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Update on Chloroplast Energetics

Concerning a Dual Function of Coupled Cyclic Electron Transport in Leaves[1]

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ABSTRACT

Coupled cyclic electron transport is assigned a role in the protection of leaves against photoinhibition in addition to its role in ATP synthesis. In leaves, as in reconstituted thylakoid systems, cyclic electron transport requires "poising," i.e. availability of electrons at the reducing side of photosystem I (PSI) and the presence of some oxidized plastoquinone between photosystem II (PSII) and PSI. Under self-regulatory poising conditions that are established when carbon dioxide limits photosynthesis at high light intensities, and particularly when stomata are partially or fully closed as a result of water stress, coupled cyclic electron transport controls linear electron transport by helping to establish a proton gradient large enough to decrease PSII activity and electron flow to PSI. This brings electron donation by PSII, and electron consumption by available electron acceptors, into a balance in which PSI becomes more oxidized than it is during fast carbon assimilation. Avoidance of overreduction of the electron transport chain is a prerequisite for the efficient protection of the photosynthetic apparatus against photoinactivation.

Despite several decades of intensive research, it is still not entirely clear how in leaves the reactions of the photosynthetic electron transport chain, which yield reductant (in the form of NADPH) and phosphate energy (in form of ATP), are geared to the reactions of stromal enzymes. These use this "assimilatory power" (1) to supply the autotrophic organism with reduced carbon, nitrogen, and sulfur at ratios varying not only with the growth, type, and nature of the plant but also with the season. Obviously, a considerable degree of metabolic flexibility is required even though metabolism comprises sequences of chemical reactions with stoichiometries that are usually both known and fixed.

H^+/e COUPLING

Although it is now abundantly clear that light-driven electron transport is coupled to the vectorial transfer of protons from the chloroplast stroma to the intrathylakoid space of the chloroplasts, and that the free energy of the proton gradient thus formed is used for ATP synthesis, neither the stoichiometry of H^+/e coupling nor that of ATP synthesis are known for certain. During linear electron transport from water to NADP, two protons are released inside the thylakoids per H_2O oxidized by PSII and at least another two by the subsequent oxidation of the plastoquinol formed as a consequence of the transfer of the two electrons of water to plastoquinone. Unfortunately, it is still not quite clear how the Cyt *b/f* complex mediates oxidation of plastoquinol. If it passes electrons of this two-electron carrier straight on to PSI, which lifts them to the redox levels of Fd and NADP, the H^+/e ratio of linear electron transport is 2. If only one electron from the plastoquinol is transferred to PSI and the other one is shuttled back to plastoquinone in the loop of a Mitchellian Q-cycle, the H^+/e ratio is 3. According to Rich (19), Q-cycle coupling is obligatory. Others consider it to be facultative, with decreasing coupling efficiency at increasing light intensities (17, 18). Crowther and Hind (4) proposed a modified Q-cycle, with electron input from the reducing side of PSI.

CONSEQUENCES OF THE H^+/ATP RATIO IN ATP SYNTHESIS

Most researchers believe that the stoichiometry of ATP synthesis is 3 H^+/ATP. If H^+/e is only 2, then insufficient ATP is formed for carbon reduction, the stoichiometry of which requires a little more than 1.5 ATP/2e in C_3 plants and 2.5 ATP/2e in C_4 plants. An auxiliary reaction capable of supplying extra ATP, such as cyclic electron transport or linear electron transport to O_2 in the Mehler reaction (2, 20) or to nitrite in nitrogen metabolism, would be required for both types of plants. However, if the H^+/e ratio were stoichiometrically fixed to a value of 3, more ATP would be formed than is required for carbon assimilation in C_3 plants but still not enough for assimilation of C_4 plants (cf. ref. 7).

With H^+/e = 3, chloroplast ATP/ADP ratios would be expected to increase to high levels in C_3 plants in the light, and partial uncoupling would be required for photosynthesis to proceed. In fact, Strotmann et al. (21) reported the existence of a naturally occurring safety valve in thylakoid membranes that is capable of releasing excessive proton pressure. However, neither the physiological function of this valve nor its

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regulation is clear. Chloroplast ATP/ADP ratios are rarely higher than 2 in leaves in which photosynthesis proceeds fast, and proton gradients increase only when CO_2 is limited by stomatal closure.

