTOSYNTHETICA 34 (4): 481-496, 1997

REVIEW

The NADPH-dependent electron flow in chloroplasts of the higher plants

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Abstract

The NADPH-dependent reduction of some photosynthetic electron carriers in the dark, and the reduction of $NADP^+$ associated with the glycolytic sequence and the oxidative pentose phosphate pathway in chloroplasts are reviewed. The postulated pathways of electron transports sensitive and insensitive to antimycin A are also evaluated. It is proposed that the electron flow, predominantly through cytochrome *bf* complex, may be also involved in the pathway of NADPH-dependent and antimycin A-insensitive back electron transport. An information on the chlororespiration in higher plants is also included.

Additional key words: antimycin A; chlororespiration; cyclic electron flow, glycolytic reaction sequence; NADPH oxidation; oxidative pentose phosphate pathway; reverse electron flow.

Introduction

In chloroplasts of higher plants an electron flow through a linear electron transport system contributes to the release of two protons into the thylakoid lumen and to the reduction of 1/2 $NADP^+$. Additionally, the cyclic electron transport around PS1 is also responsible for a vectorial proton transport from the stroma into the lumenal side of a thylakoid. The electrogenic proton gradient generated in these ways across the thylakoid membrane is involved in the synthesis of ATP (for recent reviews see Skulachev 1994, Bendall and Manasse 1995).

Received 10 July 1996, *accepted* 18 November 1996

Abbreviations: Ant A - antimycin A; cyt - cytochrome; cyt b_{6H} - cytochrome b_6 high potential; cyt b_{6L} - cytochrome b_6 low potential; DBMIB - dibromothymoquinone (2,5-dibromo-3-methyl-6-isopropyl-*p*-benzoquinone); DCCD - dicyclohexylcarbodiimide; DCMU - 3-(3',4'-dichlorophenyl)-1,1-dimethylurea; E_m7 - midpoint redox potential at pH 7; Fd - ferredoxin; Fd_{red} - reduced ferredoxin; FNR - ferredoxin:$NADP^+$ oxidoreductase; FQR - ferredoxin:plastoquinone reductase; PC - plastocyanin; PS1 - photosystem 1; PS2 - photosystem 2; PQ - plastoquinone.

Acknowledgment: This paper was financially supported by the Committee for Scientific Researches (KBN), grant no. 6P04A 049 09.

Although the general mechanisms of cyclic and non-cyclic electron transport systems have been established, still there are many problems remaining, *e.g.*, little do we know about mutual interactions between different pathways contributing to the reduction or oxidation of NADP(H) in chloroplasts. Particularly some mechanisms should be employed in the course of regulating the $NADP^+$ reduction associated with the photosynthetic electron transport chain, and that associated with glycolysis or the oxidative pentose phosphate pathway operating in chloroplasts. It is also a matter of debate whether a part of a typical electron transport chain could work in the reverse direction *in vivo* on account of the NADPH that may be formed during the oxidation of, *e.g.*, glyceraldehyde-3-phosphate into glycerate-3-phosphate, and if so, in which way is this process important for regulating the $NADPH/NADP^+$ ratio in chloroplasts. Some of these problems will be reviewed briefly.

The $NADP^+$ reduction in glycolytic and oxidative pentose phosphate pathways of chloroplasts

