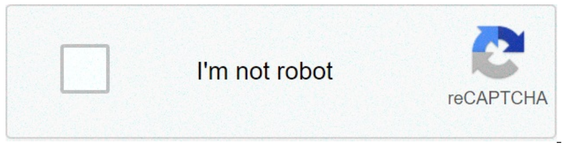


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# Light reaction of photosynthesis

Understanding:• Absorption of light by photosystems generates excited electrons• Transfer of excited electrons occurs between carriers in thylakoid membranes The light dependent reactions use photosynthetic pigments (organised into photosystems) to convert light energy into chemical energy (specifically ATP and NADPH)These reactions occur within specialised membrane discs within the chloroplast called thylakoids and involve three steps:Excitation of photosystems by light energyProduction of ATP via an electron transport chainReduction of NADP+ and the photolysis of waterStep 1: Excitation of Photosystems by Light EnergyPhotosystems are groups of photosynthetic pigments (including chlorophyll) embedded within the thylakoid membranePhotosystems are classed according to their maximal absorption wavelengths (PS I = 700 nm ; PS II = 680 nm)When a photosystem absorbs light energy, delocalised electrons within the pigments become energised or 'excited'These excited electrons are transferred to carrier molecules within the thylakoid membrane Understanding:• Excited electrons from Photosystem II are used to contribute to generate a proton gradient• ATP synthase in thylakoids generates ATP using the proton gradient Step 2: Production of ATP via an Electron Transport ChainExcited electrons from Photosystem II (P680) are transferred to an electron transport chain within the thylakoid membraneAs the electrons are passed through the chain they lose energy, which is used to translocate H+ ions into the thylakoidThis build up of protons within the thylakoid creates an electrochemical gradient, or proton motive forceThe H+ ions return to the stroma (along the proton gradient) via the transmembrane enzyme ATP synthase (chemiosmosis)ATP synthase uses the passage of H+ ions to catalyse the synthesis of ATP (from ADP + Pi)This process is called photophosphorylation – as light provided the initial energy source for ATP productionThe newly de-energised electrons from Photosystem II are taken up by Photosystem I Understanding:• Excited electrons from Photosystem I are used to reduce NADP• Photolysis of water generates electrons for use in the light dependent reactions Step 3: Reduction of NADP+ and the Photolysis of Water Excited electrons from Photosystem I may be transferred to a carrier molecule and used to reduce NADP+This forms NADPH – which is needed (in conjunction with ATP) for the light independent reactionsThe electrons lost from Photosystem I are replaced by de-energised electrons from Photosystem IIThe electrons lost from Photosystem II are replaced by electrons released from water via photolysisWater is split by light energy into H+ ions (used in chemiosmosis) and oxygen (released as a by-product) Overview of the Light Dependent ReactionsThe light dependent reactions occur within the intermembrane space of the thylakoidsChlorophyll in Photosystems I and II absorb light, which triggers the release of high energy electrons (photo activation)Excited electrons from Photosystem II are transferred between carrier molecules in an electron transport chainThe electron transport chain translocates H+ ions from the stroma to within the thylakoid, creating a proton gradientThe protons are returned to the stroma via ATP synthase, which uses their passage (via chemiosmosis) to synthesise ATPExcited electrons from Photosystem I are used to reduce NADP+ (forming NADPH)The electrons lost from Photosystem I are replaced by the de-energised electrons from Photosystem IIThe electrons lost from Photosystem II are replaced following the photolysis of waterThe products of the light dependent reactions (ATP and NADPH) are used in the light independent reactionsLight Dependent Reactions Analogy Z SchemeThe energy changes (oxidation / reduction) that occur during photosynthesis may be represented as a Z scheme:First vertical bar: Photosystem II electrons are energised by light (electrons replaced by photolysis of water molecules)Diagonal bar: Electrons lose energy as they pass through an electron transport chain (synthesising ATP)Second vertical