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REVIEW

Chloroplast and photosystems: Impact of cadmium and iron deficiency

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Abstract

Chloroplasts utilize photons from solar radiation to synthesize energy-rich molecules of ATPs and NADPHs, which are further used in active cellular processes. Multiprotein complexes (MPCs), including photosystems (PSII and PSI), and the cellular architecture responsible for generation of the proton motive force and the subsequent photophosphorylation, mediate the task of ATP and NADPH synthesis. Both photosystems and other multiprotein assemblies are embedded in thylakoid membranes. Advances in techniques used to study structural biology, biophysics, and comparative genomics and proteomics have enabled us to gain insights of structure, function, and localization of each individual component of the photosynthetic apparatus. An efficient coordination among MPCs is essential for normal functioning of photosynthesis, but there are various stressors that might directly or indirectly interact with photosynthetic components and processes. Cadmium is one of the toxic heavy metals that interact with photosynthetic components and damage photosystems and other MPCs in thylakoids. In plants, iron deficiency shows similar symptoms as those caused by Cd. Our article provides a general overview of chloroplast structure and a critical account of Cd-induced changes in photosystems and other MPCs in thylakoids, and suggests the possible mechanisms involved in mediating these changes. The connection between Cd-induced Fe deficiency and the elevated Cd toxicity under the Fe-deficient condition was also discussed.

Additional key words: grana; light-harvesting complex; photosynthesis; stroma; thylakoids.

Introduction

High-resolution images of thylakoids in chloroplasts and their individual components, including PSII, PSI, LHCII, Cyt b_6f, and ATPase, provide insights into structure, function, and possible inter-relation dynamics of these multiprotein complexes (MPCs) embedded in the thylakoid membrane. A consolidated model of *Arabidopsis* thylakoid protein complexes has been provided in Fig. 1 (from Allen *et al*. 2011), which also depicts Rubisco complex that is responsible for assimilation of carbon dioxide into the biosphere (Andersson and Backlund 2008). Thylakoid membrane forms an elongated flattened-capsular structure enclosing a lumen. Extensive folding and occasional stacking (overlapping) of the membranes create a unique but inhomogeneous structural network; the stacked and unstacked thylakoids known as grana and stroma lamellae, respectively (Dekker and Boekema 2005). The PSII core complex (Umena *et al.* 2011) contains four large membrane-intrinsic subunits called PsbA, PsbB, PsbC, and PsbD. In addition, PsbO, PsbP, and PsbQ are membrane-extrinsic subunits. The peripheral antenna of PSII consists of two types of peripheral proteins constituting the major LHCII antenna complex, in a trimeric state (Butler and Kühlbrandt 1988). In addition, three minor antenna complexes Lhcb4 (CP29), Lhcb5 (CP26), and Lhcb6 (CP24) usually occur in the monomeric form. The dimeric PSII core associates with a variable number of peripheral antenna proteins to form the PSII-LHCII supercomplexes (Boekema *et al*. 1995).

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Abbreviations: MPC – multiprotein complex; TIC – translocons at inner membrane of chloroplast; TOC – translocons at outer membrane of chloroplast; BNP – blue native PAGE; SDS – sodium dodecylsulphate; PAGE – polyacrylamide gel electrophoresis; *pmf* – proton motive force; PMF – peptide mass fingerprinting; iTRAQ – isobaric tag for relative and absolute quantitation; CP – chloroplast.
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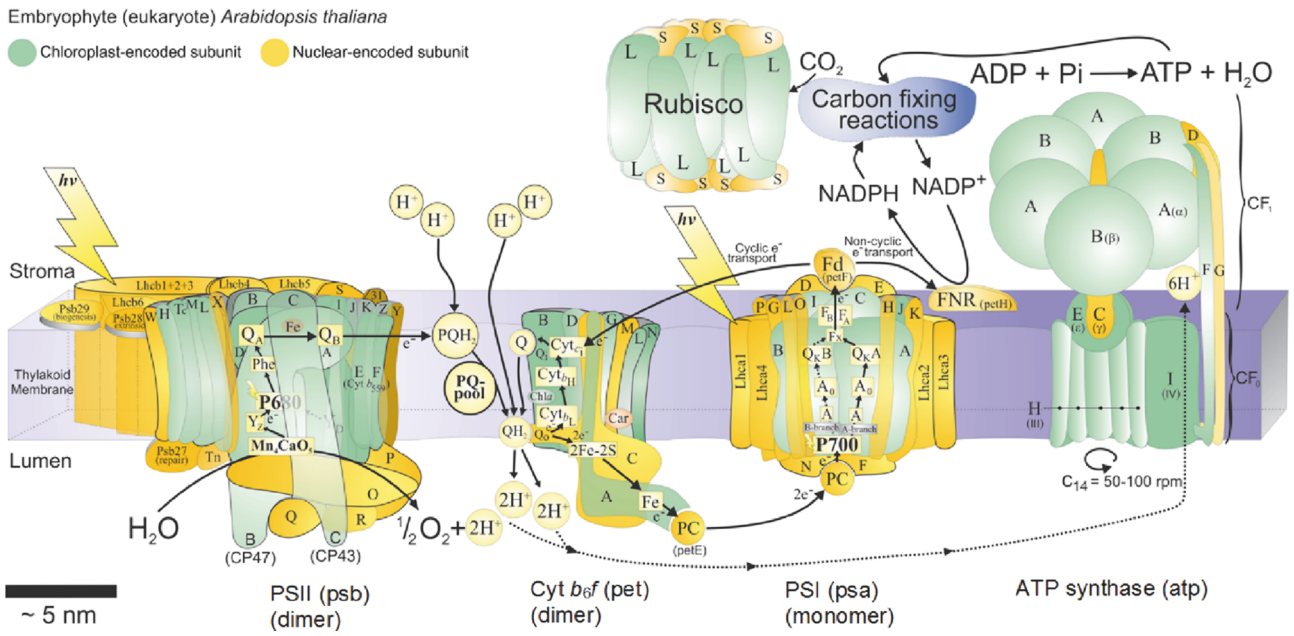