The hexoses cannot be effectively transported from chloroplasts to other cell compartments under irradiation due to the envelope impermeability of the inner membrane. Instead they are transformed into starch granules. In the dark, the starch granules are degraded *via* hydrolytic or phosphorolytic pathways into glucose or glucose-1-phosphate, respectively, which, in turn, can be converted into triose phosphates and glycerate-3-phosphate in a glycolytic reaction sequence and/or oxidative pentose phosphate cycle operating in chloroplasts (Krause and Bassham 1969, Kelly and Latzko 1977, Kaiser and Bassham 1979, Kow *et al.* 1982, Schnarrenberger *et al.* 1995). These C-3 components are the major species exported from chloroplasts to cytosol. The transport in question is associated with a phosphate translocator activity, a 60 kDa protein (which consists of two identical subunits) occurring in the inner membrane of the envelope (see Flügge and Heldt 1991). The apparent K_m values for the transport of these substrates as well as a countertransport of inorganic phosphate are between 0.1 and 0.4 mM (Heldt and Flügge 1987, Flügge and Heldt 1991). After irradiation, only the efflux of 3-phosphoglycerate from chloroplasts is restricted due to the alkalization of chloroplast stroma (Flügge and Heldt 1991). In fully developed chloroplasts, the starch degradation to glyceraldehyde-3-phosphate, dihydroxyacetone phosphate, and glycerate-3-phosphate takes place predominantly in the dark since there occurs a thioredoxin- or NADPH-mediated photodeactivation of glucose-6-phosphate dehydrogenase or phosphofructokinase, respectively (*e.g.*, Ashton *et al.* 1980, Cséke *et al.* 1982). However, the starch degradation is not inhibited completely in light; the inhibition may vary from approximately 15 % to approximately 80 %, depending on the P_i level (Stitt and Heldt 1981). Więckowski *et al.* (1989) suggest that at earlier stages of etioplast (or amyloplast) transformation to chloroplast these processes may proceed more actively even under irradiation because rapid degradation of storage materials can be observed. Thus, the oxidative pentose phosphate pathway and at least a part of the glycolytic pathway contribute to the reduction of $NADP^+$ in chloroplasts.

The continuous operations of both pathways require a concomitant oxidation of NADPH which can be achieved by the activities of some NADPH-dependent reactions, *e.g.*, enzymatic reductions of glutathione or oxaloacetate (see Więckowski and Panz 1989), as well as by the reduction of nitrite to ammonia (Kow *et al.* 1982). One can observe even some competition for the utilization of reducing equivalents from NADPH by different NADPH-dependent reactions (Więckowski and Panz 1989). The components reduced in these ways can be exported to the cytosol mainly *via* malate/oxaloacetate and/or glutamate/α-ketoglutarate shuttles (for a review see Anderson 1982). According to Kow *et al.* (1982) and others, the oxidation of NADPH is also associated with the reduction of Fd, which, in turn, can interact with molecular oxygen as in pseudocyclic electron transport (Arnon *et al.* 1961, Telfer *et al.* 1970, Kobayashi and Heber 1994, *etc.*). The oxidation of reduced spinach Fd by O_2 proceeds with a half-time of 6-20 s at oxygen concentrations ranging from 0.065 to 0.650 mM (Hosein and Palmer 1983) and it usually does not exceed the value of 0.260 $\mu mol(O_2)\ s^{-1}\ kg^{-1}(Fd)$ (Bojko and Więckowski 1995). With an increase of NADPH/$NADP^+$ ratio to approximately 19, the concurrent oxygen uptake rate associated with the Fd_{red} oxidation increased to *ca.* 11.1 $mmol(O_2)\ s^{-1}\ kg^{-1}(Chl)$ (Hosler and Yocum 1987). Thus, the autooxidation of spinach Fd_{red} is rather slow, and it cannot be responsible for the high rate of oxygen uptake observed under certain conditions, *e.g.*, in thylakoids isolated from chloroplasts at earlier stages of their biogenesis (Więckowski and Fiedor 1990, Bojko and Więckowski 1995). Although the efficiency of Fd_{red} oxidation may be higher in a whole leaf or intact chloroplasts due to the ascorbate peroxidase activity catalyzing ascorbate oxidation by H_2O_2 (an intermediate in the reaction $Fd_{red} + O_2$) to monodehydroascorbate (Hormann *et al.* 1994), it is now supposed that these oxygen uptake processes might only partially reflect the oxidation of reduced Fd as proposed by Mehler (1951), Good and Hill (1955), Arnon *et al.* (1961), Telfer *et al.* (1970), Marsho *et al.* (1979), Egnéus *et al.* (1975), Kow *et al.* (1982), Hosein and Palmer (1983), Hormann *et al.* (1994), Kobayashi and Heber (1994), and others. Some other reduced carriers of the photosynthetic electron chain could also interact with molecular oxygen (see Egnéus *et al.* 1975) including Fe-S centres (Elstner and Heupel 1974, Hosein and Palmer 1983), plastocyanin (Björkman 1966), quinols (Thorne and Boardman 1971, Cadenas *et al.* 1977, Sugioka *et al.* 1988), and some other components associated preferentially with the inner part of the thylakoid membrane (see Egnéus 1975, Gruszecki *et al.* 1995), since the O_2 diffusion is 2-3 fold higher in lipid bilayers than in water (Subczyński *et al.* 1991).