bar: Photosystem I electrons are energised by light (electrons used to reduce NADP+) Skip Nav Destination PDF Split View Article contents Figures & tables Video Audio Supplementary Data Plant photosynthesis channels some of the most highly reactive intermediates in biology, in a way that captures a large fraction of their energy to power the plant. A viable photosynthetic apparatus must not only be efficient and robust machinery, but also well integrated into the plant's biochemical and physiological networks. This requires flexibility in its responses to the dramatically changing environmental conditions and biochemical demands. First, the output of the energy-storing light reactions must match the demands of plant metabolism. Second, regulation of the antenna must be flexible to allow responses to diverse challenges that could result in excess light capture and subsequent photoinhibition. Evidence is presented for the interplay of two types of mechanistic flexibility, one that modulates the relative sensitivity of antenna down-regulation to electron flow, and the other, which primarily modulates the output ratio of ATP/NADPH, but also contributes to down-regulation. Light is captured by a set of light-harvesting complexes (LHCs) that funnel light energy into photochemical reaction centres, photosystem (PS) I and PSII (Fig. 1) (see review by Ort and Yocum, 1996). Special subsets of chlorophyll molecules in these photosystems are excited by light energy, allowing electrons on them to be transferred through a series of redox carriers called the electron transfer chain (ETC), beginning from the oxygen evolving complex (OEC) of PSII (which oxidizes H2O and releases O2 and protons) (Diner and Babcock, 1996), through the plastoquinone (PQ) pool, the cytochrome (cyt) b6f complex (Sacksteder et al., 2000) and plastocyanin (PC), and finally through PSI (Malkin, 1996). Electrons from PSI are transferred to ferredoxin (Fd), which, in turn, reduces NADP+ to NADPH via ferredoxin:NADP+ oxidoreductase (FNR) (Knaff, 1996). This linear electron flux (LEF) to NADP+ is coupled to proton release at the OEC, and 'shuttling' of protons across the thylakoid membrane by the PQ pool and the Q-cycle at the cyt b6f complex, which establishes an electrochemical potential of protons, or proton motive force (pmf) that drives the synthesis of ATP by chemiosmotic coupling through the chloroplast ATP synthase (McCarty, 1996; Mitchell, 1966). Open in new tabDownload slidePrimary routes of proton/electron flux and mechanisms of Type I and II flexibility. (A) Energy storage begins with the absorption of light energy (lightning bolts) by light-harvesting complexes (LHC) associated with photosystem (PS) II and I, respectively. Depicted is the linear electron flux (LEF, red arrows) of electrons derived from the oxidation of H2O at the oxygen evolving complex (OEC) through PSII reducing sequentially plastoquinone (PQ) to a quinol (PQH2). Bifurcated oxidation of PQH2 occurs at the cytochrome b6f complex (b6f ) where half of the electrons are linearly transferred to the NADP+/NADPH couple via plastocyanin (PC), PSI, ferredoxin (Fd), and ferredoxin-NADP+ oxidoreductase (FNR), and the other half of the electrons will return to the PQH2 pool. Proton flux (blue arrows) originates from H2O splitting at the OEC and the cyclic reduction and oxidation of PQ/PQH2, establishing an electrochemical gradient of protons across the thylakoid membrane (pmf), comprised of pH (ΔpH) and electric field (Δψ) components. Total pmf drives ATP synthesis from ADP and Pi as protons move down their electrochemical gradient through the CF1-CFO ATP synthase. Energy dissipation by qE (purple arrow) is pH-dependent due to the pH-dependent activity of violaxanthin de-epoxidase (VDE), which sequentially reduces violaxanthin (V) to zeaxanthin (Z), and protonation of PsbS. Type II mechanisms (highlighted in red) involve variability in: (i) the response of the antenna to lumen pH, (ii) the conductive properties of the ATP synthase, and (iii) the relative partitioning of pmf into Δψ and ΔpH. Type I mechanisms (B) involve alternate routes of electron transfer at the reducing side of PSI, including the water–water