Fig. 1. Major proteins and protein complexes of the chloroplast of *Arabidopsis thaliana*. Photosystem II (PSII); cytochrome b_6f (Cyt b_6f); photosystem I (PSI); ATP synthase; and Rubisco. Subunits are given single-letter names, omitting the three-letter prefix that denotes the complex of which each forms a part: psa – photosystem I; psb – photosystem II; pet (photosynthetic electron transport) – cytochrome b_6f complex and secondary electron carriers; atp – ATP synthase; and rbc – Rubisco. Polypeptide subunits encoded in the chloroplast are marked *in green*, while those in the nucleus are shown *in yellow*. A high-resolution colour version of this figure is available on http://dx.doi.org/10.1016/j.tplants.2011.10.004 (Allen *et al*. 2011, reproduced with permission).

The PSI core complex, occurring in the monomeric form with two functional moieties namely the core complex (reaction centre, RC) and light-harvesting complex (LHCI) (Ben-Shem *et al.* 2003, Busch and Hippler 2011), contains large subunits PsaA and PsaB (forming central heterodimer), three membrane-extrinsic subunits PsaC, PsaD, and PsaE, and several membrane-intrinsic subunits PsaF-H, PsaI-L, PsaN, and PsaN. PsaN is the extrinsic protein of PSI that is exposed to thylakoid lumen. PSI binds to LHCI, membrane-bound peripheral antenna consisting of four different polypeptides Lhca1 to Lhca4. However, although the occurrence of Lhca5 and Lhca6 has been reported, their binding in the complex has not been confirmed (Jansson 1999). PSI-LHCI occurs in complexes which is evident from the fact that LHCI subunits bind in one cluster at the side occupied by the PSI-F and PSI-J core complex subunits (Boekema *et al*. 2001, Ben-Shem *et al.* 2003). LHCI shows some heterogeneity including the occurrence of Lhca1 and Lhca4 isomers (*e.g.*, in tomato), and/or existence of only one gene for each Lhca1-4 subunit with two additional homologous genes encoding Lhca5 and Lhca6 as in *Arabidopsis* (Jansson 1999, Jensen *et al*. 2007). The complex is formed by PSI core and LHCI (PSI-LHCI); it has comparatively stronger association than the PSI core with LHCII in supercomplex of PSI-LHCI-LHCII (Qin *et al.* 2011). Another MPC, the cytochrome (Cyt) b_6f complex, contains eight to nine polypeptide subunits (Zhang and Whitelegge 2001). The Cyt b_6f complex receives electrons from PSII through plastoquinone and passes them to PSI by reducing plastocyanin or cytochrome c_6. Thus, protons are taken up from the stroma and generate an electrochemical gradient across the membrane to boost synthesis of ATPs at the expense of reducing equivalents through mediation of the Q-cycle. Further, ferredoxin $NADP^+$ oxidoreductase can bind to Cyt b_6f complex to provide connectivity with ferredoxin-dependent cyclic transport of electrons through the main electron-transport chain (Zhang and Whitelegge 2001). Further, chloroplastic ATP synthase, belonging to the family of F-type ATP synthases and known as CF_0-CF_1-ATP synthase, is another thylakoid MPC responsible for synthesis of ATPs by utilizing the proton motive force (*pmf*) over the thylakoid membrane. The α- and β-subunits of each of the three noncatalytic proteins constitute the F1 headpiece, whereas the γ-subunit fills the central shaft connected to the *c* subunit that occurs as a multimer (Dekker and Boekema 2005). Thus, both types of thylakoids, stromal as well as granal, are the structures constituted by lipid bilayers and anchored proteins, which play crucial roles in running the major part of photosynthesis. Induction of thylakoid stacking seems to be regulated by Mg^{2+} (Qin *et al.* 2011). Among the genes that encode for the proteins of thylakoids and those of the stroma, some are located in the genome and others in the plastome (Jansson *et al*. 1992, Jansson 1994,