At low ATP/ADP ratios, flexible Q-cycle activity may make the participation of auxiliary ATP-producing reactions in C_3 photosynthesis unnecessary (17, 18). It should be noted that photosynthesis does not demand a high ratio of NADPH to NADP or a high phosphorylation potential of the chloroplast adenylate system. On the contrary, light-dependent enzyme activation permits photosynthesis to proceed at high rates in the presence of a relatively oxidized chloroplast NADP system and at phosphorylation potentials that never even approach those possible when isolated thylakoids are illuminated with ATP, phosphate, and a proper electron acceptor or a catalyst of cyclic electron flow such as pyocyanine. However, in brightly illuminated leaves, when CO_2 is limited by partial or even full closure of stomata (as is often the case under water stress, particularly in Mediterranean or desert climates), linear electron flow declines and electron pressure in the thylakoid system is bound to increase because the light reaction of PSII, which pumps electrons, is essentially irreversible as long as oxidized acceptors are available. A decrease of the pool of oxidized plastoquinone may suppress operation of the Q-cycle because the redox potential gradient between the high potential *b* heme in the Cyt *b/f* complex and plastoquinone decreases, particularly if the proton gradient is large. Full reduction of available electron acceptors in the electron transport chain, when CO_2 is limiting, is known to lead to rapid photoinactivation and subsequent photodestruction. It can be avoided (or checked) only by the internal generation of electron acceptors, by the diversion of electron flow to an available alternative electron acceptor or by control of the activity of PSII.

It appears that in leaves all three possibilities are realized. Ribulose bisphosphate carboxylase in the chloroplast stroma is a bifunctional enzyme. It can oxygenate ribulose bisphosphate as well as carboxylate it. Through oxygenation, when CO_2 is limiting, there is internal generation of electron acceptors. Oxygenation, together with the rest of the photorespiratory pathway, results in carbon loss. Electrons provided by the electron transport chain and derived from water oxidation are, together with ATP, consumed both during carbon gain and carbon loss. Actually, during the release of one molecule of CO_2 in photorespiration, twice as much NADPH and ATP is consumed than during fixation of one molecule of CO_2. Thus, behind closed stomata, carbohydrate oxidation and photosynthetic assimilation of the CO_2 released during photorespiration guarantee continuous electron flow. However, the maximum rate of this electron flow is distinctly below the maximum electron transport rate possible when open stomata permit easy access of external CO_2 to the photosynthetic apparatus. If electron flow made possible by internal cycling of CO_2 contributes to the protection against photoinactivation (9), it certainly cannot do so simply by using and degrading excess light energy in the established pathways of photochemistry.

There is also the possibility of diverting electrons to an acceptor other than CO_2. However, at the CO_2 compensation point (i.e. the CO_2 concentration at which photorespiratory CO_2 release and photosynthetic CO_2 consumption balance each other), although atmospheric O_2 concentration is about 210,000 μL/L of gas phase and CO_2 only between 35 and 50 μL/L, O_2 is still a poor electron acceptor compared with CO_2. Electrons react with O_2 mainly at the level of PSI. Reoxidation of reduced Fd by molecular O_2 yields reactive O_2 radicals that are detoxified by superoxide dismutase and ascorbate peroxidase (20). It appears that, in isolated chloroplasts, in the absence of so-called Mehler reagents and of CO_2, the maximum electron transport from water to O_2 is not much more than about half of the electron transport made possible in leaves by photorespiratory and photosynthetic CO_2 turnover behind closed stomata. In leaves, O_2 reduction may be less than in isolated chloroplasts, because the chloroplast NADP system remains partially oxidized even when stomata are closed. Relatively low electron pressure in PSI in this situation is also indicated by the high oxidation state of the electron donor pigment of PSI, P700, under water stress and high-intensity illumination.

