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Minireview

Irrungen, Wirrungen? The Mehler reaction in relation to cyclic electron transport in C3 plants

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Abstract

Plants not only evolve but also reduce oxygen in photosynthesis. Considerable oxygen uptake occurs during photorespiration of C3 plants. Controversies exist on whether direct oxygen reduction in the Mehler reaction together with associated electron transport is also a major sink of electrons when leaves are exposed to sunlight. Here, preference is given to the view that it is not. Whereas photorespiration consumes ATP, the Mehler reaction does not. In isolated chloroplasts photosynthesizing in the presence of saturating bicarbonate, the Mehler reaction is suppressed. In the water – water cycle of leaves, which includes the Mehler reaction, water is oxidized and electrons flow through Photosystems II and I to oxygen producing water. The known properties of coupled electron transport suggest that the water – water cycle cannot act as an efficient electron sink. Rather, by contributing to thylakoid acidification it plays a role in the control of Photosystem II activity. Cyclic electron transport competes with the Mehler reaction for electrons. Both pathways can help to defray possible ATP deficiencies in the chloroplast stroma, but play a more important role by making intrathylakoid protein protonation possible. This is a necessary step for the dissipation of excess excitation energy as heat. Linear electron flow to oxygen relieves the inhibition of cyclic electron transport, which is observed under excessive reduction of intersystem electron carriers. In turn, cyclic electron transport replaces functions of the linear pathway in the control of Photosystem II when oxygen reduction is decreased at low temperatures or, experimentally, when the oxygen concentration of the gas phase is low. Thus, cyclic electron flow acts in flexible relationship with the water–water cycle to control Photosystem II activity.

Introduction

In 1888, the classical German novelist Theodor Fontane published a novel describing the conflict between what is commonly considered realities of life and the – often fruitless – attempts to overcome them. An only approximate translation of the title 'Irrungen und Wirrungen' may be 'Errors and Complications.'

In 1951, the late Alan Mehler (Figure 1) observed that chloroplasts can use oxygen as an electron acceptor in a Hill-type reaction. The reaction sequence, as it slowly became apparent, is:

$$H_2O + 2\ O_2 \rightarrow 2\ O_2^- + 2\ H^+ + 1/2\ O_2,$$
$$2\ O_2^- + 2\ H^+ \rightarrow H_2O_2 + O_2$$

and, in the presence of catalase:

$$H_2O_2 \rightarrow H_2O + 1/2\ O_2.$$

Since the overall electron transport reaction which involves both Photosystems II and I is

$$H_2O + 2\ O_2 \rightarrow H_2O + 2\ O_2,$$

net gas exchange is absent. For this reason, Daniel Arnon termed the underlying electron transport reaction pseudocyclic electron transport to distinguish it from cyclic electron transport around Photosystem I, which does not involve gas exchange (Arnon 1977). In contrast to cyclic electron transport, oxygen reduction by Photosystem I in the Mehler reaction results in the production of potentially toxic active oxygen

Figure 1. Professor Alan H. Mehler at the symposium given in his honor on the occasion of his retirement from Howard University, Washington, DC, on November 16, 1995. The Mehler reaction originated from the Institute of Radiobiology and Biophysics of the University of Chicago. Courtesy of Professor Thomas Smith, Howard University.

species, which require enzymic detoxification. Like cyclic electron transport, pseudocyclic electron transport is coupled to transthylakoid proton transport. When measured in the presence of ADP and phosphate, it is accompanied by ATP formation.

Where are the errors and where are the complications? Whereas the thylakoid suspensions used in early work were contaminated with catalase, intact chloroplasts do not contain this enzyme. Instead, the presence of ascorbate peroxidase and of high concentrations of ascorbate (AA) result in:

$$H_2O_2 + 2\ AA \rightarrow 2\ MDA + 2\ H_2O.$$

The resulting ascorbate radical monodehydroascorbate (MDA) is reduced by the chloroplast electron transport chain according to:

$$H_2O + 2\ MDA \rightarrow 2AA + 1/2\ O_2.$$

Again, net gas exchange is zero in the full reaction sequence, but as the additional electron transport from water to MDA is coupled to vectorial proton transport, the transthylakoid proton gradient is larger than in the earlier version of the reaction sequence. The altered reaction sequence involving AA oxidation and the reduction of the resulting MDA has been pioneered by Kozi Asada and termed water/water cycle (Asada 1999).