Agne and Kessler 2007, Waters and Langdale 2009). The regulation of chloroplast genes encoding thylakoid proteins is highly coordinated and regulated by the redox status of organelle and the environment (Allen and Pfannschmidt 2000, Choquest *et al*. 2001, Minai *et al*. 2006, Rochaix 2013). These MPCs, packs of proteins and pigments, perform nonsubstitutable, and perhaps life-driving and life-sustaining functions. However, development of human society and its zeal for invention-led industrialization, besides the natural leaching sources, have eroded the land and contaminated it with toxic metals including cadmium. These toxic metals intervene with and affect the chloroplast and its components, ultimately posing a threat to net global photosynthesis. The level of toxic-metal-induced impact on photo-synthesis and the photosynthetic apparatus can be assessed only by studying the mechanisms involving actual targets in the MPCs, thylakoids, and chloroplasts. Cadmium is also known to hinder biogenesis of chloroplasts and organizational changes in MPCs induce 'Fe-deficiency-like' symptoms. This review critically evaluates the general structure of chloroplasts and MPCs (with emphasis on photosystems) and the impact of Cd stress and Fe deficiency on thylakoids and photosystems.

Structure of chloroplasts

Chloroplasts in leaf homogenates or leaf sections can be easily identified under a light microscope as distinctly green organelles. In mesophyll tissues, including palisade cells, they are present in abundance, suspended in the cytoplasm and mostly appressed towards the cell wall. Transmission electron microscopy (TEM) has revealed the presence of a double membrane or envelope, encapsulating the stroma that contains enzymes necessary for various metabolic reactions. Among the metabolic processes responsible for a number of physiochemical activities, some are associated with carbon fixation, fatty-acids biosynthesis, nitrogen and sulfur metabolism, and also with the expression of the chloroplast's own genes. The outer membrane of the chloroplast provides not only mechanical support to the entire unit, but is largely responsible for trafficking metabolites and proteins into the chloroplast, besides receiving cross-talk cues at its surface. The inner membrane is comparatively more complex and serves as a barrier largely between stroma and cytoplasm. It harbors transporters for import of proteins, metabolites (*e.g*., phosphates), and certain lipid-synthesizing enzymes.

Thylakoids, which are suspended within the stroma of the chloroplast, form an elaborately interconnected network of folded photosynthetic membranes forming nonappressed (unstacked) and appressed (stacked) regions; latter visible as 'little pouches' called grana. The fine structure of thylakoids exhibits unique architecture. Thylakoid membranes show a huge but orderly repeated occurrence of four basic MPCs, including LHCs, which is obligatory for successful completion of the light phase of photosynthesis. These MPCs comprise two types of photosystem (*e.g*., PSII and PSI that are multiple protein subunits binding pigment molecules), Cyt *b*/*f* complexes, and ATP synthase complexes. A sequential arrangement of these MPCs ensures photosynthetic electron transport. However, heterogeneity in sequential arrangement has been a proven feature (Nevo *et al*. 2012). The term "lateral heterogeneity" refers to the observation that grana and stroma lamellae differ in their protein composition. PSII and LHCII are concentrated in the grana, while PSI with its associated LHCI and the chloroplast ATP synthase are localized in the unstacked thylakoid regions, *i.e*., the stromal lamellae and grana-end membranes. The Cyt b_6f complex can be found in both appressed and non-appressed regions of thylakoids (Jensen and Leister 2014).

Collectively, these MPCs in thylakoids enable harvesting of light by initiating electron flow from H_2O molecules to $NADP^+$, thereby converting solar energy into chemically usable forms, a phenomenon that has profound implications for initiation and sustenance of life. The core process starts with the selective absorption of light by accessory photosynthetic pigments and chlorophyll (Chl). In order to generate ATP molecules, the ATP-synthase complexes ensure passage of protons from thylakoid lumen into stroma as a result of the subsequently generated *pmf*.

