The most important reaction for most life forms on earth is oxygenc photosynthesis. In this process, light energy drives the oxidation of water and the transport of extracted electrons along an electron transport chain embedded in the thylakoid membranes for the generation of NADPH and ATP. The accumulation of reactive oxygen species occurring particularly under high light intensities is an inherent side effect of the light reactions and leads to oxidative damage especially of the D1 core subunit of photosystem II, but also of the PsbH and D2 core subunits.1,2 A total collapse of the photosynthetic machinery as a consequence of PSII damage is prevented by the light-dependent turnover of the D1 protein in a process referred to as the PSII repair cycle. As excellent reviews on the PSII repair cycle have been published previously,3-9 we aim here to provide a focused review of the topic including the most recent developments.

Disassembly of PSII mega- and supercomplexes and migration of PSII monomers into stroma lamellae

Most of PSII is located to stacked grana regions, where it is organized in supercomplexes consisting of dimeric PSII cores associated with LHCII antennae10 (Fig. 1). Two PSII supercomplexes may laterally assemble into a so-called megacomplex.11,12 PSII supercomplexes may also form semi-crystalline arrays, an arrangement that appears to be supported by interactions between the flat stromal surfaces of PSII dimers, LHCII trimers, and minor LHCs and their counterparts in supercomplexes located in the opposite membrane of a granal stack.13 Because bulky proteases and ribosomes cannot access the ~3.2 nm stromal gap between stacked membranes, the repair of photodamaged PSII needs to take place in stroma exposed lamellae. To provide access for the repair machinery to photodamaged D1 buried in PSII supercomplexes, megacomplexes or semicrystalline arrays, the latter first need to be disassembled, the thylakoid membranes unfolded, and released PSII monomers transported to stroma lamellae.14 To run efficiently, these processes require the light-dependent specific phosphorylation of PSII core subunits D1, D2, CP43 and PsbH.15-19 Phosphorylation of these PSII core subunits takes place at their N-terminal threonine residues and is catalyzed mainly by the state transition kinase 8 (STN8).20,21 The efficient disassembly of PSII megacomplexes also requires an Lhcb-binding protein that is localized to the stroma and to thylakoid membranes and termed thylakoid formation 1 (THF1) in Arabidopsis,22,23 non-yellow coloring 4 (NYC4) in rice,24 and Psb29 in cyanobacteria.25 As phosphorylated D1 is more resistant to degradation than its non-phosphorylated form,26 efficient degradation of photodamaged D1 requires its dephosphorylation.27,28 D1 dephosphorylation is likely driven by more than one phosphatase.29 One of them is the stroma-exposed, membrane-extrinsic PP2C-like PSII core phosphatase (PBCP).29,30 Another is a not yet cloned, membrane intrinsic PP2A-like phosphatase, which is negatively regulated from the luminal side by the cyclophilin TLP40/CYP38.31,32 Accordingly, PSII core subunits and LHCII are less phosphorylated in cp38 mutants.33

After PSII core monomers containing photodamaged D1 have migrated laterally from grana stacks into stroma lamellae, CP43 as well as the oxygen evolving complex (OEC) are released to generate a CP43-free PSII monomer at least composed of the D1/D2/CP47 proteins, the oxygen evolving complex (OEC) are released to generate a CP43-free PSII monomer at least composed of the D1/D2/CP47 proteins, the cytochrome b559 subunits PsbE and PsbF, and the PsbI protein34 (Fig. 1). The low quantum yield of PSII 1 (LQY1) and the hypersensitive to high light 1 (HHL1) proteins have been proposed to cooperate in facilitating CP43 release from photodamaged PSII core monomers.35 Both proteins have been claimed to exist only in land plants. They are intrinsic membrane proteins that are enriched...
in stroma lamellae and accumulate in high light. They interact with each other and with CP43 and CP47 in PSII monomers containing and lacking CP43. The PSB28 protein is extrinsically attached to thylakoid membranes and interacts mainly with CP43-free PSII complexes and to a smaller degree with PSII monomers and non-assembled CP47. Analyses of cyanobacterial psb28 mutants have led to differing conclusions: while Dobakova et al. (2009) assigned a role of PSB28 in linking chlorophyll biogenesis with its incorporation into CP47 and PsaA/PsaB, Sakata et al. (2013) assigned it a role in stabilizing CP43-free PSII monomers during assembly, which is important at elevated temperatures for the efficient repair of photodamaged PSII.