The oxygen consumption by preparation of isolated thylakoids in the dark and in the presence of externally supplied FNR, Fd, and DCMU increases up to 60 % when adding NADPH. This NADPH-stimulated oxygen uptake in the dark is insensitive to inhibition by Ant A but it is partially inhibited (*ca.* 15 %) by DCCD (Bojko *et al.* 1996). This might support the notion that reducing equivalents from NADPH are transported through a portion of the cyclic electron transport chain to the sites of O_2 reduction.

The NADPH-dependent reduction of some photosynthetic electron carriers

Under aerobic conditions, the NADPH stimulates the Fd- and FNR-dependent cyclic electron transport (and cyclic photophosphorylation) causing maintenance of Fd in a reduced form and decrease in the PS2 activity (Forti and Rosa 1971, Arnon and Chain 1979). An externally added NADPH is involved in the reduction of some photosynthetic electron carriers in osmotically broken chloroplasts kept in the dark. For example, the NADPH stimulates the reduction of plastoquinone (Mills *et al.* 1979a,b, Groom *et al.* 1993), the electron acceptor of PS2 designated Q (Arnon and Chain 1979), cyt b_6 (Arnon and Chain 1979), cyt *f* (Chain 1979), the Rieske Fe-S centre (Malkin and Chain 1980), and $P700^+$ (Rurainski and Stauder 1984, Rurainski *et al.* 1985, Więckowski *et al.* 1989). Most of these processes take place in the dark and they also depend on the presence of exogenous FNR and Fd. Ferredoxin and cyt b_6 are involved in the electron transport from NADPH to the primary electron acceptor of PS2 and it is inhibited essentially by Ant A and DCMU, but this process is insensitive to the action of quinone-analogue DBMIB (Arnon and Chain 1975, 1979). The physiological significance of the back electron transport from NADPH to some photosynthetic electron carriers under irradiation or in the dark is a matter of speculation. Asada *et al.* (1992) found that efficient $P700^+$ re-reduction *in vivo* in the angiosperms required the electron flow from stroma, perhaps from NADPH, because the electron supplying from Fd_{red} was too slow to be effective when the electron input by PS2 assembly was blocked. The pool size of electrons available to $P700^+$ reduction in chloroplasts of maize was approx. 2.5-fold larger than in the case of *Hedera helix* (Asada *et al.* 1993). In maize, the NADPH may be generated not only in the pathway of glucose-1-phosphate to triose phosphate, but also during the oxidation of malate to oxaloacetate.

The transport mechanisms of the reducing equivalents from NADPH to certain photosynthetic electron carriers

What is (are) the mechanism(s) of the electron flow from NADPH to different electron carriers? We can simply assume that a part of a typical cyclic electron chain is engaged in this process and FNR can catalyze the reaction in the reverse direction as compared with typical reaction sequences, which means that FNR might be engaged in the oxidation of NADPH instead of its reduction. The diaphorase activity of FNR has been established *in vitro*, *e.g.*, in the presence of artificial electron acceptors like ferricyanide, methyl viologen, cyt *c*, DBMIB, or some others (see Forti 1977, Carillo and Vallejos 1987, Bowyer *et al.* 1988, Bojko and Więckowski 1995). Furthermore, in the presence of FNR inhibitors (*e.g.*, an antibody to FNR, *N*-ethylmaleimide) the reduction of primary acceptor of PS2 is also inhibited (Mills *et al.* 1979a,b). However, there is a controversy as to further sequence events of the electron transport (for reviews see Hope 1993, Bendall and Manasse 1995). Two cyclic electron transfer pathways are discussed in the literature: the Ant A-sensitive one and Ant A-insensitive one (Hosler and Yocum 1985, 1987, Więckowski *et al.*

1989, Asada *et al.* 1990, Ravenel *et al.* 1995). Hosler and Yocum (1985) have found that the P/O value diminishes in the presence of Ant A but only when reduced Fd is oxidized by O_2, and it does not decrease in the preparations supplemented with FNR and $NADP^+$. Thus, the FNR activity seems to be involved only in the Ant A-insensitive cyclic electron flow. The Ant A-insensitive cyclic photophosphorylation does not depend on the NADPH/$NADP^+$ ratio, whereas the activity of Ant A-sensitive one increases with the increase of this ratio, particularly when it becomes higher than 5.0 (Hosler and Yocum 1987).