Development of chloroplasts

Chloroplasts embody a huge population of proteins with numerous important functions. Around 90% of the thousands of proteins residing in plastids may not be native but encoded by the nucleus and imported from the cytosol post-translationally (Lopez-Juez and Pyke 2005, Ling *et al*. 2012). In other words, the chloroplast contains its own genetic system and may synthesize up to 10–20% of the organellar proteins (Robinson *et al*. 1998). Translocons at the outer envelope of chloroplasts (TOC), comprising of several members with various structure and molecular mass, recognize chloroplast pre-proteins and initiate the process of their translocation (Li and Chiu 2010, Ling *et al*. 2012). The TOC machinery is composed of Omp85 (outer membrane protein, 85 kDa)-related channel Toc75 and the receptor guanosine triphos-phatases Toc34 and Toc159 (Ling *et al*. 2012). It has been demonstrated that receptors protrude into the cytosol, where different isoforms come in contact with

pre-proteins having varied specificity. In *Arabidopsis thaliana* ('at'), the major isoforms are atToc33 and atToc159, which recognize precursors of the photosynthetic apparatus found in abundance, whereas the minor isoforms are atToc34 and atToc132/atToc120, which recognize and deal with housekeeping pre-proteins (Jarvis *et al*. 1998, Ivanova *et al*. 2004). The profile of receptor-protein isoforms in the cell depends on the stage of plastid development and nutritional requirement of developing and mature plastids (Ling *et al*. 2012).

Thus, the development of mature, photosynthetically active chloroplasts from precursors involves highly coordinated processes executed in different cell compartments. The process of chloroplast differentiation comprises of (*1*) light perception and subsequent expression of nuclear and plastid genes; (*2*) biosynthesis of enzymes, signal recognition particles (ribonucleoproteins), lipids, and pigments; (*3*) import of suitable pigment-binding proteins, such as Chl *a/b*-binding proteins, into developing chloroplasts; (*4*) insertion of these proteins into thylakoid membranes through protein targeting or protein sorting; and (*5*) assemblage of proteins and binding of pigments finally to form the functional pigment-multiprotein complexes (López-Juez 2007, Waters and Langdale 2009). Thylakoid membranes constitute a 3D-network, which ultimately takes a cylindrical but flattened shape to form grana that are linked to one another by the stroma lamellae (Adam *et al*. 2011). Protein composition and the arrangement of photosynthetic complexes within the thylakoid membranes also contribute to the final structure of the chloroplast (Rumak *et al*. 2010). Therefore, the various features of the assembly, such as the lateral separation of LHCII and PSII from PSI and ATP synthase, decide the final structure and arrangement of the appressed and nonappressed thylakoids within the chloroplasts. The specific arrangement and abundance of MPCs give rise to a specific structure of thylakoids, which may be a characteristic feature of chloroplasts of a given plant species. However, the arrangement of thylakoid and grana can be modulated by different environmental factors (Garstka *et al*. 2007, Rudowska *et. al*. 2012). It is now known that composition of light-harvesting antenna controls the macrostructure and dynamics of thylakoid membranes (Goral *et al*. 2012).

The biochemical and physical structure of chloroplasts during differentiation has been studied (Lochmanova *et al*. 2008). Some studies are based on proteomic and functional analysis (Kleffmann *et al*. 2004, Rudowska *et al*. 2012), whereas others have focused the environmental influence on ultrastructure and composition of MPCs (Qureshi *et al*. 2010, Basa *et al*. 2014).

Structure of photosystems

As mentioned earlier, photosystems (PSI and PSII) are pigment-multiprotein assemblies embedded in thylakoid membranes. Their numbers indicate the order in which they were discovered, and not the order of electron transfer. PSI and PSII exhibit some physical, chemical, functional, and structural differences as described below.

Organization of PSI: PSI is a complex of multisubunit, transmembranal protein located in cyanobacteria and thylakoid membranes (Busch and Hippler 2011). It mediates the transport of light-driven electron across the thylakoid membrane, from plastocyanin or Cyt c_{553} to ferredoxin (Jordan *et al*. 2001). Both PSI and PSII are organized into supercomplexes with varying amounts of membrane-bound peripheral antenna complexes (Kouřil *et al.* 2012, van de Meene *et al*. 2012). PSI consists of a monomeric core complex associated with four different LHCI proteins and contains binding sites for LHCI and/or LHCII complexes. In cyanobacteria, the complex consists of two large subunits (PsaA and PsaB) that form the reaction centre, three extrinsic subunits (PsaC-E), and a number of small intrinsic units (PsaF, PsaI-M, and PsaX). Of these, PsaA and PsaB coordinate the organic factors of electron-transport chain (ETC) and most of the PSI light-harvesting pigments. In higher plants, three additional and larger intrinsic membrane proteins (PsaG, PsaH, and PsaO) and one additional extrinsic protein (PsaN) replace PsaM and PsaX (Dekker and Boekema 2005, Hihara and Sonoike 2013). The thylakoid multiprotein complexes, such as PSI, Cyt b_6f, and ferredoxin, also contain iron-sulphur clusters (2Fe-2S or 4Fe-4S) (Balk and Pilon 2011).

The PSI complex occurs as a trimer in cyanobacteria and prochlorophytes and has no LHCI complexes. However, in higher plants and green algae, PSI probably occurs in the monomeric form (Gardian *et al*. 2011). In cyanobacteria, PsaL is known to be essential for the formation of PSI trimers, while PsaI and PsaJ are required for correct organization of PsaL and PsaF (Zolla *et al*. 2007).