Degradation of photodamaged D1

Two types of chloroplast proteases act cooperatively in the degradation of the D1 protein from CP43-free PSII monomers lacking the OEC (Fig. 1). The first type of protease is the membrane-anchored heterohexameric FtsH metalloprotease that is composed of the 4 isomers FtsH1, FtsH2, FtsH5 and FtsH8 in Arabidopsis; and of the 2 isomers FtsH1 and FtsH2 in Chlamydomonas. As an exoprotease, FtsH binds to the N-terminal end of D1 at the stromal side and drives D1 degradation in an ATP-dependent manner. It was proposed that the access of FtsH to photodamaged D1 is constrained if D1s N-terminal threonine is phosphorylated, therefore explaining why efficient D1 degradation requires its dephosphorylation. The second type of proteases belong to the Deg family of proteases, which are ATP-independent serine proteases that are inactive as monomers and may assemble into proteolytically active oligomers. In Arabidopsis 3 chloroplastic homologs of the Deg family (Deg1, Deg5 and Deg8) are localized in the thylakoid lumen and cleave damaged D1 within different loops connecting the transmembrane helices. Yet another Deg protease referred to as Deg7 cleaves D1 within a stromal loop. The generation of additional N- and C-terminal ends by the action of Deg endoproteases is thought to enhance D1 degradation via FtsH. D1 degradation is also assisted by the thylakoid lumen protein TLP18.3, presumably by its phosphatase activity and apparent ability to interact with lumenal Deg1. Moreover, TLP18.3 was reported to be important for the efficient dimerization of repaired PSII monomers.

De novo synthesis and assembly of D1 into PSII cores

After degradation of the damaged D1 protein, a new copy of D1 is inserted into CP43-free PSII monomers by de novo synthesis (Fig. 1). To this end, the signal recognition particle 54 (cpSRP54) targets the ribosome nascent D1 chain to cpFTSY at stroma-exposed thylakoid membranes where the protein is cotranslationally inserted into CP43-free PSII via the cpSECY translocase. cpSECY interacts with the conserved integral membrane protein ALB3 which in turn is required for the membrane insertion and assembly of D1 into PSII reaction centers. Translation of the psbA mRNA is attenuated by the PDI6 protein disulphide isomerase, thus leading to a slowing down of the repair process.

