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Alternative electron transport pathways in photosynthesis: a confluence of regulation

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Photosynthetic reactions proceed along a linear electron transfer chain linking water oxidation at photosystem II (PSII) to CO_2 reduction in the Calvin–Benson–Bassham cycle. Alternative pathways poise the electron carriers along the chain in response to changing light, temperature and CO_2 inputs, under prolonged hydration stress and during development. We describe recent literature that reports the physiological functions of new molecular players. Such highlights include the flavodiiron proteins and their important role in the green lineage. The parsing of the proton-motive force between ΔpH and Δψ, regulated in many different ways (cyclic electron flow, ATPsynthase conductivity, ion/H^+ transporters), is comprehensively reported. This review focuses on an integrated description of alternative electron transfer pathways and how they contribute to photosynthetic productivity in the context of plant fitness to the environment.

Introduction

The photosynthesis power plant converts the radiant energy of light into electrochemical energy, ultimately used to reduce atmospheric CO_2 into C_3 intermediates, then C_6compounds, serving as the building blocks for all organic molecules found in plants. These energy rich stocks are much more easily broken down for food or burned off as thermal energy than they are synthesized. We know a lot about the molecular processes of photosynthesis primary energy conversion, involving a series of transmembrane proteinsencompassing light harvesting complexes, photosystems, cytochrome b_6f complex and adenosine triphosphate (ATP) synthase. In the last 10–20 years, with the flourishing of molecular genetics, a few additional players have come into play that intriguingly are as important as the primary reactions, because they allow plants to endure fluctuating conditions in the wild. These are often referred to as 'alternative electron transport pathways', and play an indispensable regulatory role for photosynthesis.

Photosynthetic organisms use alternative electron transport to respond rapidly to changes to their environment. The general consensus is that these pathways balance photosynthetic electron transfer so that light energy, converted in the form of ATP and nicotinamide adenine dinucleotide (phosphate) (NADPH), is optimally used for CO_2 fixation or safely dissipated as heat. If, for instance, the electron carriers become over-reduced, O_2 can replace CO_2 as a terminal electron acceptor, creating reactive oxygen species (ROS). Over longer time frames, alternative pathways are a resource to acclimate to a variety of physiological conditions while their activity also limits the potential of photosynthetic yields [1]. They can also play moonlighting roles in non-green tissues, catalyzing essential redox reactions [2]. To be

comprehensive, we chose to provide information on the whole spectrum of pathways that have been identified, studied and recently reported in the literature but we focus here only on the contribution of alternative pathways to the regulation of the light photosynthetic reactions. Figure 1 provides a 'beginners guide' to these pathways with the most salient points about the proteins involved and how they are currently recognized to function. Our purpose is to show how these pathways interconnect and we describe this as a bioprocess-engineering problem in Figure 2. Recent improvements in whole systems techniques are starting to help explain the redundancy and relatedness of these pathways (see Box 1).