The high oxidation status of PSI under conditions in which a greater level of reduction would be expected is made possible by the control of electron flow from PSII (8, 11, 14, 23, 24). Control becomes strong when access of CO_2 to the photosynthetic apparatus is restricted. It relaxes when CO_2 becomes available.

CONTROL OF ELECTRON FLOW

Control is exerted at two different levels, i.e. by a direct effect on PSII, which diminishes its activity, and by decreasing electron transfer from PSII to PSI. Both modes of control require formation of a transthylakoid proton gradient larger than that needed to satisfy the ATP requirement of carbon reduction (for a review, see ref. 23). When a decreased proton gradient causes loss of control, photoinhibition of electron transport proceeds rapidly (15). Two methods are available to monitor changes in the magnitude of the transthylakoid proton gradient in intact leaves. One involves measurements of Chl fluorescence during intermittent flashing with saturating light and the other one involves recording changes in the scattering of light by the thylakoid membranes. Neither signal is unambiguous; interpretation requires circumspection (3, 16). Nevertheless, the so-called nonphotochemical fluorescence quenching contains a major component that indicates acidification of the intrathylakoid space.

As would be expected from the thermodynamics of ATP synthesis and the ATP requirement of carbon assimilation, considerable acidification is indicated by fluorescence quenching at light intensities that are still far from saturating photosynthesis. Under the same conditions, light scattering does not increase appreciably. However, when light saturation is approached, or when intercellular CO_2 decreases to low levels during stomatal closure, light scattering increases steeply toward a saturation level, while fluorescence is quenched further. Thus, light scattering and fluorescence differ in their sensitivity as indicators of the transthylakoid proton gradient (or intrathylakoid acidification), with light scattering being the more useful indicator of the formation of a proton gradient larger than that required to satisfy the ATP requirements of carbon assimilation (3).

Obviously, when excitation of PSII is in excess of the electron requirement of carbon, nitrogen, and sulfur assimilation reactions, electron supply and electron demand must be brought into proper balance. Protection against photoinactivation demands a balance in which excessive reduction of the electron transport chain is avoided. In fact, P700 in the reaction center of PSI is more oxidized in leaves receiving a high photon flux density at the CO_2 compensation point than in leaves photosynthesizing in air under otherwise comparable conditions. If control of electron flow (which prevents swamping of PSI with electrons) is based on the formation of a large transthylakoid proton gradient, it can be asked which electron transport reaction permits formation of such a gradient under conditions of restricted acceptor availability when stomata are closed under water stress.

FORMATION OF A TRANSTHYLAKOID PROTON GRADIENT UNDER ACCEPTOR LIMITATION OF ELECTRON FLOW

By itself, the interplay of photorespiratory and assimilatory electron flows cannot create a proton gradient large enough for efficient control of electron transport to PSI and beyond, because both carbon assimilation and photorespiration consume ATP and NADPH at a ratio of approximately 1.5. As mentioned above, assimilation of CO_2 can proceed in the absence of an appreciable increase in light scattering, whereas a large increase in light scattering is brought about, at comparable light intensities, in leaves experiencing partially or fully closed stomata.

Even though nitrogen assimilation during photosynthesis of actively growing plants can support rates of electron transport that approach 10% of the rate of electron transport to CO_2, photosynthetic nitrite reduction, which does not require ATP, cannot account for the formation of a large proton gradient, because in leaves it is strictly coupled to carbon assimilation (13). It ceases when stomata close.