Organization of PSII: PSII is another highly ordered pigment-multiprotein complex (Umena *et al*. 2011, Nickelsen and Rengstl 2013) that uses light energy for splitting molecular water into its chemical components (to initiate electron flow in oxygenic photosynthesis), including oxygen that sustains life on the Earth. PSII exists *in vivo* in the thylakoid membrane as a dimer; each monomer contains polypeptide subunits with length varying according to species (Shi and Shröder 2004, Dekker and Boekema 2005, Kramer and Evans 2011, Bricker *et al*. 2012, Shi *et al*. 2012). A concerted assembly of at least 20 different polypeptides is incorporated with various organic and inorganic cofactors (Nickelsen and Rengstl 2013). The concentration of PSII in thylakoid membrane, as compared to PSI and antenna

complexes, varies with organism, temperature, altitudes, light intensity, and spectral wavelength to maintain the ratio of the reductant *vs*. the need for *pmf* and ATP (Kramer and Evans 2011) and the developmental stage of the chloroplast. It has been suggested that the proton concentration gradient regulates energy distribution between the photosystems (Tongra *et al*. 2014). In cyanobacteria, PSII is found throughout the thylakoid-membrane system but in the primitive cyanobacterium, *Gloeobacter violaceus*, it is localized in cytoplasmic membrane, as thylakoid membranes are absent (Nakamura *et al*. 2003). In higher plants and green algae, at least three extrinsic (soluble) subunits are associated with the lumenal side of PSII: PsbO (33 kDa, also known as Mn-stabilizing protein), PsbP (23 kDa), and PspQ (16 kDa). Interestingly, PsbO is conserved in cyanobacteria but homologues CyanoP and CyanoQ replace PsbP and PsbQ. In addition, PSII in cyanobacteria contains soluble subunits PsbU (12 kDa) and PsbV (Cyt c_{550}), which are not reported from green algae and higher plants (Roose *et al*. 2007, Bricker *et al*. 2012). The members of Rhodophyta and Bacillariophyta also contain PsbU and PsbV in addition to PsbO, PsbP, and a homolog of PsbQ (*i.e*., PsbQ') (Bricker *et al*. 2012).

Cadmium toxicity in plants

Cadmium is a nonessential element that negatively affects photosynthetic efficiency, plant metabolism, growth, and development. Numerous sources, including heating systems, metal-working industries, power stations, urban traffic *etc*., release Cd into the environment. It is used widely in plastic stabilizers, electroplating, paints, and nickel-cadmium batteries (Sanità di Toppi and Gabrielli 1999). Due to its high solubility in water (Pinto *et al*. 2004), Cd is easily taken up by roots and transported to leaves through the xylem. Highly deleterious and abundantly available, Cd is ranked as number 7 among the top 20 toxic substances (Yang *et al*. 2004). Like other nonessential metal ions, Cd is supposed to be transported in plants *via* cation-transport systems, which are members of the ZIP and Nramp families or Ca^{2+} channels and transporters (Clemens 2001, Perfus-Barbeoch *et al*. 2002, Nocito *et al*. 2007). Most plants are sensitive even to low concentrations of Cd; it disturbs/inhibits the physiological and molecular mechanisms, such as photosynthesis, respiration, plant-water relation, nitrogen assimilation, cell division and elongation, sulphur and phosphate metabolism, and plant growth and development, through which plants display adaptive responses to environmental stress (Prasad and Strzałka 1999, Sanità di Toppi and Gabbrielli 1999).

Cadmium can alter the uptake of important soil minerals by plants by affecting the availability of other minerals. Once taken up, Cd induces oxidative stress, alters cellular antioxidants, affects adversely stomatal conductance, the size, frequency, and ultrastructure of stomata and chloroplasts, photosynthetic pigment contents, and rates of transpiration and photosynthesis (Sandalio *et al.* 2001, Bashir *et al*. 2013). It may also cause a variety of toxicity symptoms to plant tissues/ organs, ranging from wilting, chlorosis, retarded growth and senescence to cell death. Cellular toxicity caused by Cd may be attributed to its interaction with many reactions; Cd may interact with thylakoid protein complexes (Qureshi *et al*. 2010, Basa *et al*. 2014), carbohydrate metabolism (Sanità di Toppi and Gabrielli 1999), S-assimilation (Bashir *et al*. 2013), nitrate absorption and reduction (Hernández *et al*. 1997), water balance (Costa and Morel 1994, Perfus-Barbeoch *et al*. 2002), enzyme catalysis (van Assche and Clijsters 1990), photosynthesis (Siedlecka and Krupa 1996, Küpper *et al*. 2007), and cellular defence (Qureshi *et al*. 2007). The major cause of toxicity seems to be the extreme capability of Cd to bind to sulfhydryl groups of proteins (Villiers *et al.* 2011), which causes inactivation of proteins and enzymes. Moreover, Cd might induce stress (Qadir *et al*. 2004) by the formation of reactive oxygen species (ROS). It also interferes with –SH bonds, glutathione metabolism, and redox-active metal displacement from proteins (Cho and Seo 2005, Bashir *et al*. 2013). Such indications have emerged from nutrient-limiting studies with the objective to assess the impact of various nutrients on Cd-induced stress, especially of sulphur and nitrogen (Bashir *et al.* 2013, Basa *et al.* 2014, Sebastian and Prasad 2014a), which are important for synthesis of amino acids including those containing sulphur.