In the Ant A-sensitive pathway, the electron from Fd_{red} probably reaches the Q_r site on the cyt *bf* complex (Böhme and Cramer 1972). According to many authors, this reaction is inhibited by a low concentration (1 mM) of Ant A (cf. Arnon and Chain 1975) which is bound at the Q_r site (near the heme b_H) of the cyt *bf* complex, similarly as it is in cyt bc_1 complex in mitochondria (see Allred and Stachelin 1986, O'Keefe 1988), and suppresses the oxidation of this heme (Meinhard and Crofts 1983, De Wolf *et al.* 1988, Tokutake *et al.* 1994). The electron from heme b_H participates, together with that derived from heme b_L (the Q-cycle), in the reduction of PQ (Furbacher *et al.* 1989). Two electrons derived in sequence from the heme b_L or from hemes b_L of two cooperating monomers of the cyt *bf* complexes (Cramer *et al.* 1991, Malkin 1992, Huang *et al.* 1994) may reduce the plastoquinone. The plastoquinol is oxidized (through semiquinone) at the Q_0 site of the cyt *bf* complex, and further steps of the electron transport and proton translocation proceed as in a typical non-cyclic electron flow (see Malkin 1992, Szczepaniak 1994). Hosler and Yocum (1985) have established the FNR and cyt b_{563} being involved only in a pathway insensitive to Ant A. However, the FNR could be easily associated with the cyt *bf* complex, and this may also contribute to regulation of the electron flow in cyclic and non-cyclic pathways (Shahak *et al.* 1981, Clark *et al.* 1984). Nevertheless, participation of FNR in the cyclic electron transport has not been confirmed in many experiments, whereas involvement of cyt *bf* in the cyclic electron flow has been confirmed with specific inhibitors, such as DBMIB, 2-nonyl-4-hydroxyquinoline N-oxide (see Bendall and Manasse 1995), although the detailed mechanism of the electron and proton transports by this complex has not been fully elucidated since the specificities of these inhibitors are questionable (for discussion of this question see Trebst 1980). However, the cyt b_H (E_m7 = -45 mV, peak absorbance at 563.2 nm), located towards the stromal side of the thylakoid membrane, can be reduced by Fd_{red}, whereas the other heme (b_L, E_m7 = -150 mV, peak absorbance at 565 nm), which is located on the lumenal side of the cyt *bf* complex, is not reducible under comparable conditions (Lam and Malkin 1982, Clark and Hind 1983, Furbacher *et al.* 1989, Kramer and Crofts 1994). DBMIB inhibits the oxidation and reduction of cyt b_6 and this suggests that plastoquinone participates in the redox processes associated with this complex (Crowther and Hind 1980).

On the contrary, Bendall *et al.* (1971), Bendall and Manasse (1995), Chain (1982), Lam and Malkin (1982), Cleland and Bendall (1992) and others have suggested that the cyt *bf* complex is not reduced directly by Fd_{red}, or that its reduction is extremely slow. According to Moss and Bendall (1984), *e.g.*, the cyt *b* is reduced by the plastoquinol pool that had been earlier reduced on the outer surface of the thylakoid

membrane in the presence of FQR or by both FNR and FQR. This enzyme(s) is considered to be localized outside the cyt *bf* complex, and this way is believed to be the main pathway of cyclic electron transport which is sensitive to inhibition by Ant A and by excess of NADPH. Yet the detailed pathway of the FQR participation in the cyclic electron transport in higher plants has not been fully characterized (Moss and Bendall 1984, Bendall and Manasse 1995), and therefore further experimental evidence is needed. Yu *et al.* (1994) have found that the PsaE protein (m.m. 10 kDa) is a component of PS1 that may be involved in the cyclic electron transport. Perhaps this protein is an integral component of the FQR and contains both Fd and plastoquinone binding sites (Bendall and Manasse 1995).

Two modifications of the cyclic electron flow around PS1 have also been discovered in chloroplasts of *Chlamydomonas reinhardtii* (Ravenel *et al.* 1995). The Fd, PQ, and cyt *bf* are involved in the Ant A-sensitive pathway, whereas the other one was Ant A-insensitive, but it was mediated by NADPH and FNR. In the latter one, electrons could enter the PQ pool through the action of NAD(P)H-dependent dehydrogenases. However, some differences in the mechanisms of the cyclic electron transport in chloroplasts of the higher plants and green algae may occur (Bendall and Manasse 1995).