When intercellular levels of CO_2 decrease during stomatal closure, the increased ratio of O_2 to CO_2 not only shifts ribulose bisphosphate consumption toward oxygenation, it may also increase linear electron flow to O_2 in the Mehler reaction. Even though the rate of direct electron flow to O_2 may appear to be slow in leaves, it could, in principle, create a proton gradient large enough for control of electron flow (20) because O_2 reduction, like nitrite reduction, is unaccompanied by the consumption of ATP (for a recent review, see ref. 23). However, experiments with leaves in which both carbon assimilation and photorespiration were inhibited by glyceraldehyde have shown that the Mehler reaction alone cannot prevent what may be called "overreduction," i.e. flooding the electron transport chain with electrons (25). Also, when leaves are illuminated in CO_2-free air for a prolonged time so that endogenous reserves of carbohydrate are depleted, initially oxidized P700 becomes reduced. Nevertheless, increased light scattering and fluorescence quenching indicate formation of a large proton gradient in glyceraldehyde-inhibited leaves and in leaves illuminated in the absence of CO_2. Apparently, what is needed to prevent overreduction, which is characterized by the absence of appreciable P700 oxidation under high-intensity illumination, is either faster electron flow than is possible during O_2 reduction or a larger proton gradient than O_2 reduction (and the accompanying electron flow to monodehydroascorbate and dehydroascorbate, which regenerates the ascorbate consumed during detoxification of O_2 radicals) can provide.

ROLE OF PSI-DEPENDENT CYCLIC ELECTRON TRANSPORT

There are two lines of evidence that implicate a participation of coupled cyclic electron flow in the formation of a proton gradient large enough to provide not only extra ATP for carbon assimilation when linear electron transport and Q-cycle activity do not satisfy ATP requirements but also protection against photodestruction of chloroplasts when leaves are exposed to light and water stress. One dates back to the early work of Arnon and Whatley (see ref. 1), who observed that isolated thylakoids supplied with Fd could phosphorylate ADP under aerobic conditions in far-red light, which excites predominantly PSI. Their conclusion was that ATP synthesis was based on coupled cyclic electron transport. Because the reaction was inhibited by DCMU, which blocks linear electron transport from water, PSII activity was considered necessary to establish so-called "poising," i.e. a redox situation in which electrons, lost from the electron transport chain by reduction of an exogenous electron acceptor, would be replaced. In this way, cyclic electron transport, which competes with linear electron transport for electrons, would not run out of electrons.

It has remained unclear for a long time whether or not chloroplasts in leaves experience conditions resembling those that permit coupled cyclic electron transport and cyclic photophosphorylation in vitro in a reconstituted chloroplast system. The possibility that Q-cycle activity may be sufficient under many conditions to provide the extra ATP needed for carbon assimilation of C_3 plants has already been mentioned. In fact, Hosler and Yocum (12) observed sensitivity of photophosphorylation of thylakoids to antimycin A, an effective inhibitor of cyclic electron transport, only when O_2, and not NADP, was available as electron acceptor in addition to Fd.

However, in barley protoplasts, carbon assimilation, which was insensitive to antimycin A at low light intensities, was much decreased by antimycin A above photon flux densities of 100 μmol m^{-2} s^{-1} (6). Using a photoacoustic method, Herbert et al. (10) recently provided evidence for the occurrence of energy storage by coupled cyclic electron flow in various algae and higher plants, with the possible exception of C_3 plants. It remains unclear whether in their experiments, which involved infiltration of leaves, redox poising was really achieved for the latter group of plants. It should be noted that redox balances in thylakoids, intact chloroplasts, protoplasts, and leaves are variable and depend on experimental conditions.

In fact, redox regulation of cyclic electron transport in leaves can be demonstrated by measurements of light scattering. In leaves of a C_3 plant, light scattering was in the absence of CO_2, increased far more by far-red light than by low-intensity red light when the beams were balanced so as to produce comparable excitation of PSII (14). Scattering was decreased not only by CO_2 but also by elevated concentra-

tions of O_2. In both cases, electrons are drained from the electron transport chain. However, when O_2 was decreased to a very low level, PSII excitation did not stimulate but actually suppressed the light-scattering response induced by far-red light. This suppression results from overreduction. Excessive reduction of electron carriers must diminish cyclic electron flow because electron passage from one carrier to another requires the potential acceptor to be oxidized. Indeed, light scattering is completely suppressed and ATP/ADP ratios are decreased in leaves illuminated with high-intensity red light in the absence of O_2 and CO_2. The quenching of Chl fluorescence observed under these conditions is caused by the photoaccumulation of reduced pheophytin, which acts as quencher, rather than by thylakoid acidification.