Are there complications? An obvious one is the necessity of enzymic detoxification of reactive oxygen species, a feat perhaps not easy to achieve when low temperatures slow down enzymic reactions. Other complications will be discussed below.

Interest in the Mehler reaction has not only persisted for half a century but has actually been renewed in the light of its possible role in the photoprotection of plants. Initially, the reaction was viewed only as being capable of supplying extra ATP for carbon assimilation. This role is still under discussion (Asada 1999; Christine Foyer and Graham Noctor 2000), although evidence is mounting that in leaves the ATP requirement of photosynthetic carbon reduction and photorespiratory carbon oxidation can be largely satisfied during electron transport to nicotinamide adenine dinucleotide phosphate (NADP). It now seems that the H^+/e ratio of noncyclic electron transport is not 2 as envisaged earlier but 3 owing to Q-cycle activity (see Peter Rich 1991), and the H^+/ATP ratio is not 3, but 4 (Bernd Rumberg et al. 1990; Michel Haraux and Yaroslav de Kouchkovsky 1998). For this reason, the ATP/NADPH ratio is not 1.33, as thought earlier, but 1.5, very close to the ATP/NADPH requirement of carbon assimilation and photorespiration (Derek Bendall and Robert Manasse 1995; Heber et al. 2001). Thus, additional ATP from the Mehler reaction is scarcely needed for photosynthesis of leaves particularly as the reduction of the nitrite which is formed during nitrogen assimilation may also help to defray possible ATP deficiencies (Noctor and Foyer 1998). However, the proton gradient established during electron transport in the Mehler reaction does not power only ATP synthesis. It also permits the de-epoxidation of violaxanthin to zeaxanthin (Achim Hager 1963; Ehrhard Pfündel and Richard Dilley 1993) and is large enough to protonate chlorophyll–proteins in the thylakoid lumen. In the protonated form, these proteins bind zeaxanthin and undergo a conformational change which converts them into energy-dissipating traps that compete with the reaction center of Photosystem II for excitons (for a review, see Adam Gilmore and Govindjee 1999). Exciton pressure is thereby diverted from Photosystem II protecting this photosystem from photoinactivation.

In these roles, the Mehler reaction has a competitor. Cyclic electron transport around Photosystem I is also coupled to vectorial proton transport (Bendall and Manasse 1995). Like the Mehler reaction, it

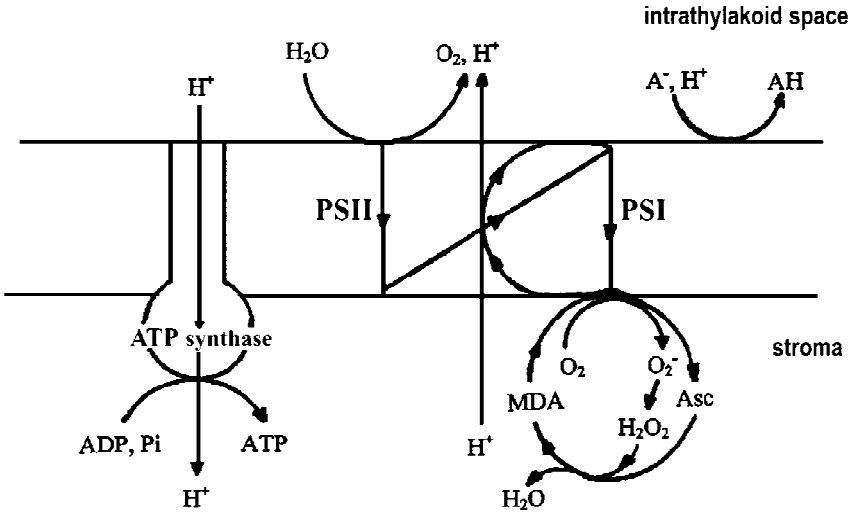

Figure 2. Schematic representation of the competing pathways of linear electron flow from water to oxygen in the water–water cycle and cyclic electron flow around Photosystem I. To come into operation, both require accumulation of reductant on the stromal side of Photosystem I (PS I), i.e. conditions in which photoassimilatory electron flows are restricted by shortage of external electron acceptors such as CO_2. Asc – ascorbate; A^- – anionic group of a thylakoid protein before and AH after protonation; MDA – monodehydroascorbate.