The plastoquinol is involved in a one-electron reduction of the Rieske FeS protein that remains in the reduced form in darkened chloroplasts (Malkin and Chain 1980). The analysis of results obtained with a model system indicates that if the Rieske Fe-S protein is in an oxidized form and cyt b_{563} in a reduced one, the plastosemiquinone can oxidize the reduced cyt b_{563} and the formed plastoquinol may reduce again the Rieske Fe-S protein (De Wolf *et al.* 1988) which, in turn, is involved in the reduction of cyt *f*. The Ant A and DCMU strongly influence the kinetics of the cyt *f* reduction and its reoxidation: in the presence of NADPH ($NADP^+$) Ant A slows down the fast component of the kinetics by *ca.* 50 % (Chain 1979).

Which pathway is involved in the reducing equivalent transport from NADPH to different electron carriers? One could presume that both Ant A-sensitive and Ant A-insensitive pathways are involved in the NADPH-dependent electron transport. Yet the NADPH-stimulated dark $P700^+$ re-reduction is insensitive to Ant A and DBMIB (Więckowski *et al.* 1989) like that of cyt *f* (Bojko *et al.* 1996). These results cannot be explained satisfactorily on the basis of the two above discussed pathways. The involvement of cyt *bf* complex was more pronounced in our experiments. We have also demonstrated that in the presence of DCMU, the NADPH-stimulated cyt *f* reduction is sensitive to DCCD treatment (Bojko *et al.* 1996). DCCD is an inhibitor of proton channels (see Lenaz *et al.* 1982, Jahns and Junge 1990) and may also contribute to the inhibition of the electron transport (Sane *et al.* 1979) including that in the cyt *bf* complex (Wang and Beattie 1991, Li *et al.* 1991). If we assume that DBMIB interacts with the cyt *bf* complex at the Q_0 site and this prevents the oxidation of plastoquinol (Trebst *et al.* 1970, Böhme *et al.* 1971, Nitschke *et al.* 1989), the plastoquinone pool might not be involved in the transport of reducing equivalents from NADPH to cyt *f* and $P700^+$ in isolated thylakoids. Under these conditions, the transport of reducing equivalents from NADPH may occur mainly through the cyt *bf* complex. The NADPH-dependent reduction of heme b_H has been

described by Furbacher *et al.* (1989), but the electron transport from heme b_H to heme b_L is energetically unfavourable. Moreover, there is also no experimental proof to confirm the assumption that the Rieske Fe-S protein or cyt *f* can be reduced by heme b_L (see Hope 1993). We tentatively assume that the third cyt *b* species in the cyt *bf* complex designated cyt b_{560} (Kramer and Crofts 1994) or cyt b_{559}* (Miyake *et al.* 1995a,b) with midpoint redox potential +47 mV could participate in the Rieske Fe-S protein (E_m7 = +300 mV) and/or cyt *f* (E_m7 = +365 mV) reductions (Fig. 1). We may also assume that, in turn, the cyt b_{560} is reducible by electrons derived from