Several factors are involved in the proper membrane insertion/folding of the newly synthesized D1 protein during PSII de novo synthesis and most likely also during repair. These include the Arabidopsis low PSII accumulation 1 protein.
(LPA1) and its Chlamydomonas ortholog repair-aberrant 27 (REP27), which are thylakoid membrane integral proteins harboring 2 transmembrane helices and 2 tetracopeptide repeat (TPR) domains.\textsuperscript{59-61} \textit{Ipa1} and \textit{rep27} mutants synthesize D1 at much lower levels than wild type and accumulate low levels of D1 and other PSII core subunits, while subunits of other thylakoid membrane complexes are unaffected.\textsuperscript{59,60,62} As judged from split-ubiquitin assays, LPA1 interacts specifically with D1 but not with D2 or ALB3.\textsuperscript{59} LPA1 has been proposed to act as a membrane chaperone that assists the correct assembly of the D1 protein into PSII during its translation.\textsuperscript{59,60} Similarly, photosynthesis affected mutant 68 (PAM68) is an integral thylakoid membrane protein housing 2 transmembrane domains. Arabidopsis \textit{pam68} mutants, like \textit{ipa1} mutants, show lower D1 synthesis rates (albeit not as low as \textit{ipa1} mutants) and accumulate PSII core proteins to 10–30% of wild-type levels.\textsuperscript{62} Unlike \textit{ipa1} mutants, \textit{pam68} mutants are impaired in the conversion of the D1 precursor into mature D1 as well as in the accumulation of larger PSII assembly states. In split-ubiquitin assays PAM68 was shown to interact with D1, D2, CP43, CP47, PsbH and PsbI as well as with the PSII assembly factors HCF136, LPA1, LPA2 and ALB3.\textsuperscript{62} Tellurite resistance C (TERC) is another integral thylakoid membrane protein harboring 8 putative transmembrane domains.\textsuperscript{63} Arabidopsis \textit{terc} mutants are unable to accumulate newly synthesized thylakoid membrane proteins, but do accumulate some Lhcbb.\textsuperscript{63,64} TERC was found to interact stably with ALB3 and at most transiently with LPA1, LPA2, and PAM68, leading to the proposal that TERC acts cooperatively with ALB3 during the co-translational insertion of thylakoid membrane proteins.\textsuperscript{64} Furthermore, the plastid-encoded, stroma lamellae localized and membrane intrinsic PsbN protein was shown to be required for the assembly of the reaction center complex during PSII de novo biogenesis, e.g. by facilitating the proper folding of the D1 and/or D2 proteins. PsbN was also shown to be required during the PSII repair cycle.\textsuperscript{65} Lumenal TLP40/CYP38 was found to interact not only with the PP2A-like phosphatase but also with PSII monomers, mostly in non-pressed regions.\textsuperscript{33,66} Arabidopsis \textit{cyp38} mutants accumulate less PSII, albeit synthesis rates of PSII subunits are not altered, but their assembly into dimers and supercomplexes is impaired and mutant plants are highly susceptible to photodamage. CYP38 has been proposed to be involved in the correct assembly of D1 (and CP43) during PSII de novo synthesis and repair. In the absence of CYP38 PSII appears to be assembled with a defect in the donor side therefore rendering it more susceptible to photodamage.\textsuperscript{33,67} Finally, high chlorophyll fluorescence 243 (HCF243) is a thylakoid membrane intrinsic protein present only in higher plants that directly interacts with D1. Arabidopsis \textit{hcf243} mutants accumulate less PSII subunits and less PSII monomers, dimers and supercomplexes. They overaccumulate the D1 precursor and exhibit increased D1 degradation rates.\textsuperscript{68} The stromal heat shock protein 70 (HSP70B) has been proposed to stabilize the PSII core complex during removal and replacement of photodamaged D1.\textsuperscript{69,70} However, HSP70B may affect PSII repair only indirectly by its function – together with co-chaperones CDJ2 and CGE1 – in controlling the assembly state of oligomeric rings and rods formed by the vesicle inducing protein in plastids 1 (VIPP1).\textsuperscript{72,73} In analogy with so-called eisosomes, VIPP1 has been proposed to organize thylakoidal lipid microdomains.\textsuperscript{74,75} Eisosomes are furrow-like invaginations of the plasma membrane enriched in sterols that in yeast are formed by the Pii1 and Lsp1 proteins.\textsuperscript{76} Both proteins form large rods (resembling VIPP1 rods) that are able to bind and tubulate liposomes \textit{in vitro}. The specific lipid environment created in microdomains formed by eisosomes attracts specific integral membrane proteins – e.g., the arginine transporter Can1 – whose efficient function depends on the specific lipid environment present in the microdomain.\textsuperscript{77} The enrichment of specific lipids in a membrane microdomain putatively formed by VIPP1 might facilitate their incorporation as structural lipids during PSII biogenesis and repair (Fig. 1). Moreover, translocases and integrases like ALB3, cpSECY and cpTAT may be enriched and their effective function dependent on the lipid environment in such microdomains. In support for such a scenario, VIPP1 and its bacterial ancestor PspA improved bacterial TAT- and Sec-mediated protein secretion.\textsuperscript{79,80} The activity of the bacterial Sec translocase was shown to strictly require the presence of anionic phospholipids and is stimulated by non-bilayer lipids.\textsuperscript{81} Moreover, the addition of recombinant VIPP1 to thylakoid membranes was shown to increase TAT-mediated protein import in vitro, although VIPP1 did not directly interact with import substrate or TAT components.\textsuperscript{82} Finally, VIPP1 was shown to interact with ALB3 in order to stimulate the formation of a D1 insertion intermediate.\textsuperscript{50,83} A malfunctioning of the translocases/integrases in the absence of VIPP1 might render D1 translation/membrane insertion inefficient. As PSII monomers were found to disappear when protein synthesis is blocked during PSII repair,\textsuperscript{34} inefficient D1 translation/membrane insertion in the absence of functional VIPP1 might explain the more pronounced disassembly of photodamaged PSII in high light-exposed \textit{HSP70B}-antisense lines compared with control or \textit{HSP70B}-overexpressor lines.\textsuperscript{71}