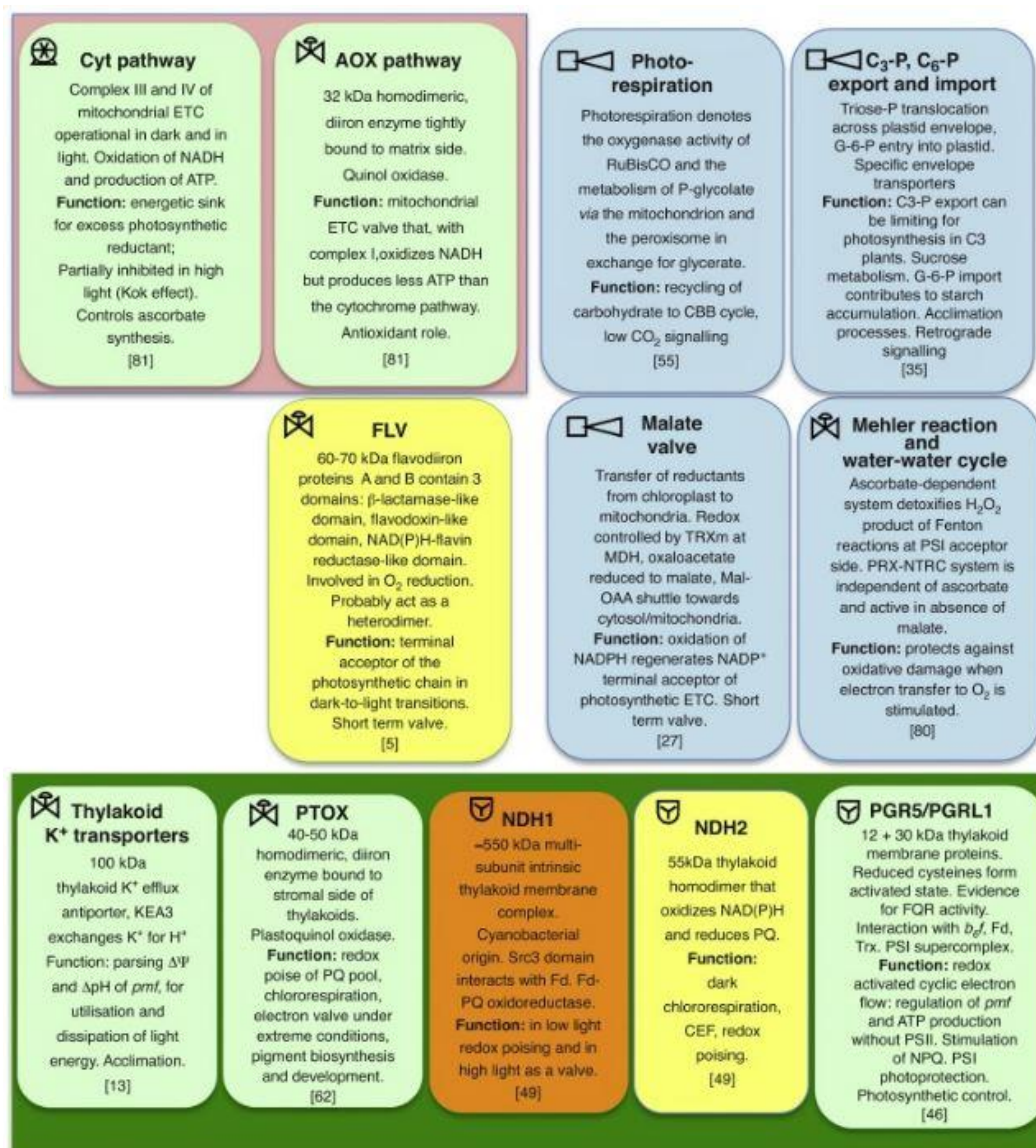
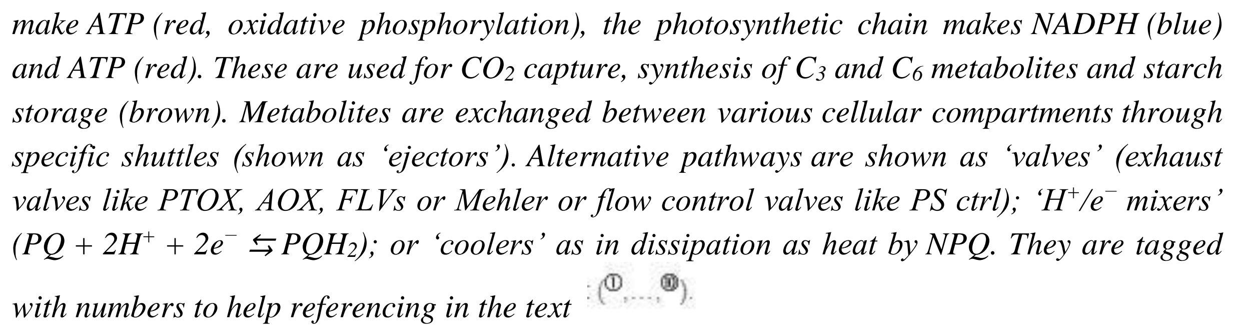


Figure 1. *A set of I.D. cards for alternative electron transport pathways organized by their localization (pink background are mitochondrial and dark green in chloroplast thylakoids) describes the structure and functions of a group of the proteins and alternative*

pathways reported in this review and shown schematically in Figure 2. We invite the reader to explore the review(s) suggested for each of these pathways for a more complete overview [5,13,27,35,46,49,55,62,80,81]. Pale green cards are proteins that are conserved in the green lineage; the yellow cards have not been found in angiosperm chloroplasts while the orange card is absent from all algae and the gymnosperms, Gnetales and Pinaceae, sequencedto date. The blue cards show pathways.