has the potential to give rise to ATP formation, zeaxanthin synthesis, and protein protonation (Heber and David Walker 1992). It competes for electrons with the Mehler reaction (Figure 2). Unlike the Mehler reaction, it does not give rise to oxygen radicals and hydrogen peroxide, which must be enzymically detoxified. Hydrogen peroxide is known to be a powerful inhibitor of photosynthesis (Werner Kaiser 1979).

Like oxygen reduction, cyclic electron transport is controlled by the redox state of electron acceptors on the reducing side of Photosystem I (Arnon and Richard Chain 1975; Heber et al. 1978). As discussed by Mordhay Avron and Joseph Neumann (1968), it requires redox poising of the chloroplast electron transport chain. In intact chloroplasts, it is inhibited not only when the acceptor side of Photosystem I is oxidized, but also when electron carriers between the photosystems become excessively reduced (Ursula Ziem-Hanck and Heber 1980).

Although a main activity of green plants is carbon assimilation, chloroplasts reduce *in situ* several electron acceptors besides CO_2. What is the role of oxygen reduction in relation to that of competing electron acceptors? In the following, discussion will be restricted to C3 plants.

The Mehler reaction in chloroplasts

The Mehler reaction can be easily shown as net oxygen uptake in suspensions of thylakoids and intact chloroplasts when some KCN is present to prevent reduction of H_2O_2 and inhibit competing electron transport reactions. As a rule, O_2 uptake rates increase as the preparations become less intact. Uptake rates of 25 μmol O_2 (mg Chl $\times$ h)$^{-1}$ are common under light saturation. In preparations of intact chloroplasts capable of high rates of CO_2-dependent oxygen evolution, maximum oxygen uptake rates are often below 10 μmol O_2 (mg Chl $\times$ h)$^{-1}$ corresponding to electron flows to oxygen of less than 20 μeq (mg Chl $\times$ h)$^{-1}$. When methylviologen is added to the chloroplasts, oxygen uptake is increased. This demonstrates that the Mehler reaction is not, or not only, controlled at the level of cytochrome b/f complex between Photosystems II and I, as has been proposed (Asada 1999). A kinetic restriction exists also on the reducing side of Photosystem I. It must be emphasized that modest concentrations of KCN do not affect electron transport, whereas catalase and ascorbate peroxidase are effectively inhibited. When KCN is absent, availability of bicarbonate or electron acceptors such as nitrite or oxaloacetate will suppress oxygen reduction under limiting light by competition for electrons (Jan Backhausen et al. 1994).

When intact chloroplasts were prepared in the presence of ascorbate so as to make detoxification of

H_2O_2 by ascorbate peroxidase possible, strong membrane energization caused by illumination was attributed to the operation of the water–water cycle (Ulrich Schreiber and Christian Neubauer 1990; Schreiber et al. 1991; Neubauer and Harry Yamamoto 1992). According to Chikahiro Miyake et al. (1998), the maximum flux of linear electron transport in the water–water cycle is 120 e^- $P700^{-1}$ s^{-1} corresponding to an electron flow of approximately 400 μeq (mg Chl $\times$ h)$^{-1}$. Such rates are commensurate with high rates of electron flow to CO_2as measured by CO_2-dependent oxygen evolution. However, it should be noted that high electron fluxes in the water–water cycle imply uncoupling because coupled electron transport unaccompanied by ATP consumption increases the transthylakoid proton gradient, which is known to control electron flow.