Cadmium may increase lipid-peroxidation levels and oxidative damage in different plant species because of an increase in ROS production or induction of lipoxygenase activity (Smeets *et al*. 2008). It is still unknown whether Cd^{2+} directly induces formation of ROS, such as H_2O_2, because Cd^{2+} is unable to catalyze the Fenton and Haber-Weiss reactions. It is just possible that Cd hinders the function of ROS-scavenging system indirectly, leading in turn to ROS accumulation. The role of NADPH oxidase as the main source of ROS under Cd stress has been demonstrated (Horemans *et al*. 2007). Imidazole, an inhibitor of NADPH oxidase activity, strongly inhibits the oxidative effect of Cd (Maksymiec and Krupa 2006).

Under normal conditions, plants maintain a precise balance between production and scavenging of oxygen species. ROS have a dual role in plant life; they are signal-modulating molecules in biological processes, such as cell cycle, signal execution into action, programmed cell death, hormone signalling, growth and development, and plant responses to biotic and abiotic stresses (Dat *et al*. 2000, Pei *et al*. 2000, Mullineaux and Karpinski 2002, Neill *et al*. 2002, Foreman *et al*. 2003, Torres and Dangl 2005, Gechev *et al*. 2006), but their overproduction may lead to oxidative destruction of cells

(Dat *et al*. 2003, Radeva *et al*. 2010). Cd causes structural and functional down-regulation of photosynthetic machinery, as it disrupts thylakoids/chloroplast biogenesis and maturation, assemblage and composition of MPCs, pigment concentration in pigment-protein complexes, proteins involved in photosynthesis, electron-transport chain, photosystems, and the Calvin cycle (Tuomainen *et al*. 2006, Kieffer *et al*. 2008, Durand *et al*. 2010, Qureshi *et al*. 2010, Basa *et al*. 2014).

Cadmium stress, photosynthesis and related metabolism

The chloroplast represents one of major target sites of abiotic stressors, including Cd and other metals/ metalloids (Dalcorso *et al*. 2010, Anjum *et al*. 2012). Cd causes distortion of chloroplasts and reduction in a size and number of grana stacks (Qadir *et al.* 2004, Hakmaoui *et al*. 2007). It enhances ROS production in the cell by influencing the activity of antioxidant enzymes, and thus alters thylakoid multiprotein complexes (*e.g*., PSI, PSII, ATPase, Cyt b_6f). Thylakoid-proteome dynamics is an active subject of photosynthesis research to determine the plant potential to modulate proteome composition under hostile environmental conditions. Abiotic stressors may impact, directly or by secondary consequences (such as oxidative stress), on photosynthetic apparatus in terms of damage to MPCs, alteration in protein-pigment, protein-protein or protein-lipid (membrane) interaction in thylakoidal MPCs (Sárvári 2005), besides an altered protein expression. The enzymes responsible for forming temporary or stable large protein complexes might be also targeted, which ultimately lowers the photosynthetic efficiency of plants. Composition (protein subunits) and structure of the protein complexes need to be studied critically for a better understanding of Cd interactions that lead to inhibition and dysfunction of photosynthetic apparatus.

The dynamic, comparatively hydrophobic and complex proteome of thylakoid membranes, and the changes induced in thylakoidal multiprotein complexes by abiotic stress have been studied extensively (Friso *et al.* 2004, Aro *et al.* 2005, van Wijk and Baginsky 2011, Basa *et al.* 2014, Tomizioli *et al.* 2014). However, only few reports attempted to elucidate the impact of Cd on the thylakoid-membrane system. Studies on spinach thylakoid protein complexes have indicated the importance of differential accumulation of LHCI and LHCII proteins during plant adaptation to different abiotic conditions (Fagioni *et al*. 2009, Andaluz *et al.* 2006). An *Arabidopsis* chloroplast-targeted Hsp101 homologue, APG6, was reported to have an essential role in chloroplast development and plant response to heat-stress (Myouga *et al*. 2006). Qureshi *et al*. (2010) have reported that iron stabilizes thylakoid protein-pigment complexes in Indian mustard during Cd stress.