Figure 2. *Process flow diagram of the biochemical reactions of photosynthetic eukaryotes. The simplified bioenergetics reactions of respiration are shown in the mitochondrion (pink shading) and the photosynthetic reactions along the thylakoid membrane (green strip) and chloroplast (green shading). Whereas the respiratory chain oxidizes NADH (blue) to*



make ATP (red, oxidative phosphorylation), the photosynthetic chain makes NADPH (blue) and ATP (red). These are used for CO_2 capture, synthesis of C_3 and C_6 metabolites and starch storage (brown). Metabolites are exchanged between various cellular compartments through specific shuttles (shown as 'ejectors'). Alternative pathways are shown as 'valves' (exhaust valves like PTOX, AOX, FLVs or Mehler or flow control valves like PS ctrl); 'H^+/e^- mixers' ($PQ + 2H^+ + 2e^- \leftrightharpoons PQH_2$); or 'coolers' as in dissipation as heat by NPQ. They are tagged with numbers to help referencing in the text :(①,…,⑩).

Box 1

Techniques that have allowed the understanding of alternative electron transfer pathways to move forward in recent years.

- ✧ **Large scale mutant collections and homologous recombination techniques in new model species**
- ✧ **Open access genome sequencing projects**
- ✧ **Open access bioinformatics tools**
- ✧ **Metabolomics and metabolite analysis**
- ✧ **Large scale RNA sequencing techniques**
- ✧ **Chlorophyll fluorescence screening techniques**
- ✧ **Improved tools for monitoring gas exchange**

Part I. Redox poising of the photosystem I (PSI) acceptor side is important in fluctuating light and when CO_2 availability changes

Cyclic electron flow around PSI, mediated by the PGR5-PGRL1 pathway (see in Figure 2), builds up a proton-motive force across the thylakoid membrane and produces ATP to meet metabolic demands of the chloroplast [3••,4,5]. It relaxes the reducing pressure at the PSI acceptor side by: (i) providing the Calvin–Benson–Bassham (CBB) cycle with ATP to reoxidize NADPH, (ii) limiting electron transfer upstream of PSI. An increased ΔpH component of the proton motive force (*pmf*), upregulates non-photochemical quenching qE and limits the excitation pressure from photosystem II (PSII). ΔpH also downregulates linear electron flow at cyt b_6f thus the term photosynthetic control (photosynthetic control (PS ctrl) in Figure 2) is used for this valve acting on both electron and proton flow. ATPsynthase conductivity, which is redox controlled and responds to ADP availability and *pmf*, is also intrinsically linked to this process [2,6,7].

Arabidopsis *pgr5* mutants show that PSI is particularly vulnerable to fluctuating light, rather than high light [8••], due to an imbalanced electron transport chain because of a lack of *pmf*regulation. In Chlamydomonas, when electrons are in excess due to limiting ATP, O_2photoreduction pathways can take up this load [4,9]. In Arabidopsis, decreasing PSII [10] or introducing a PSI acceptor side sink for electrons [11] can alleviate these effects. In Chlamydomonas [4,9] as well as in Arabidopsis [12] there is evidence that

the cytochromerespiratory pathway (cyt bc_1, cyt *c* and cyt oxidase) rather than alternative pathway(alternative oxidase—AOX) can act as a sink for excess electrons.
The *pmf* is partitioned between ΔpH and Δψ. A number of transporters that have specificity for ions, Pi and ADP/ATP have been identified in thylakoid membranes [13]. We concentrate here on the KEA3 thylakoid efflux antiporter because of its apparent specific role in evacuating protons from the lumen (decreasing ΔpH) and importing K^+ into the lumen (increasing Δψ) until a steady state is reached [14,15]. The physiological significance of KEA3 has been identified in light transitions to balance ΔpH and Δψ, an effect that would be attenuated under constant light conditions through downregulation of KEA3 via its luminal C-terminal [16,17]. The absence of KEA3 has consequences for the efficiency of photosynthetic electron transport [18], suggesting that partitioning of *pmf* into ΔpH and Δψ components is actively regulated and required for efficient photosynthesis.
Flavodiiron (FLV) proteins A and B oxidize NADPH at the expense of O_2 and serve as terminal electron acceptors at the onset of light in green algae, bryophytes and gymnosperms [9,19–21]. The characterization of cyanobacterial FLV1/3 proteins as electron acceptors from PSI [22] led to their identification in eukaryotes by sequence homology. Analysis of *flva* and *flvb* knock-out mutants in *Physcomitrella* patens and *Marchantia polymorpha*, shows that FLV activity contributes to the long-observed transient kinetics of chlorophyll fluorescence, also called Kautsky effect [23], in basal land plants and green algae at the onset of illumination [19,21]. Furthermore FLVs protect PSI integrity in fluctuating light, under these conditions both *flva* and *flvb* mutants show severe growth phenotypes [19]. An elegant approach was also used to show that FLVs could function in angiosperms in rapid dark-to-light transitions: the transformation of At*pgr5* plants with Physcomitrella FLVs protected PSI [11]. This study clearly showed that FLVs could act as a valve for electrons at the acceptor side of PSI, stimulating *pmf* and reinforced the idea that PSI photoinhibition occurs as a consequence of acceptor side limitation [24]. Interestingly however, the ΔpH-dependent component of NPQ, qE, could only be partially restored in the *pgr5* knock-out FLV expressing transgenic lines, reportedly because the parsing of the *pmf*between ΔΨ and ΔpH was weighted toward ΔΨ. As already suggested [25] the down-regulation of PSII activity via qE is not the major effector in PSI photoprotection. However, the complementarity of CEF and qE to acceptor side poising in algae may be crucial [26]. The fact that the FLV proteins are a dispensable valve in angiosperms, begs the question of why algae, bryophytes and gymnosperms have retained it.
Malate plays a central role in chloroplast metabolism in the light. It is required for C4 photosynthesis as the C4 intermediate that delivers CO_2 to ribulose-1,5-bisphosphate carboxylase oxygenase (RuBisCO) via the activity of NADP-malic enzyme in bundle sheath cells. The 'malate valve' , serves a role in C3 photosynthesis whereby chloroplast malate dehydrogenase (NADP-MDH) is activated by reduced thioredoxins and inactivated by $NADP^+$. The translocation of malate toward mitochondria via the oxaloacetate/malate transporter (AtpOMT1 in Arabidopsis) provides a short term regulatory response when NADPH production exceeds its consumption in the chloroplast [27]. While the Arabidopsis *mdh* mutant