Chloroplast energization occurs not only during noncyclic electron transport. Cyclic electron transport has been shown to proceed concurrently with electron transport to oxygen in the Mehler reaction (Yoshichika Kobayashi and Heber 1994). Apparently, increased reduction of donors on the acceptor side of Photosystem I permits not only reduction of oxygen but also flow of electrons into the cyclic pathway. There is a not yet fully resolved discrepancy, as Henning Hormann et al. (1994) have reported also that the extended water–water cycle inhibits cyclic electron flow. However, in their assays, 15 mM ascorbate was used as substrate for ascorbate peroxidase. Metal-ion-catalyzed oxidation of ascorbate produces ascorbate radicals which, by oxidizing reduced ferredoxin, drain electrons from the cyclic pathway. This rather artificial situation questions the physiological significance of the observations. It is known that oxidation at the acceptor side of Photosystem I inhibits cyclic electron transport.

Cyclic electron transport has been shown to proceed even together with linear electron flow when oxaloacetate serves as electron acceptor for illuminated intact chloroplasts in addition to oxygen (Boris Ivanov et al. 1998). Oxaloacetate is reduced to malate by NADP-dependent malate dehydrogenase, which is a light-controlled enzyme that becomes active at elevated NADPH/NADP ratios (Renate Scheibe 1987, 1990). The observations demonstrate that cyclic electron transport can occur when oxidized NADP is still present. In fact, carbon assimilation of intact chloroplasts or protoplasts has been shown to be sensitive to antimycin A, an inhibitor of ferredoxin-dependent cyclic electron flow (Heber et al. 1978; Bob Furbank and Peter Horton 1987; Backhausen et al. 1994). Only methylviologen, which is a very efficient electron acceptor, suppresses cyclic electron transport effectively.

Even if so-called intact chloroplasts have retained their envelopes during isolation, they are not really as intact as they were inside the cells. This is apparent not only from altered chlorophyll fluorescence kinetics but also from generally increased reduction of the components of the electron transport chain in the light.

Although both the water–water cycle and cyclic electron transport can be shown to proceed in intact chloroplasts, the real question is when and under which conditions they occur in leaves, and how effective the water–water cycle is as a sink for electrons. Obviously, these question cannot be answered unequivocally by work with intact chloroplasts.

The Mehler reaction *versus* cyclic electron transport in leaves of C3 plants

In air, the ratio of CO_2 to oxygen is about 0.0016. Nevertheless, the quantum efficiency of carbon assimilation as measured in limiting light is remarkably high even in C3 plants and, when viewed together with photorespiratory electron flow, close to the efficiency expected if almost every exciton trapped in a reaction center causes a redox reaction. The intermediate electron acceptor of both assimilatory carbon reduction and photorespiratory carbon oxidation, NADP receives electrons from reduced ferredoxin. As the latter reacts only slowly with oxygen (Asada 1999), electron flow from reduced ferredoxin to oxygen is unlikely in the presence of oxidized NADP. In fact, Asada (1999) has proposed that reduced flavin enzyme is the main electron donor to oxygen in intact chloroplasts and green cells. When it was found that the quantum efficiency of energy conversion in Photosystem I was similar to that of Photosystem II during carbon assimilation (Jeremy Harbinson et al. 1989; Bernard Genty et al. 1989), the possibility of cyclic electron transport occuring in leaves of C3 plants was largely discounted. Extra electron flow giving rise to extra thylakoid energization was attributed either to the water–water cycle (Giorgio Forti 1999; Asada 1999) or to electron flow during nitrogen assimilation (Noctor and Foyer 1998). However, the affinity of the Mehler reaction for oxygen is low. Apparent Km values for leaves are between 75 and 100 μm O_2, corresponding to 6–8% O_2 in the gas phase (Asada