cycle (WWC) and cyclic electron flow around PSI (CEF1). The WWC uses the same electron transfer pathways as normal LEF except at the reducing side of PSI it reduces O2 to which is subsequently detoxified to H2O. As depicted, four carrier pathways have been proposed for the cycling of electrons from PSI back to the PQ pool (CEF1): (1) a ferredoxin-PQ oxidoreductase (FQR), (2) a NADPH-PQ oxidoreductase (NDH), (3) oxidation of Fd by a FNR/b6f super complex, and (4) oxidation of, for example, Fd by a newly discovered haem associated with the stromal side of the b6f complex.Following the absorption of photons by chlorophyll, the transfer of excitons to reaction centre chlorophyll and the initiation of electron transfer must be well regulated to prevent 'over-excitation' of the photosystems (i.e. more excitation than can be processed by the reaction centres), which favours the formation of highly reactive species and photoinhibition of the photosynthetic machinery (Anderson and Barber, 1996; Kramer and Crofts, 1996). In general, overexcitation of PSII is prevented largely by antenna down-regulation, which dissipates excess excitation energy as heat. This involves a series of processes, which are collectively termed non-photochemical exciton quenching (NPQ) and typically measured by the quenching of chlorophyll a fluorescence (reviewed by Maxwell and Johnson, 2000). Under most physiological conditions, the major form of NPQ is termed qE, for the 'quenching' of light energy in the antenna that is dependent on the 'energization' of the thylakoid membrane (reviewed by Horton et al., 1996; Müller et al., 2001; Owens, 1996; Yamamoto and Bassi, 1996). Activation of qE involves at least two processes (Fig. 1): (i) the conversion of the xanthophyll carotenoid violaxanthin to antheraxanthin and zeaxanthin, catalysed by violaxanthin deepoxidase (VDE) (Eskling et al., 2001); and (ii) protonation of amino acid side-chains on an antenna-associated, chlorophyll binding protein, PsbS (Li et al., 2004). Both of these processes are activated by acidification of the lumen by the ΔpH component of pmf. In this analysis, the proton gradient is considered to equilibrate across the entire continuous lumenal space, i.e. it is not necessary to invoke proton domains to explain these data. Thus, pmf not only drives the synthesis of ATP, but is also a key signal for feedback regulation of the light reactions. The need for modulation of down-regulatory sensitivity (qE-modulation) qE sensitivity is defined as the responsiveness of qE to LEF, because both parameters are readily and frequently measured using chlorophyll fluorescence measurements. Alternatively, under most conditions NPQ may be substituted for qE, since qE makes up a significant fraction of NPQ. If the light reactions behaved in a static fashion, qE sensitivity would be constant, i.e. qE would be a continuous function of LEF. However, such rigidity in down-regulation of the photosynthetic apparatus would leave it prone to catastrophic failure (Asada, 1996; Heber and Walker, 1992; Kanazawa and Kramer, 2002). For example, if photosynthesis became limited by the lack of PSI electron acceptors, as might be expected under conditions of metabolic stress, LEF and its proton pumping will be attenuated. A static model would predict a decrease in qE, precisely under the conditions where photoprotection is needed most to prevent the build-up of reduced intermediates, which could lead to 'acceptor side' photoinhibition (Anderson et al., 1997). Clearly, a more flexible model must be invoked to account for the response of antenna regulation to the fluctuating physiological status of the plant (Horton, 1989; Horton et al., 1999).Indeed, such flexibility has been demonstrated in C3 plants (Avenson et al., 2004; Kanazawa et al., 2001; Kanazawa and Kramer, 2002). Rather than a continuous relationship, as the static model would predict, a series of distinct curves was observed, with qE becoming increasingly more sensitive to LEF as [CO2] was lowered (Kanazawa and Kramer, 2002). Physiologically, this is desirable because the availability of PSI electron acceptors, and thus overall LEF, is expected to decrease with decreasing