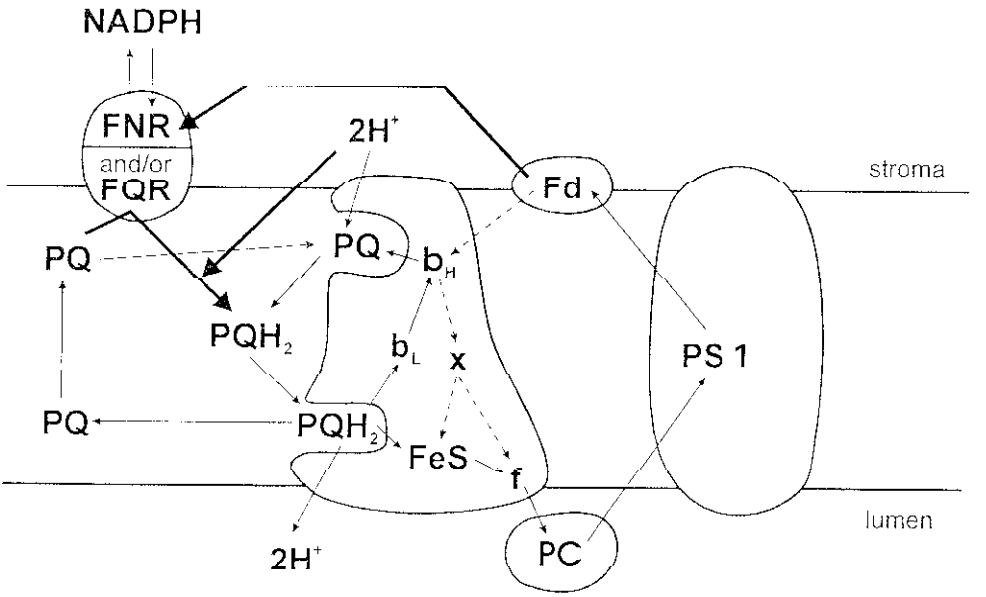

Fig. 1. Tentative scheme of the photosynthetic cyclic electron transport routes at the side of cytochrome *bf* complex: *thick lines* - pathway with involvement of ferredoxin:plastoquinone reductase (FQR) and/or ferredoxin:$NADP^+$ oxidoreductase (FNR) (see also Więckowski and Bojko 1996); *broken lines* - pathway with involvement of cytochrome b_{6H} and hypothetical electron carrier (x), presumably cytochrome b_{560}; *thin lines* - pathway with involvement of cytochrome b_{6H} and cytochrome b_{6L} (Q-cycle). Thin lines indicate also common parts in all three pathways discussed in this review. b_H - high potential form of cytochrome b_6; b_L - low potential form of cytochrome b_6; FeS - the Rieske Fe-S protein, *f* - cytochrome *f*; Fd - ferredoxin; FNR - ferredoxin:$NADP^+$ oxidoreductase; FQR - ferredoxin:plastoquinone reductase; PC - plastocyanin; PQ - plastoquinone; PQH_2 - plastoquinol; PS1 - photosystem 1; x - unidentified electron carrier.

*Cyt b_{559} (high potential form) is probably associated with the PS2 reaction centre (*e.g.*, Rich and Bendall 1980, Klimov *et al.* 1995) although its function in the PS2 activities is still not clear. However, some results indicate that a similar or the same type of cyt b_{559} (predominately a low potential form) may also be associated with other protein complexes occurring in thylakoid membranes (Peters *et al.* 1983, Baroli *et al.* 1991, McNamara *et al.* 1995) including the cyt *bf* complex (Miyake *et al.* 1995a,b).

the cyt b_H (E_m7 = -45 mV) and (?) cyt b_L (E_m7 = -150 mV). Thus, there may be some experimental proofs suggesting different pathways of the electron transport from Fd_{red} to cyt *f* in chloroplasts (Fig. 1). Their relative activities might depend on the stage of chloroplast development as well as on the quality of isolated chloroplasts used for the experiments.

It is a matter of debate if the modifications of the cyclic electron flow operate equally around all types of PS1. Evidence has accumulated for the existence of at least two kinds of PS1 complexes designated PS1α and PS1β (Svensson *et al.* 1991, Wollenberger *et al.* 1994, 1995). It has been argued that the first one derives from the grana lamellae and is responsible for the oxygenic electron flow and $NADP^+$ reduction, whereas the second one derives from stroma lamellae and is involved mainly in the cyclic electron flow and cyclic photophosphorylation (Albertsson *et al.* 1990). Rurainski (1981) and Rurainski *et al.* (1984) have also suggested that three components in the kinetics of $P700^+$ re-reduction derive from two kinds of the PS1 reaction centres: "μs components" (average relaxation times 18 or 150 ms) can only be involved in linear electron transport terminating in the $NADP^+$ reduction, whereas the "ms component" (with an average relaxation time approximately 15 ms) is engaged in the cyclic electron transport. NADPH influences only the turnover of the P700 [ms]. In isolated and washed thylakoids the time range of $P700^+$ reduction is extended to several seconds judging from the dark decay of the light induced g = 2.0026 EPR signal (Więckowski *et al.* 1979), and under comparable conditions the NADPH stimulated $P700^+$ reduction is insensitive to Ant A. The rate of NADPH-stimulated and Ant A-insensitive $P700^+$ reduction is higher at the earlier stages of chloroplast development (Więckowski *et al.* 1989) and at these stages the $P700^+$ turnover does not depend on the rate of electron donation from PS2 (Więckowski *et al.* 1979). Presumably it is related to the domination of non-appressed lamellae over that of the appressed ones at these stages of chloroplast biogenesis (for a review see Ryberg *et al.* 1993) and under these conditions the electron flow through the cyt *bf* complex from NADPH-Fd to $P700^+$ may be more pronounced.