Being closely similar with other elements, Cd can replace Ca, Fe, and Zn in a number of proteins. It may replace Zn ions in metal-containing enzymes, such as carbonic anhydrase (Grzyb *et al*. 2004) and Zn fingers, the DNA-binding proteins (Vallee *et al.* 1991). It can substitute Fe^{2+} in [2Fe-2S] clusters (Iametti *et al*. 1996) and/or Ca^{2+} (Bouckaert *et al.* 2000, Watanabe *et al*. 2003). Since pigments are essential for stability of MPCs, binding of Cd to –SH groups of pigment-biosynthesis enzymes inhibits availability of pigments. Cd has a major effect on light-harvesting Chl *a*/Chl *b* protein complex II (Krupa 1987). It inhibits photosynthesis by reducing PSII activity, which eventually suppresses quantum yield and electron transport (Sebastian and Prasad 2014a). It affects adversely the photo-assimilatory pathways, such as carbon fixation, by influencing the enzymes involved, *i.e*., Rubisco. It may also replace the central Mg ion in the Chl molecule (Baryla *et al*. 2001). However, there are factors that limit Cd-mediated toxicity or Cd accumulation in plants (Sebastian and Prasad 2014b,c).

Effect of Cd on photosystems and other MPCs

All the metals studied so far have shown to be the potential inhibitors of PSII, whereas PSI appears to be less sensitive and more capable of maintaining physiological activity under environmental stress (Huang *et al*. 2010). Effects of Cd on PSI activity vary in different cyanobacteria and higher plants (Zhou *et al*. 2006, Fagioni *et al.* 2009). For example, PSI activity was inhibited in *Microcystis* sp. (Atri and Rai 2003), increased in *Microcystis aeruginosa* (Zhou *et al*. 2006), and unaffected in *Synechocystis* PCC 6803 (Tůmová and Sofrová 2002) under exposure to Cd. Several studies suggested that cyclic electron flow (CEF) protects PSI from Cd toxicity (Zhou *et al*. 2006, Qian *et al*. 2009). Thus, the retention of PSI yield, despite a high Cd concentration, may be attributed to the CEF, suggesting it to be an important mechanism for prevention of PSI limitation at the acceptor side (Wang *et al*. 2013).

On the other hand, PSII in higher plants is more susceptible to metal ion exposures, although some studies (Wang *et al*. 2013) have suggested that PSI, instead of PSII, is the prime site of damage. Pagliano *et al.* (2006) demonstrated that Cd does not affect the structure of PSII, although there is a decline in PSII electron transfer activity and F_v/F_m. They suggested that Cd promotes light-induced damage to PSII at the donor side as proved by a mobility shift of D1 protein. In the case of

Chlamydomonas reinhardtii, Cd-mediated inhibition of PSII activation was attributed to the binding of Cd^{2+} to the essential Ca^{2+}-site in PSII during photoactivation (Faller *et al.* 2005). Cd-induced iron deficiency is suggested to be a possible reason for greater damage to PSI (Siedlecka and Baszyński 1993, Timperio *et al*. 2007). This may be due to ROS generation in thylakoids, destroying the LHCI antenna and the Fe-S centres of PSI (Michel and Pistorius 2004). Prolonged Fe deficiency resulted in remodeling of antenna complexes and disconnection of LHCI antenna from PSI in *Chlamydomonas* (Moseley *et al*. 2002). Cd drastically reduced the amount of PSI protein in spinach leaves upon early exposure and resulted in disappearance of monomeric and multimeric aggregates of PSI supercomplexes after exposure for 10–15 days (Fagioni *et al.* 2009). The presence of modified amino acids in polypeptide chains of PsaA/PsaB proteins was revealed, thus explaining the accumulation of incomplete monomeric units leading to disruption of PSI-supercomplexes into separate PSI reaction centres and LHCI monomers in spinach (Fagioni *et al.* 2009).

In another study, a progressive decline in PSI and the consequent disappearance of supercomplexes has been observed (Qureshi *et al*. 2010); greater damage occurred to the antenna proteins of PSI, while PSII antenna proteins were less affected. However, Cd stress led to a decline in PSII core monomer with a subsequent increase in PSII supercomplex. The Cyt b_6f was also affected strongly. Apart from the thylakoid complexes, Rubisco is adversely affected by Cd (Qureshi *et al*. 2010). A decline of only 2.5% was observed in the Rubisco content of spinach chloroplasts (Siedlecka and Krupa 1999), but a drastic loss of both the large and small subunits of Rubisco appeared in *Chlamydomonas* (Gillet *et al*. 2006). Cd caused 40% decline of Rubisco activity in cyanobacterial spheroplasts.