**Reassembly of CP43**

After replacement of the photodamaged D1 protein by a newly synthesized copy, CP43 is reassembled to form a PSII core monomer still lacking the OEC (Fig. 1). Low PSII accumulation 3 (LPA3) partitions to stroma and thylakoid membranes, where it interacts stably with LPA2 and ALB3 and apparently transiently with CP43.\textsuperscript{84} Arabidopsis \textit{ipa3} mutants are impaired in the synthesis of CP43 – presumably due to rapid degradation of the newly synthesized protein – and accumulate PSII core subunits only to ~30% of wild-type levels. LPA3 appears to cooperate with LPA2 in the correct folding and assembly of CP43 into PSII reaction centers. Accordingly, \textit{ipa2/ipa3} double mutants were completely blocked in the biogenesis of PSII beyond the CP43-free assembly intermediate. As LPA3s association with thylakoid membranes increases in high light, LPA3 has been proposed not only to play a role during CP43 de novo biosynthesis, but also in the reassembly of free CP43 into repaired PSII complexes.\textsuperscript{85} Arabidopsis/maize mesophyll-enriched thylakoid protein 1 (MET1) and its Chlamydomonas ortholog thylakoid enriched fraction 30 (TEF30) contain TPR and PDZ-domains, are induced by high light, and are located to the stromal side of thylakoid membranes where they interact mostly with PSII monomers.\textsuperscript{85,86} MET1 was shown to interact
with CP43 and CP47 via their exposed stromal loops.\textsuperscript{85} $\text{met1}$/\text{tef30}$ \text{mutants}$ do not display obvious phenotypes under standard growth conditions, but show a defect in PSII repair under high light conditions in that D1, D2, and CP43 are degraded faster than in wild type, PSII supercomplex formation is impaired, and free CP43 accumulates.\textsuperscript{85,86} While Arabidopsis \textit{MET1} has been proposed to play a role in PSII core assembly during de novo biogenesis and repair,\textsuperscript{87} Chlamydomonas \textit{Tef30} has been assigned a function only in PSII repair.\textsuperscript{86} These functions may lie in the (re)assembly of D1 and/or CP43 into PSII cores during repair, in preventing repaired PSII to undergo futile cycles of degradation and repair, or in driving the migration of repaired PSII out of repair zones to allow dimer and supercomplex formation to proceed.

\textbf{Reassembly of the OEC}

Following the reassembly of CP43, a prerequisite for subsequent binding of the manganese cluster and assembly of the OEC is the processing of the D1 precursor by the luminal endopeptidase \textit{cTPA}, which removes the 1.5–2 kDa C-terminal extension from the precursor.\textsuperscript{87,88} The \textit{Psb27} protein from \textit{Thermosynechococcus elongatus} was shown to interact with PSII complexes containing newly synthesized D1.\textsuperscript{89} The interaction with PSII occurs mainly via binding of Psb27 to the D1 C-terminus and to a luminal domain of CP43.\textsuperscript{90} Arabidopsis and \textit{Synechocystis psb27} mutants contain functional PSII under standard growth conditions, but are impaired in the recovery of PSII activity after high-light exposure.\textsuperscript{91,92} This indicates that Psb27 binds to PSII complexes following repair and facilitates formation of the Mn-cluster. Interestingly, there is another PSB27 homolog in Arabidopsis termed low PSII accumulation 19 (LPA19). Like Psb27, LPA19 is peripherally attached to the luminal side of thylakoid membranes where it binds to the soluble C-terminal segment of the D1 protein.\textsuperscript{93} Under standard growth conditions, Arabidopsis \textit{lpa19} mutants accumulate reduced levels of PSII core subunits and show a defect in D1 precursor processing. This indicates that LPA19 facilitates the processing of the D1 precursor during PSII de novo biogenesis, presumably by preventing the premature binding of the extrinsic proteins of the OEC to the D1 precursor, while PSB27 performs this task during PSII repair.\textsuperscript{93}

\textbf{PSII supercomplex formation after repair}

After reassembly of the OEC, repaired PSII monomers need to migrate back into stacked membrane regions for further assembly into dimers and supercomplexes. Luminal immunophilin \textit{FKBP-20} was suggested to be involved in this process during PSII de novo synthesis and repair, as Arabidopsis \textit{fkbp-20} mutants are stunted, more susceptible to photodamage at high light and accumulate more PSII monomer/dimers at the expense of PSII supercomplexes.\textsuperscript{94} Another protein involved in PSII supercomplex formation appears to be the phosphoprotein \textit{PSB33}, which is an intrinsic thylakoid membrane protein harboring a Rieske-like domain facing the stroma. \textit{PSB33} was found in complexes containing D1, D2, CP43 and LHCII and has been proposed to mediate the interaction between PSII core complexes and LHCII. Accordingly, Arabidopsis \textit{psb33} mutants accumulate more PSII dimers and monomers at the expense of PSII supercomplexes. Moreover, \textit{psb33} mutants are more susceptible to photoinhibition and impaired in PSII repair. They show defects in PSII core subunit phosphorylation, non-photochemical quenching and state transitions.\textsuperscript{95} Finally, the 6.1 kDa single membrane domain protein \textit{PSBW} has been proposed to be essential for the formation of PSII supercomplexes and semicrystalline arrays in plants.\textsuperscript{96} The lack of the latter in \textit{psbW} mutant plants is accompanied with strongly reduced PSII core phosphorylation and increased susceptibility of PSII to photodamage and impaired repair, suggesting a role of macromolecular organization of PSII also in the PSII repair process.