In the presence of high-intensity far-red light, low-intensity red light, and O_2, light scattering can thus be decreased either by decreasing electron acceptor availability at the reducing side of PSI (which leads to overreduction) or by increasing it (which favors linear electron flow). Optimum energization of the thylakoids can be shifted toward greater acceptor availability (more CO_2 or O_2 in the gas phase) simply by increasing the photon flux density of the red light. Such an increase would replenish electrons lost from the cyclic pathway to NADP as NADPH becomes more rapidly reoxidized by increased carbon assimilation and/or photorespiration. At intermittent levels of light scattering, in the presence of predominantly far-red background illumination, brief flashes of high-intensity red light cause transient increases in light scattering (14). This increase is dependent on the intensity of the far-red background light. It is inferred that these flashes cause transient increases in electrons available for cycling around PSI. Significantly, whereas light scattering is transiently increased after a flash, Chl fluorescence is decreased, indicating increased radiationless energy dissipation. This quenching of Chl fluorescence shows that PSI-dependent electron flow can control the activity of PSII.

The responses of light scattering of leaves to PSI light and to O_2 and CO_2 are best explained by the concept of poising by Arnon and Whatley (see ref. 1). Coupled cyclic electron flow requires a balanced redox situation that is characterized by the simultaneous availability of electrons at the reducing side of PSI and of oxidized electron carriers in the cyclic pathway. Because electrons can be donated from the low redox potential of Fd to plastoquinone, even if the plastoquinone pool is largely reduced, cyclic electron transport can still proceed when electron donation to plastoquinone in a Q-cycle has already become ineffective. Yet, because NADP drains electrons from the cyclic pathway, coupled cyclic electron transport is unlikely to occur when the chloroplast NADP system is largely oxidized. In isolated intact spinach chloroplasts, about 20% of extractable NADP is reduced even in the dark (22). On illumination, if CO_2 is available, NADP reduction is increased only briefly. After the induction phase, NADP is scarcely more reduced in the light than it was in the dark. In the absence of CO_2, on the other hand, considerable reduction persists in the light (22). Such reduction, if it also occurs in leaves, would permit electrons to enter the cyclic pathway because Fd/NADP reductase is inhibited allosterically by NADPH, permitting electrons to accumulate at the level of Fd (23).

Recent determinations of quantum efficiencies also favor the view that cyclic electron transport contributes to the large proton gradient that is formed in leaves when CO_2 is not freely available (8). Fluorescence and P700 measurements in pea leaves revealed a larger decline in the quantum efficiency of PSII than in that of PSI as photon flux density was increased. The relationship between the quantum efficiencies of the two photosystems was linear in air, but not linear in the absence of CO_2, with a larger proportion of electrons passing through PSI as irradiance was increased. This is another indication of the occurrence of cyclic electron flow under electron acceptor limitation.

The conventional view that if cyclic electron transport occurs in vivo it would help to meet the ATP demand of photosynthetic carbon assimilation scarcely applies to conditions of strict acceptor limitation. There is obvious justification for such a view only if the high demand for ATP in C_4 photosynthesis is to be considered (cf. ref. 7). In both C_3 and C_4 plants, the conditions for poising must be met if cyclic electron flow is to contribute to thylakoid energization. In C_3 photosynthesis, in which Q-cycle activity may make a participation of cyclic photophosphorylation in carbon reduction unnecessary under many conditions, we suggest that a main function of cyclic electron transport is to build up a proton gradient capable of controlling electron pressure in the electron transport chain. Overreduction, with its damaging consequences, is prevented in water-stressed leaves exposed to high irradiances by the concerted action of the transthylakoid proton gradient, which controls electron flux from PSII, and by electron drainage at the reducing end of the electron transport chain (9). Phosphoglycerate (formed during carboxylation and oxygenation of ribulose bisphosphate), O_2, and oxidized ascorbate all function as main electron acceptors of linear electron flow (2, 20, 25). In C_4 plants, cyclic electron transport also contributes to the higher ATP requirement of C_4 photosynthesis when CO_2 is available (7). At the CO_2 compensation point, which is much lower in C_4 plants than in C_3 plants, residual linear electron flow is maintained in C_4 plants on the basis of the same principles that have been described for C_3 plants, with the only differences being that cycling of CO_2 occurs between bundle sheath cells, which evolve CO_2 by photorespiration, and mesophyll cells, which have the greater share in refixation, and that rates of electron flow supported by cycling will be lower than in C_3 plants.