does not show a growth phenotype [28], the *Atpomt1* plastid envelope transporter mutant suffers a short-term photoinhibition phenotype when transferred from low light to high light, conditions where the malate valve would be the most important [29]. It is interesting to note that AtpOMT1 also transports 2-oxaloglutarate, a trafficking linked to nitrogen metabolism and photorespiration. A redox activated malate dehydrogenase (MDH) is found in Chlamydomonas and lower plants [30,31] but the assessment of its contribution to the strong interaction between photosynthesis and respiration [4,32] is awaiting specific mutants.

Part II. Alternative pathways act as constitutive valves in low CO_2, high light, cold, salt and drought stress

Triose-phosphates synthesized from CO_2 in the CBB cycle are directed toward sucrose for export and/or kept in the chloroplast for starch synthesis at a rate that depends on RuBisCOrates and RuBP turnover [33]. At variance with the malate valve that only acts on $NADP^+$/NADPH levels, triose-phosphate translocation (TPT) also balances Pi, ADP and ATP . ATPsynthase conductivity and *pmf* at steady state depends on the availability of these substrates, therefore Triose-P shuttling has consequences on electron and proton transfer [34]. Chloroplast envelopes have large families of TPTs and a number of translocators and mutants have been characterized [35]. In Arabidopsis *tpt* mutants, an increase in transient pools of starch is witnessed by a futile cycle of starch synthesis and degradation. Mutants can use this transient starch pool as a buffer, but it becomes saturated in high light [36,37]. The rice *Ostpt1* mutant is unable to sustain such a compensatory pathway and has a stunted growth phenotype at all light regimes [38]. The balance of phosphorylated sugars inside and outside the chloroplast has a regulatory role in acclimation [39]: arresting either chloroplast export of triose-P in *tpt* mutants or translocation of glucose-6-phosphate (via GPT2) into the chloroplast in *gpt2* mutants and are both associated with a defective acclimation response. This is observed at the transcriptional and metabolic level resulting in an inability to upregulate photosynthetic electron transfer when transferred to high light [36,37,39].

NADPH dehydrogenase (NDH1) is a multi-subunit complex resembling the mitochondrialcomplex I. Compelling evidence shows that despite its name and its evolutionary origin it oxidizes ferredoxin rather than NADPH and uses plastoquinone (PQ) as an electron acceptor [40]. There is evidence that its role would be rather in cyclic electron flow and steady state redox poising in low light in C3 species [41] and its high accumulation and complementarity to proton gradient regulation 5/like 1 (PGR5/PGRL1) is supported in C4 species [42–45]. NDH1 pathway would be minor under high light conditions in C3 plantswhere the PGR5 pathway would be dominant [46]. The type-2 NDH2, a true NADPH dehydrogenase, accumulates in thylakoids of green algae and some gymnosperms in the absence of the type-I NDH. It would appear to have the same function in algae as in C3 plants in redox poising but also as a valve under anaerobic conditions [47–49]. Under conditions where sustained PSI acceptor-side limitation occurs, increasing evidence suggests that the *pmf* mostly induced by PGR5-CEF and parsed between $\Delta\Psi$ and ΔpH by KEA3, would control PSII photoinhibition [4,10,50–52].