CO2; to maintain reasonable levels of photoprotection, qE should become more sensitive to LEF. The need to balance ATP/NADPH ratios With LEF to NADP+, ATP synthesis and NADPH production are coupled, and within a static model the output ratio of ATP to NADPH would be fixed. However, this would work only in a system where consumption of ATP and NADPH occurs at the same fixed ratio; that is, their relative consumption by chloroplast metabolism (including fixation of carbon, nitrogen, phosphorus, and sulphur) and other plastid maintenance processes continuously matches output by energized thylakoids. Yet each individual process imposes a different demand for ATP/NADPH. Again, this leaves a static model susceptible to failure in cases where differential flux is required to respond to the changing demands on the chloroplast. If shortage of a single metabolite decreases relative metabolic flux through the pathway that fixes it, then the demand for ATP versus NADPH may change. Also, the resulting mismatch between production and consumption ratios would create 'back pressure' on the light reactions from excess product (ATP or NADPH) or lack of substrate (ADP+Pi, NADP+), sensitizing the photosynthetic apparatus to photoinhibition. Therefore, contrary to a static model, a certain measure of flexibility in the LEF output ratio is expected in order to compensate for changes in demand.The need for balancing mechanisms is further exemplified by potential mismatch between the LEF-dependent ouput and the demand of CO2 fixation. If one considers only LEF, the ATP/NADPH ratio is defined by the proton coupling stoichiometries for the ETC (H+/e−) and that for ATP synthesis (H+/ATP, termed n) (Allen, 2002; Kramer et al., 2003). There is strong evidence that H+/e− for LEF remains at 3 under physiological conditions (Sacksteder et al., 2000). New information about the structure and mechanism of the ATP synthase implies that n is likely to be 4.67 (reviewed by Allen, 2002; Kramer et al., 2003). With these stoichiometries, ATP/NADPH should be 1.3, which as discussed later, would provide insufficient ATP to support CO2 fixation in C3 plants. Without flexible responses, even larger supply–demand mismatch would occur in species using modified CO2 fixation strategies, for example, in plants with some types of C4 photosynthesis.As discussed in (Kanazawa and Kramer, 2002) and extended here, there are several models that could, together or separately, account for qE modulation (Fig. 1), some of which will also affect the output ratio of ATP/NADPH, and these were termed Type I flexibility mechanisms. Other mechanisms will have no effect on the ATP/NADPH output ratio, and these were termed Type II flexibility mechanisms. This distinction is critical for understanding the relative roles of these processes. Type I: Flexibility mechanisms affecting the ATP/NADPH ratio In accordance with the general model for electron and proton transfer, any process increasing the rate of proton translocation into the lumen will tend to activate qE by increasing pmf. If such processes supplement proton flux supplied by LEF, they will increase qE sensitivity as it has been defined here. They will also tend to increase the ATP/NADPH ratio, because the resulting increase in proton flux will drive more ATP synthesis (Fig. 2), without a net increase in the reduction of NADP+. There have been several proposals for this type of mechanism. Open in new tabDownload slideRelationships between energy-transduction and qE sensitivity. As determined by its sensitive components, PsbS and VDE, qE (and thus NPQ) will be a function of lumenal pH. As pH drops from ~6.5 to ~5.8, qE will continuously increase to saturation. If the steady-state pH of the stroma is constant, then qE will be a function of ΔpH. Therefore, factors affecting the extent to which ΔpH forms will influence qE induction. Depicted are simplified schematics of chloroplastic energy transduction with proton and electron fluxes indicated in blue and red, respectively. The table indicates relative changes in ATP output, NADPH output, pmf, and ΔpH (NC indicates no change). The pmf (and by extension ΔpH) will depend, in part, on the steady-state