Differences between stroma and grana lamellae concern not only the composition and activity of PS1 complexes, *e.g.*, according to Romanowska and Albertsson (1994, 1995), the cyt *bf* complex from stroma lamellae is enriched with plastocyanin and 4 kDa protein as compared to that isolated from grana lamellae, whereas an additional 15 kDa protein occurs in the cyt *bf* complex isolated from grana lamellae. The Rieske proteins, having isoelectric points 5.1 and 5.4, were isolated from grana and stroma membranes, respectively (Yu *et al.* 1994). The tightly bound type of FNR dominates in stroma lamellae and this type may be involved predominantly in the cyclic electron transport, whereas the loosely bound one dominates in the grana region where the non-cyclic electron flow dominates (Nielsen *et al.* 1995, Yu *et al.* 1995). The bound form of FNR has its V_{max} approximately ten time lower than the free one in the NADPH oxidation activity (Nielsen *et al.* 1995).

General remarks

The results discussed above indicate that in chloroplasts of higher plants the NADPH, generated in glycolytic and/or oxidative pentose phosphate pathways or supplied externally, can be used for the reduction of some photosynthetic electron carriers, and that cyt *bf* may be involved in this process, although the details of this mechanism are not known. We also do not know whether in all cases this reverse electron flow is strictly energy- or ΔpH-dependent as suggested by some authors (see Shahak and Avron 1986). It cannot be ruled out that the NADPH driven electron transport is not associated with ATP hydrolysis, and it may even contribute to the proton transport across the thylakoid membranes (Wang and Beattie 1991) which may stimulate the ATP synthesis, as it has been found in the chloroplasts of bundle-sheath cells of C_4 plants (Leegood *et al.* 1981). The NADPH-stimulated photophosphorylation is only slightly sensitive to Ant A (Woo *et al.* 1983), whereas in mesophyll cells of the same plant species a high rate of Fd-dependent and Ant A-sensitive cyclic electron flow is observed (Miyake *et al.* 1995a,b).

If this NADPH-stimulated electron transport occurs indeed *in vivo* and plays any role in maintaining NADPH/ATP ratio at a certain level in the dark, the system accepting electrons from electron carriers should operate between Fd and PC. We cannot exclude a possibility that it is associated with the oxygen uptake which occurs in chloroplasts as discussed above, and this may concern particularly the earlier stages of etioplast to chloroplast transformation (Egnéus 1975).

Now the question arises whether the NADPH oxidation and O_2 consumption is in any way coupled with chlororespiration which has been found in cyanobacteria and green algae (see Bennoun 1982, Cotton *et al.* 1983, Stürzl *et al.* 1984). Some results indicate the existence of residual activity of chlororespiration also in chloroplasts of higher plants (Garab *et al.* 1989, Havaux *et al.* 1991, Singh *et al.* 1992, Asada *et al.* 1992). However, a final experimental proof for this surmise is still lacking. The NAD(P)H dehydrogenase has been found in thylakoids isolated from green algae chloroplasts (Viljoen *et al.* 1985, Mi *et al.* 1992, 1994). Such dehydrogenase [NAD(P)H-plastoquinone oxidoreductase] has recently been found in thylakoids of barley (Cuello *et al.* 1995), maize (Funk and Steinmüller 1995), pea, spinach (Sazanov *et al.* 1995), and potato (Guedeney *et al.* 1995), although its role *in vivo* has not been quite well defined. Moreover, in chloroplast genome of higher plant species eleven *ndh* genes have a high sequence homology to those occurring in mitochondrial genome and encoding subunits of respiratory NADH:ubiquinone reductase (complex 1) (Ohyama *et al.* 1986, Shinozaki *et al.* 1986, Berger *et al.* 1993; for a review see Friedrich *et al.* 1995) which is thought to be an analogous enzyme to chloroplast FQR. To our knowledge no information is available on the existence of specific oxidases in thylakoids of higher plants that would be involved in the chlororespiratory pathway. One could presume that the same reduced electron carriers (*e.g.*, plastoquinone) could be non-enzymatically oxidized by molecular oxygen in the dark.

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