Carbon concentrating mechanisms (CCM) are present in both C4 plants as well as algae via different mechanisms that require extra ATP per CO_2 fixed. In Chlamydomonas a clear correlation is found between assimilation of air levels of CO_2 and cyclic electron flow [53]. Less defined grana stacks are observed as constitutive traits both in Chlamydomonas and in bundle sheath cells of some C4 plants favoring increased rates of cyclic electron flow [54]. Interestingly, bundle sheath cells accumulate high levels of both NDH and PGR5 proteins [42–45].

In the absence of CCM or C4 structure the oxygenase activity of RuBisCO becomes non-negligible. Photorespiration involves metabolic reactions in the chloroplast, peroxisomeand mitochondrion that represent an integrated network involving carbon and nitrogen metabolism to maintain the CBB cycle active [55]. It can be seen as a photosynthetic valve essential under drought stress [27] that would act at the metabolic level [56] and transcriptional level, with recent data suggesting metabolites produced by photorespiration act in a signaling pathway regulating stomatal opening [57]. At the metabolic level, photorespiration is highly connected to other alternative pathways: (i) under high-O_2 and low-CO_2 (photorespiratory conditions) mitochondrial activity shows recruitment of the alternative pathway (AOX) rather than the cytochrome pathway [58,59]; (ii) the same signals trigger both photorespiration and the malate valve in continuous high light. Arabidopsis *mdh* mutants are not light sensitive and this was explained by an upregulation of photorespiration and ROS detoxification [28]; the ATP levels in *mdh* mutants would be conserved via upregulation of nitrogen metabolism and glycolysis [60]; (iii) under the same conditions when Arabidopsis plants are subjected to low light an interplay occured between photorespiration, Mehler reaction and the malate valve; while under high light, CEF contribution makes up the ATP demand [61].

The chloroplast counterpart of AOX is plastid terminal oxidase (PTOX) , bound to the thylakoid membrane, oxidizing PQH_2 and reducing O_2 to H_2O [62]. In the dark activity of type-2 NDH to reduce plastoquinone at the expense of NADPH poises the pool by a mechanism known as chlororespiration [62]. In the light, PTOX would serve as a valve for oxidizing the PQ pool, maintaining PSII active and potentially contributing to *pmf* by H^+release in the lumen from water splitting [63,64]. To accept electrons from PSII without overproduction of ROS, PTOX would have to be localized within PSII microdomains accessible to quinone diffusion, that is, grana stacks or margins [65,66]. Although, PTOX seemed to be addressed to the lamellae in non-stressed Arabidopsis plants [67], recent studies suggest a control by stromal pH that may allow PTOX conditional access to plastoquinols [68]. Lodgepole pine uses PTOX and FLV proteins as the major O_2photoreduction pathways during acclimation to cold to generate ΔpH for NPQ [69]. PTOX activity can enhance cyclic electron flow in PTOX overexpressor mutants by oxidizing PQH_2thereby providing PQ as an electron acceptor for ferredoxin [65,70]. In cold stressed tropical plants where PSII is photoinhibited, an upregulation of PTOX and PGR5 is observed, providing some physiological relevance to the interplay between these pathways [71].

Conclusions

The study of photosynthesis identified pathways that were auxiliary to linear electron flow. However, the molecular identification of these pathways came from diverse methods and sometimes occurred in an unexpected manner: ferredoxin-mediated cyclic photophosphorylation (CEF) was identified in isolated spinach thylakoids [72], NDH1 was identified from sequencing of the Tobacco chloroplast genome [73], *pgr5* from a chlorophyll fluorescence screen in Arabidopsis [74], PTOX was found in *ghost* mutants of tomato [75,76]. Whole genome sequencing of members of the green lineage outside the angiosperms identified the FLV proteins by homology with cyanobacterial FLVs [77]. Similar genetic lesions can cause very different phenotypic traits in different organisms, for example, an absence of PTOX was found to result in colorless tomatoes or variegated Arabidopsis leaves [76,78,79], a finding that expanded the alternative pathways reach to developmental processes. The diversity of these observations has enriched our knowledge on the ins and outs of the alternative pathways in a large panel of photosynthetic organisms. Nonetheless, it should not distract us from the similarities that have been shown to exist at the molecular level. The real challenge now is to devise a combination of quantitative and physiological approaches to place each of these pathways back into the integrated network of plant metabolism and to decipher their roles in response to environmental cues.

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