rate of proton accumulation. Supplementing the rate of proton accumulation through CEF1 (A) or WWC (B) will increase pmf, the rate of proton efflux and, consequentially, the rate of ATP synthesis. However, since electrons on the reducing side of PSI return to the PQ/PQH2 pool via CEF1 or to water via WWC, NADPH output does not change. Since at steady-state, the rate of efflux will equal the rate of accumulation, pmf will also depend on how conductive the membranes are to proton flux. Thus, decreasing conductivity (C) will require an increase in pmf to balance proton accumulation with efflux. Since the steady-state rate of proton flux does not change in proportion to electron flux to NADPH, the relative outputs of ATP and NADPH remain constant. Finally, if, under most conditions the ΔpH partition is approximately 50% of pmf, collapsing the electric field component through counterion movements (D) would require an increase in ΔpH to sustain steady-state proton flux. In all cases, the sensitivity of qE to LEF (qE/LEF) increases. Changes in the H+/e− ratio for LEF The Q-cycle is a catalytic mechanism which couples electron transfer through the cyt b6f complex to the translocation of protons from the stroma to the lumen (reviewed by Kurisu et al., 2003; Sacksteder et al., 2000). For each electron transferred through LEF, one proton is released into the lumen from water oxidation, and one proton is taken up during PQ reduction at the QB site of PSII and released when PQH2 is oxidized at the Qo site of the cyt b6f complex. An additional proton is translocated by the Q-cycle, making the overall H+/e− stoichiometry for LEF 3. Although several authors have proposed that the Q-cycle is facultative (reviewed by Berry and Rumberg, 1999; Cornic et al., 2000; Ivanov, 1993; Kramer and Crofts, 1993; Sacksteder et al., 2000), disengaging it (see review by Sacksteder et al., 2000) would lower the H+/e− ratio to 2, thereby lowering the pmf generated by LEF and, consequently, the ATP/NADPH output ratio and qE sensitivity.On the other hand, in vitro mechanistic studies of the cyt b6f complex indicated that the Q-cycle was very likely obligatory (Kramer and Crofts, 1993; Rich, 1988). Furthermore, comparisons of estimated fluxes of protons with LEF and with electron flux through the cyt b6f complex in vivo suggested a constant H+/e− ratio from low to saturating light intensities (Sacksteder et al., 2000). It was concluded that the Q-cycle is ptobably continuously engaged under normal, non-stressed photosynthetic conditions.These arguments are bolstered by recent structural studies of the mitochondrial cyt bc1 complexes (Zhang et al., 1998) (which are homologous to the chloroplast cyt b6f complex) and cyt b6f complexes (Kurisu et al., 2003; Stroebel et al., 2003) which have led to proposals that the 'Rieske' iron-sulphur protein 'gates' electron transfer by undergoing large-scale conformational changes during catalysis, essentially forcing the complex to shuttle protons via the Q-cycle (reviewed by Roberts et al., 2001; Zhang et al., 1998). It was concluded that there is a strong mechanistic basis for a constant H+/e− ratio at the cyt b6f complex and that differential engagement of the Q-cycle probably does not account for ATP/NADPH balancing or for variable sensitivities of down-regulatory processes. Alternate electron transfer cycles Various light-driven cyclic electron transfer pathways have been proposed to translocate protons across the thylakoid and thus drive ATP production or initiate qE in the absence of NADP+ reduction. Two of the pathways, cyclic electron flow around PSI (CEF1) and the water-water cycle (WWC), have gained support in recent years and are discussed here. Cyclic electron flux around PSI CEF1 bypasses the photosynthetic Z-scheme by involving only one of the two photosystems, PSI. Light excites PSI, resulting in reduction of its FeS centres and oxidation of its primary chlorophyll donor, P700. Just as in LEF, the oxidized \(\mathrm{P}_{700}^{+}\) is reduced by electrons from the PQ pool, via the cyt b6f complex and PC (Bendall and Manasse, 1995). Electrons on the reducing side of PSI eventually reduce PQ, completing the cycle. There is