1999). This means that little oxygen is reduced when leaves are illuminated in an atmosphere containing not 21 but only 1% or 2% oxygen. Under these conditions, not only photorespiration but also oxygen reduction in the water–water cycle is suppressed. Although total linear electron flow is reduced in 1% or 2% O_2/0.034% CO_2, carbon assimilation is increased owing to the increased CO_2/O_2 ratio. Nevertheless, scattering of 535 nm light by leaves is increased as well as oxidation of P700 in Photosystem I, indicating increased control of Photosystem-II activity (Harbinson and Foyer 1991; Heber et al. 1992). Obviously, electron flow to oxygen is not essential for effective Photosystem II control. Another electron transport reaction capable of controlling the activity of Photosystem II must be responsible. Light scattering changes were analyzed in 1968 at the Carnegie Institution of Washington (Heber 1969). At that time, increased light scattering was already recognized to reveal energy-dependent conformational changes in the chloroplasts of illuminated leaves, presumably owing to an increased transthylakoid proton gradient. Much later the conformational changes were recognized as resulting from the protonation of chlorophyll–protein complexes which permit zeaxanthin binding and the formation of trapping centers in the Photosystem-II antenna. These compete with the reaction centers for excitons dissipating excess excitation energy harmlessly in the form of heat (Krishna Niyogi 1999; Xiao-Ping Li et al. 2000). Thus, increased light scattering indicates formation of a proton gradient large enough to control Photosystem-II activity by competitive energy capture outside the reaction centers.

When far-red light which is absorbed by Photosystem I (but not, or much less so, by Photosystem II) promoted light scattering of leaves in a nitrogen atmosphere, it was concluded that this indicated the action of cyclic electron transport (Heber 1969). Inhibition of light scattering by oxygen under far-red illumination then led to the premature conclusion that cyclic electron flow cannot operate in leaves in the presence of air levels of oxygen. This view can no longer be held because electron flow through Photosystem II is so slow under far-red illumination that oxygen can drain electrons from the cyclic pathway at the acceptor side of Photosystem I. This effect does not occur when electrons lost to oxgen either during photorespiratory carbon oxidation or the water–water cycle are replaced by electrons coming from Photosystem II. This reestablishes the balanced redox situation necessary for cyclic electron transport. In fact, far-red light is, apparently by supporting coupled cyclic electron transport, sufficient to suppress the activity of Photosystem II in predarkened leaves even when 21% oxygen is present (Gabriel Cornic et al. 2000). Predarkening had the effect of deactivating light-regulated enzymes of the carbon cycle. Inhibition of Photosystem-II activity was relieved when the enzymes became active. In this situation, the acceptor side of Photosystem I is opened and electron flow to CO_2 and oxygen inhibits cyclic electron transport (Cornic et al. 2000). Thus, the concept of redox poising, which had been developed for chloroplasts by Bruce Grant and Bob Whatley (1967), is valid also for leaves.

The question still remains under which physiological conditions the specific redox situation required for the operation of cyclic electron transport is established. Obviously, photosynthesis does not normally occur in a gas atmosphere containing low oxygen. When the petiole of illuminated leaves is cut in air, water supply is suddenly interrupted. Stomata close and linear electron flow through both photosystems decreases owing to decreased CO_2 availability. Simultaneously, not only Photosystem II control increases but also the quantum efficiency of charge separation in Photosystem I relative to that in Photosystem II. This indicates a shift from linear to cyclic electron transport (Ulvi Gerst et al. 1995). Apparently, stomatal closure under constant illumination increases electron pressure on the reducing side of Photosystem I permitting electron flow into the cyclic pathway. A similar shift towards increased electron flux through Photosystem I relative to that through Photosystem II is observed when CO_2 is removed from air (Harbinson and Foyer 1991).

When control of Photosystem II as indicated by increased nonphotochemical fluorescence quenching was compared in barley leaves under strong illumination and saturating CO_2 with electron flow through Photosystems I and II, large differences in responses both to light and temperature were observed (Joanne Clarke and Giles Johnson 2001). Control of Photosystem II was relatively independent of temperature between 10 and 35 °C, while electron flow through Photosystem II declined more with decreasing temperature than electron flow through Photosystem I. The latter was similar at 21% and 2% oxygen irrespective of light intensity, whereas electron flow through Photosystem II was insensitive to a reduction in oxygen content only at low, but not at high light intensities, or when the temperature was reduced to 10 °C. Clarke and Johnson (2001) concluded that the Mehler reac-

tion is not important in maintaining a thylakoid proton gradient capable of controlling Photosystem II activity. Cyclic electron transport appeared to dominate the thylakoid energization that permitted radiationless dissipation of excess excitation energy.