ROLE OF THE PROTON GRADIENT IN THE DISSIPATION OF EXCESS EXCITATION ENERGY

With regard to the protection of the photosynthetic apparatus, it is still largely a matter of conjecture how a low intrathylakoid pH might bring about increased light scattering and decreased fluorescence, which indicates increased radiationless dissipation of excess excitation energy (11, 20, 23), but it seems clear that protonation reactions are involved in both cases. There is excellent correlation between fluorescence quenching and the level of thylakoid zeaxanthin formed from violaxanthin at a low intrathylakoid pH (5). Increased light scattering also appears to depend on the previous formation of zeaxanthin.

In leaves, only a small part of the scattering change is now

thought to be due to chloroplast shrinkage (an osmotic response resulting from loss of cations during cation/proton exchange across the thylakoids). Rather, most of it is attributed to conformational change of thylakoid proteins (initiated by a protonation reaction). It is conceivable that such a conformational change exposes Chl to an aqueous environment. It may be remembered that the high quantum yield of fluorescence from Chl extracted into a moderately hydrophobic solvent, such as ethanol, is dramatically decreased when the solvent is made more hydrophilic by the addition of water. In this situation, fast radiationless degradation of light energy outcompetes fluorescence. A direct relationship, if it exists, among zeaxanthin formation, changes in the conformational state of thylakoid proteins, and the quenching of Chl fluorescence in leaves still remains to be elucidated. However, it is certain that the fluorescence quenching, observed when the intrathylakoid space is acidified, indicates a decrease in PSII activity.

Arnon (1) was the first to obtain evidence that cyclic electron transport is related to the control of PSII activity. However, deactivation of reaction centers is only part of the control exercised by a large proton gradient that decreases the intrathylakoid pH (23). Reaction centers remaining active will continue to reduce plastoquinone. Oxidation of plastoquinol, which is coupled to the liberation of protons into the intrathylakoid space, must now occur against the "back pressure" of a high internal proton concentration, which slows it down. In vitro, "photosynthetic control" of electron flow at this level can be relieved (together with control of PSII activity) by uncouplers or by ADP (the phosphorylation of which decreases the proton gradient).

However, the term photosynthetic control is misleading; it never "controls" photosynthesis, but it is necessary to protect photosynthesis. It is a self-adjusting device that, with the participation of cyclic electron flow and electron flow to O_2 etc., sets up a proton gradient large enough to check overreduction of the electron transport chain, which is seen as reduction of P700 under high-intensity illumination. Without control of PSII, overreduction would occur whenever photon flux densities are beyond the capacity of leaves to utilize electrons in reductive reactions. Photoinhibition occurs at irradiances that overtax the capacity of photosynthetic control to prevent excessive reduction of electron carriers. As long as it does not lead to much protein damage in PSII, photoinhibition actually contributes to the protection of the photosynthetic apparatus, because reaction centers, closed by photoinhibition, act as quenchers of fluorescence, contributing to the radiationless dissipation of light energy and decreasing electron pressure in the thylakoid system. In sunlight, even appreciable photoinhibition of PSII does not necessarily result in decreased photosynthesis, because under these conditions electron flux is limited by the rate of plastohydroquinone oxidation at the level of the Cyt *b/f* complex and not by PSII. Only when light becomes limiting does photoinhibition result in decreased photosynthetic yields. Protein components of PSII, damaged during excessive irradiation, can be replaced by newly synthesized components. Irreversible photodestruction of the photosynthetic apparatus follows only when repair and replacement mechanisms are overtaxed. Whereas some degree of photoinhibition is of common occurrence, but scarcely a factor of great importance for photosynthetic productivity in temperate climates during the growth period, permanent damage is a rare event in nature and may occur only under the most extreme conditions of illumination, drought, and/or cold.

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