no net reduction of Fd or NADP+ but flux of electrons through the cycle will translocate protons to the lumen, resulting in pmf, which can drive ATP synthesis and activate qE.At least four pathways have been proposed to link the reducing side of PSI with the PQ pool (Fig. 1B, paths 1–4). First, a linkage may occur via a ferredoxin-PQ oxidoreductase (FQR) (path 1), a pathway that has been shown to be sensitive to antimycin A (Bendall and Manasse, 1995). Recently, Shikanai and coworkers (Munekage et al., 2002) identified an Arabidopsis mutant, pgr5, lacking antimycin A-sensitive Fd reduction of the PQ pool, preliminary evidence that the PGR5 gene product may be involved in FQR-mediated CEF1. Second, an enzyme homologous to complex I of mitochondria and bacteria (Edwards and Walker, 1983; Kubicki et al., 1996), NAD(P)H-PQ oxidoreductase (NDH) (path 2), has been suggested to be involved in CEF1, but its role in vivo remains ambiguous, as suggested by deletion studies under normal (Endo et al., 1999; Horvath et al., 2000) and stress conditions (Barth and Krause, 2002; Sazanov et al., 1998). However, evidence presented by Shikanai and coworkers (Munekage et al., 2004) suggests that paths 1 and 2 act in parallel. Third, Cramer and co-workers (Zhang et al., 2001) suggested that, based on the copurification of FNR with the b6f complex, an FNR/b6f super complex (path 3) may operate in a third type of CEF1, a pathway that has been verified in vitro (Zhang et al., 2001) but the details of which remain unresolved (Kramer, 1990). Lastly, based on recent structures of the b6f complex (Kurisu et al., 2003; Stroebel et al., 2003), an unexpected haem group in between bH and the stromal phase has been identified, hinting at a role for this extra haem in mediating electron transfer from the reducing side of PSI (path 4), although a physiological pathway has yet to be identified (Stroebel et al., 2003). While several potential PQ reduction pathways have been identified, none can be established as dominant, nor can specific roles for the individual pathways be identified. Indeed, it is possible that the PQ reductase activities serve functions other than photosynthetic (Sazanov et al., 1998). In vivo estimates of CEF1 rates Care must be taken before accepting in vitro rates as reflecting those that can occur in vivo, especially since CEF1 is known to be well-regulated and a measurable change in its relative rate may appear only under special conditions. There is strong evidence for participation of CEF1 in ATP synthesis in green algae (e.g. Chlamydomonas) and cyanobacteria (Depege et al., 2003; Finazzi et al., 2002), as well as in C4 plant bundle sheath chloroplasts (Kubicki et al., 1996). However, the situation in C3 vascular plants is clearly unresolved, with the bulk of the evidence pointing to only minor contributions of CEF1 under steady-state conditions.Several groups have estimated CEF1 rates in C3 vascular plants under steady-state conditions. These measurements are difficult because the electrons flow in a cycle, and no readily measurable, stable products are formed. One approach to indicate the activation of CEF1 is to estimate steady-state transthylakoid ΔpH using pH-indicator dyes, or the onset of qE with LEF. The argument is that at a given LEF, CEF1 will increase pmf, thereby decreasing lumen pH, and thus increasing qE (Cornic and Briantais, 1991; Heber, 2002). However, it is argued below that such effects can equally result from the engagement of Type II mechanisms, which have been shown to alter the relationship between LEF and steady-state pmf, as well as between pmf and qE.Most commonly, the relative fluxes of electrons through different parts of the electron transfer chain are compared to estimate the relative engagements of LEF and CEF1. In steady-state LEF, the rates of electron transfer through PSII should equal that through PSI (Genty et al., 1990; Klughammer and Schreiber, 1994; Kramer and Crofts, 1996; Ort and Baker, 2002) or the cyt b6f complex (Klughammer and Schreiber, 1994; Sacksteder and Kramer, 2000). The engagement of CEF1 should increase electron flux through PSI over that through PSII. Likewise, the ratio of proton translocation