Controversies regarding *in vivo* rates of electron transport supported by the water–water cycle

Several reports attribute to the water–water cycle an important role as an electron sink in illuminated leaves (Barry Osmond and Grace 1995; Klaus Biehler and Heinrich Fock 1996; Asada 1999). Such a role is not easy to reconcile with coupled vectorial proton transport during its electron transport reactions, which should be expected to control electron flow by feedback action. The notion of a sink function of the water–water cycle rests mainly on measurements of $^{18}O_2$ uptake by photosynthesizing leaves, which have as main components photorespiration, Mehler reaction and mitochondrial respiration. The latter is usually assumed to be similar in light and dark, so that corrections for mitochondrial oxidation may be made. Photorespiration is assumed to be suppressed in the presence of saturating CO_2. If not carefully verified, this can be an erroneous assumption. Increased CO_2 is known to decrease stomatal aperture. Persisting photorespiratory oxygen uptake behind partially closed stomata will be wrongly attributed to the Mehler reaction. Indeed, some published values for oxygen uptake by leaves photosynthesizing near light saturation in the presence of increased CO_2 are surprisingly, if not suspiciously, high. In a table published by Osmond and Grace (1995), oxygen uptake by leaves of *Hirschfeldia, Phaseolus*, and *Helianthus* was 26, 18, and 18 μmol m^{-2} s^{-1} respectively, i.e. close to values of carbon assimilation. Assuming that 1 mg chlorophyll corresponds to a leaf area of 25 cm^2, $^{18}O_2$ uptake is then between 230 to 160 μmol (mg Chl $\times$ h)$^{-1}$ corresponding to a flux of electrons in the water–water cycle of 920–640 μeq (mg Chl $\times$ h)$^{-1}$. These very high values are particularly remarkable as they were measured in the presence of what was thought to be saturating CO_2, i.e., the presence of a competing electron acceptor. It is known that effective electron acceptors decrease not only cyclic but also pseudocyclic electron transport (Paul Behrens et al. 1982; Furbank and Murray Badger 1983; Backhausen et al. 1994). Biehler and Fock, trying to avoid the pitfalls of high CO_2, measured oxygen reduction in a combined $^{18}O2/^{14}CO_2$ approach. They calculated photorespiratory oxygen uptake from the ^{14}C appearing in glycolate. Their values for the Mehler reaction (close to 9 μmol O_2 uptake m^{-2} s^{-1} in water-stressed leaves) are just half those measured in high CO_2 by other authors. Even they appear to be overestimates as photorespiratory oxidation of unlabeled carbohydrate was not considered. Clarke and Johnson (2001) observed no substantial decrease in electron flow through Photosystem II at 10 °C when the oxygen concentration was reduced from 21% to 2%. They concluded that the Mehler reaction is active only at temperatures above 10 °C. In another approach to assess the significance the water–water cycle in relation to that of photorespiration, Sari Ruuska et al. (2000) compared oxygen uptake of wild-type tobacco plants with that of transgenic plants which had reduced activities of ribulose bisphosphate carboxylase/oxygenase. They failed to obtain evidence for significant Mehler reaction, even when reduced photorespiration should have favored direct oxygen reduction.

Summarizing a survey of the heterogenous literature, Foyer and Noctor (2000) and Badger et al. (2000) concluded that Mehler-type oxygen uptake represents 10% of total linear electron flow in C3 plants or less. Actually, the data of Ruuska et al. (2000) suggest that only a trickle of electrons reduces oxygen directly, while the observations of Clarke and Johnson (2001) actually indicate absence of the Mehler reaction at low temperatures. When this occurs, linear electron flow supported by carbon assimilation/photorespiration must establish the redox balance necessary for cyclic electron transport (Ji-Tuo Wu et al. 1991).