\textbf{Factors with yet unknown roles in PSII repair or the protection of PSII from high light}

The functional mechanism of some proteins with apparent roles in PSII photoprotection and repair is still unclear. One of them is ROC4, a stromal cyclophilin.\textsuperscript{97} Arabidopsis \textit{roc4} mutants show no phenotypes under growth light, but reduced growth and yellowing of leaves when exposed to high light at noon. The sensitivity of PSII to high light is the same in mutants as in wild type, but PSII repair is slower in the mutants, suggesting a role of ROC4 in PSII repair.\textsuperscript{98} The \textit{PSBP-like 1} (\textit{PPL1}) protein is considered to be the higher plant ortholog of the cyanobacterial cyanoP protein and is located mainly as free protein in the thylakoid lumen. Arabidopsis \textit{ppl1} mutants are impaired in the recovery of PSII activity after high light exposure suggesting a yet undefined role of \textit{PPL1} in the PSII repair cycle.\textsuperscript{99} Finally, the light-inducible maintenance of PSII under high light 1 (\textit{MPH1}) protein contains a transmembrane domain and was found to be equally distributed between grana cores, grana margins and stroma lamellae.\textsuperscript{100,101} MPH1 was shown to interact with PSII monomers containing D1, D2, CP43 and CP47 but lacking LQY1, and upon high light-exposure MPH1 was demonstrated to interact also with PSII supercomplexes. Arabidopsis \textit{mph1} mutants do not show phenotypes under growth light, but are more susceptible to photoinhibition at high light intensities: they accumulate less PSII supercomplexes, RC47, and PSII monomers, and PSII core subunits are less phosphorylated than in wild-type plants. MPH1 has been suggested to be present only in land plants and to be involved in the protection of PSII from photodamage rather than in PSII repair.\textsuperscript{101}

\textbf{Differences between chloroplasts and cyanobacteria regarding PSII de novo synthesis and repair}

Regarding both, de novo synthesis of PSII and repair, clear differences exist between chloroplasts and cyanobacteria. A first example regarding PSII de novo synthesis is \textit{YCF48}, the cyanobacterial homolog of chloroplast \textit{HCF136}. While Arabidopsis \textit{hcf136} mutants fail to accumulate any PSII core subunit,\textsuperscript{102,103} PSII complexes do form in \textit{Synechocystis ycf48} mutants.\textsuperscript{104} The same appears to be true also for \textit{PsbN}: while there are severe PSII assembly defects in tobacco \textit{psbN} mutants,\textsuperscript{65} no obvious additional effects were reported when \textit{psbN} had been deleted
alongside with psbH in Synechocystis. Similarly, Arabidopsis pam68 mutants exhibited much stronger PSI assembly defects than Synechocystis mutants lacking the PAM68 homolog Slr0933.

Regarding PSII repair there is an example for a protein involved in the repair cycle in cyanobacteria that lacks obvious homologs in the green lineage. The TPR-domain protein Slr0151 was found to be integral to both thylakoid and plasma membranes of Synechocystis. It interacts with the D1 and CP43 proteins but not with D2 and CP47 and has been proposed to be involved in the PSII repair cycle by enhancing D1 synthesis as well as the (dis)assembly of PSII.

In conclusion, we have learned much about the molecular functions of proteins involved in PSII repair in the past 2 decades. However, the ever increasing number of proteins assigned to be involved in PSII repair indicates that the picture is far from complete. Although we have tried to associate the various factors with particular repair intermediates in Fig. 1, this assignment is only tentative and we need to learn much more about the molecular mechanisms that drive a repair factor on and off a particular PSII repair intermediate. Moreover, we need to learn where exactly PSI biogenesis and repair take place and how sites of biogenesis and repair are defined and organized.

Disclosure of potential conflicts of interest
No potential conflicts of interest were disclosed.

Funding
This work was supported by the Deutsche Forschungsgemeinschaft (Schr 617/9–1).

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