to LEF should increase with the engagement of CEF1 (Sacksteder et al., 2000). The fraction of overall photosynthetic energy storage attributable to PSII will change with the engagement of CEF1 (Herbert et al., 1990). Unfortunately, each of these techniques measures CEF1 only as a fraction of LEF and is only sensitive to changes in the ratio of CEF1:LEF (Bendall and Manasse, 1995; Kramer and Crofts, 1996), and low rates are not readily detected. A number of studies using such assays have found little evidence for changes in the fractional turnover of CEF1 in steady states as conditions were altered, and thus the general consensus appears to be that, in C3 vascular plants, CEF1 is either negligible or a fairly constant fraction of steady-state LEF (Genty et al., 1990; Herbert et al., 1990; Klughammer and Schreiber, 1994; Kramer and Crofts, 1996; Ort and Baker, 2002; Sacksteder and Kramer, 2000). On the other hand, in more recent papers other groups have reported substantial rates of CEF1 (15–100% of LEF) during photosynthetic induction (Joliot and Joliot, 2002) or anaerobiosis (Joet et al., 2001) or under high light, low temperature conditions (Clarke and Johnson, 2001) or drought stress (Golding and Johnson, 2003). The water-water cycle (WWC) In the WWC, electrons extracted from H2O by PSII are transferred through the ETC to PSI, where O2 acts as the terminal acceptor forming superoxide ( \(\mathrm{O}_{2}^{\cdot-}\), Fig. 1B, WWC). is dismutated to hydrogen peroxide and dioxygen, a reaction that is catalysed by superoxide dismutase (SOD), and the hydrogen peroxide is reduced to H2O by ascorbate peroxidase, thereby completing the cycle. Since O2 is reduced more slowly by Fd than FNR, the WWC has been proposed to operate to a higher extent when concentrations of NADP+ are low. Although the WWC produces no net reductant, it does generate pmf, which may serve to drive ATP synthesis or to initiate down-regulation (Asada, 1996).Because it shares nearly all reactions with LEF, the WWC is very difficult to distinguish from LEF (Heber, 2002) and thus it is not surprising that issues concerning the relative contribution of the WWC to overall electron transfer have not yet been resolved. Much of the literature (Foyer and Noctor, 2000; Heber, 2002) suggests that, in vivo, the WWC is a relatively minor contributor to LEF. An estimate based on a survey of more recent work (Badger et al., 2000) suggests that, at most, WWC operates at 10% of LEF of C3 photosynthesis, even under conditions of extreme stress. Moreover, others have observed little to no WWC under conditions that should favour NADPH accumulation, such as lowered RUBISCO levels (Ruuska et al., 2000) or low temperatures (Clarke and Johnson, 2001).By contrast, higher flux capacities for WWC have been observed in isolated chloroplasts of C3 plants (Backhausen et al., 2000; Badger et al., 2000), suggesting that conditions which favour WWC may not be simple to produce in vivo. However, there is evidence for the active engagement of the WWC in conjunction with CEF1 in rice leaves, during photosynthetic induction (Makino et al., 2002). It was suggested that the supplemental proton flux was required to generate additional ATP for the initiation of the Calvin–Benson cycle from a dark-adapted state. Furthermore, suppressed expression of thylakoid-associated Cu/Zn-SOD in Arabidopsis suppressed photosynthetic activity and growth, which is consistent with the need for detoxification of generated by photosynthesis (Rizhsky et al., 2003). While this observation supports the presence of the WWC in vivo, it does not necessarily support a role for the WWC supplementing pmf during steady-state photosynthesis. Type II: Flexibility without altering ATP/NADPH output ratio While Type I mechanisms could be modulators of qE, effective engagement would require them to comprise a large fraction of total electron flux, leading to mismatch in supply and demand for ATP and NADPH. By contrast, Type II mechanisms, as depicted in Fig. 1, allow the regulation of qE sensitivity without perturbing the ATP/NADPH ratio. Alteration of qE response to lumen pH One way to alter qE sensitivity would be to change the response