Conclusions

Photosynthesis not only depends on sunlight, but is also endangered by sunlight. When light flux exceeds the capacity of the photosynthetic apparatus for photochemical energy conservation, dissipative pathways become essential for avoiding photoinactivation. The reaction center of Photosystem II is a highly effective light-driven electron pump. The electrons it takes from water must be transported to and consumed by external acceptors to avoid damaging reduction of electron carriers. In photorespiration, oxygen can serve as an effective electron sink in addition to carbon assimilation because coupled electron flow to oxygen is linked to photorespiratory ATP consumption.

This prevents proton accumulation in the thylakoids but makes it impossible for photorespiration to control the activity of Photosystem II by feedback action. Direct univalent oxygen reduction by the Mehler reaction leads to the production inside the chloroplasts of potentially dangerous oxygen species but is not accompanied by ATP consumption. Therefore, coupled noncyclic electron flow in the water–water cycle increases the transthylakoid proton gradient. Although this makes the Mehler reaction unsuitable to serve as an efficient electron sink, it gives it a role in the control of the activity of Photosystem II because thylakoid acidification is a necessary step in the formation of energy-dissipating traps in the antenna of Photosystem II which decrease exciton pressure on the reaction center.

Reports ascribing to the water–water cycle a role as an effective electron sink must be viewed with great caution because it is not clear to what extent photorespiratory oxygen uptake was clearly distinguished from Mehler-type oxygen uptake. A reaction competing not only for electrons with the Mehler reaction but also for a role in photoprotection is coupled cyclic electron flow. Both linear electron flow to oxygen and cyclic flow are activated only when partial inaccessibility of external electron acceptors increases electron pressure on the reducing side of Photosystem I. Whereas cyclic electron flow is inhibited when electron carriers between the photosystems are strongly reduced, electron flow to oxygen is not under such restriction. By mediating the oxidation of intersystem electron carriers, the Mehler reaction can make cyclic electron flow possible when no other electron acceptor is available. It acts as a poising agent for cyclic electron flow. This appears to be an important if not the major function of the water–water cycle.

Exposed to a constantly changing and occasionally hostile environment, threatened by loss of water at high temperatures or by freezing while simultaneously exposed to strong irradition, leaves need flexible mechanisms to remain functional while coping with adversity. Their situation is translated by Richard Walker, son of David Walker of chloroplast fame, into a picture also reflecting the situation of the scientist who wishes to understand their mechanisms (Figure 3). The difference between leaves and scientists is that the former dance the rope not only successfuly but also gracefully, while the scientist, wishing to understand complexity, may twist his legs, stumble and fall from the rope. However, he will correct mistakes and try again. With increasing experience, he may even learn to keep his balance and escape a continuation of the Irrungen, Wirrungen which are described above.

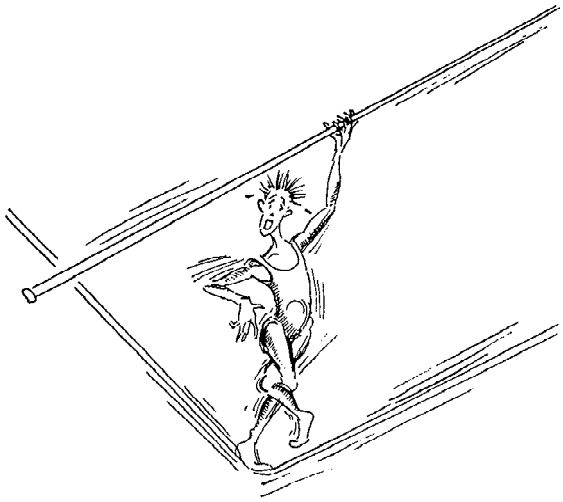

Figure 3. Dance on the rope. Courtesy of Richard Walker, son of Professor David Walker, formerly Director of the Robert Hill Institute of Sheffield University, who used to be called Alan by Robin Hill but David by all his other friends.

Figure 4. The author (Ulrich Heber) in an atypical pose. Normally, he would hold a wine glass in his hand.

Figure 4 (requested by the Editor Govindjee) shows an atypical photograph of the author of this contribution. A normal one would show him with a wine glass in his hand.

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