capacity of qE to lumen pH. Over developmental time-scales, the differential accumulation of antenna and xanthophyll components has been shown to alter qE sensitivity (Demmig-Adams and Adams III, 1996). Hypothetically, more dynamic changes in qE sensitivity could occur though alterations in the pH response of the molecular components of qE. For example, covalent modification of VDE or PsbS could shift either pH dependence of VDE or pKas of protonatable groups on PsbS, respectively. Alternatively, components in the membrane could be modified, affecting the propensity of LHCs to aggregate or associate with the xanthophyll components, processes which have been linked to exciton dissipation by qE (reviewed by Horton et al., 1996). The predicted outcome, in all cases, would be a range of sensitivities of qE to ΔpH. However, in tobacco, a constant relationship was observed between qE and estimates of light-driven pmf changes, over conditions where qE sensitivity was substantially altered by changing CO2 levels (Kanazawa and Kramer, 2002), while under extreme acceptor limiting conditions qE was a continuous function of ΔpH (Avenson et al., 2004). These observations suggest that a constant relationship exists between lumen pH and qE and that modifications in antenna response do not account for short-term changes in qE sensitivity, under these conditions. The importance of pmf composition for modulating qE response Since qE is triggered by the ΔpH, but not the Δψ (electric field) component of thylakoid pmf, one way to change qE sensitivity would be to alter the manner in which pmf is stored. The chemisomotic mechanism, first described by Peter Mitchell, states that pmf is thermodynamically composed of the sum of the ΔpH and Δψ potentials (Mitchell, 1966). Many of the earlier characterizations of pmf were performed by monitoring ATP synthesis in intact thylakoids as a function of ΔpH produced by pH jump and/or by measuring ΔpH-dependent uptake of radiolabelled or fluorescent amines (Davenport and McCarty, 1986; Junesch and Gräber, 1985; Schuldiner et al., 1972). While useful for defining the thresholds of activation and other energetic parameters, these studies ignored and actively suppressed the Δψ component of pmf through the use of uncouplers and/or relatively high concentrations of counterions. Direct measurements of Δψ, made using salt-filled microelectrodes (Vredenberg and Tonk, 1975), helped to popularize the notion that it contributed little or negligibly to steady-state pmf, despite changes observed in vivo in the electrochromic shift (ECS) (Finazzi and Rappaport, 1998; Joliot and Joliot, 1989; Sacksteder et al., 2000) or measurement of Δψ-dependent ATP synthesis (Hangarter and Good, 1982; Junesch and Gräber, 1991), which suggested the contrary. Lately, it has been argued that under permissive conditions, it is unlikely that ΔpH solely comprises pmf (reviewed in Cruz et al., 2001; Kramer et al., 1999). In essence, a ΔpH requirement of 2–3 to activate ATP synthesis (Kramer and Crofts, 1989) yields a lumen pH that is inconsistent with the pH sensitivities of PSII and PC and with the pH-dependent rates of VDE and cyt b6f, observed in vivo.In much of the authors' recent work, the ECS has been exploited as an endogenous probe for changes in transthylakoid Δψ during light-to-dark transitions (Avenson et al., 2004; Cruz et al., 2001; Kanazawa and Kramer, 2002; Sacksteder et al., 2000). The relevance of the ECS to pmf was first reported by Junge and Witt (1968). ECS refers to a Δψ-induced 'shift' in the absorption spectrum of pigments (i.e. chlorophyll and carotenoids) embedded in the thylakoid membrane. The peak of the difference spectrum occurs at 515–520 nm and has been shown to be a linear indicator of the strength of the transthylakoid Δψ (Witt and Zickler, 1973). One particular advantage of using the ECS is that it is non-invasive, allowing in vivo measurements on intact leaves. Generally, two techniques were employed when using ECS to probe pmf, both of which are variations of Dark Interval Relaxation Kinetic (DIRK) analysis (Sacksteder and Kramer, 2000). The DIRK technique uses brief (

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