Cd-induced Fe deficiency

Cadmium has been shown to induce Fe deficiency by interfering mainly with Fe uptake from roots to shoots (Yoshihara *et al*. 2006). It is suggested that Cd competes with Fe for uptake by roots (Fodor *et al*. 1996, Lombi *et al*. 2002), ultimately restricting Fe availability in the plant. Cd treatment causes over-expression of some Fe-deficiency responsive genes (Yoshihara *et al*. 2006). Interestingly, a cell membrane–bound Fe transporter capable of transporting both Fe and Cd has been identified and isolated (Lombi *et al*. 2002, Thomine *et al*. 2003). It appears, however, that besides inducing Fe-deficiency-like symptoms, Cd has its own mechanism of cellular toxicity targeting the specific sites (*e.g*., amino acid residues) on MPCs. Moreover, Fe deficiency increases susceptibility of MPCs to Cd (Qureshi *et al.* 2010, Basa *et al.* 2014) either through its interaction with S of Fe-S clusters in proteins of MPCs (Qureshi *et al*. 2010, Bashir *et al*. 2013) or at the level of sulphate transporter gene expression (Astolfi *et al*. 2012). This suggests that Cd not only induces Fe deficiency but also causes stress leading to damages in the cell. However, more evidence is needed to understand the mechanism of uptake competition between Fe and Cd, and how Fe deficiency enhances Cd toxicity and *vice versa*.

Synergistic effects of Cd and Cd-induced Fe deficiency

As we know, Cd heavily disturbs the homeostasis of several essential metal ions, especially of Fe, and induces a moderate to strong Fe deficiency in leaves. Cd has been shown to inhibit Fe uptake even in the presence of metal-chelating agents (Fodor *et al*. 1996, 2005). Iron deficiency, induced or accompanied by Cd, significantly altered the photosynthetic apparatus in cucumber (Fodor *et al*. 1996) and poplar (Solti *et al*. 2008) plants. The presence of Fe lowers the damaging impact of Cd stress. This protection might stem from the competition of Fe with Cd for intake and availability of sufficient amount of Fe for assemblage of Fe-S clusters (Qureshi *et al*. 2010). Roth *et al*. (2006) also demonstrated that adequate amount of Fe tends to diminish Cd impacts on photosynthesis and reduces Cd accumulation in leaves. Iron supply during Cd exposure thus helps plants to minimize the Cd-stress symptoms. However, a high concentration of Cd causes a devastating and nonspecific destruction of all MPC subunits related to all four photosynthetic complexes, despite the presence of Fe. This nonspecific damage to photosystems and other MPCs is ascribed to ROS production at large, recorded during Fe sufficiency, Fe deficiency, and Cd treatments (Qureshi *et al*. 2010).

The overproduction of ROS destroys most proteins at random and forces the cell to strengthen its tolerance mechanisms at the cost of growth (Bashir *et al*. 2013); eventually, the cell slips into early irreversible senescence (Pietrini *et al*. 2003), as it was observed in the Cd-treated *Arabidopsis* (Sarry *et al*. 2006), spinach (Timperio *et al*. 2007), Indian mustard (Qureshi *et al*. 2010), and sugar beet (Basa *et al*. 2014). In the absence of Fe, Cd caused a strong damage to the entire photosynthetic apparatus and only a small amount of antenna proteins and some ATPase subunits were retained (Qureshi *et al*. 2010). One of the possible reasons of stress aggravation might be the reduced amount of xanthophylls, a well-known antioxidant (Timperio *et al.* 2007). Changes in the monomer-trimer equilibrium of major PSII antenna suggest that Fe deficiency also decreases the content of violaxanthin, which represents the first adaptive adjustment to Fe

deficiency and has a role in light-dissipation mechanisms. When violaxanthin starts to recover, a *de novo* formation of Lhcb and Lhca takes place (Timperio *et al*. 2007). Thus, the level of ROS produced either by Fe deficiency or due to Cd stress goes beyond the quenching capacity of xanthophyll pigments due to their relatively low content and the ROS start to attack all proteins of MPC complexes of photosynthetic apparatus. Exceptionally, proteins that are the most abundant and hydrophobic in nature might survive this devastating attack of ROS (Qureshi *et al*. 2010).

It has been suggested that Cd stress induces Fe deficiency in leaves, which strongly affects photosynthesis (Siedlecka and Krupa 1999, Larbi *et al*. 2002, Qureshi *et al*. 2010, Basa *et al*. 2014); during the period of Cd exposure, losses to thylakoid MPCs and photosynthetic activity are closely related to availability of Fe (Sárvári *et al*. 1999, Shao *et al*. 2006, Solti *et al*. 2008, Qureshi *et al*. 2010, López-Millán *et al*. 2013, Basa *et al*. 2014). Cd severely impairs Fe supply in leaves, inhibiting enzymatic steps in Chl biosynthesis (Larbi *et al*. 2002, 2006), including the production and function of Chl *a* oxygenase (Tanaka *et al*. 1998). Complexes containing PSI and LHCII during both Cd treatment and Fe deficiency are more prone to damage (Andaluz *et al*. 2006, Timperio *et al*. 2007, Basa *et al*. 2014). PSI and LHCII, being the most abundant thylakoid complexes, are strongly influenced by the decrease in leaf Chl. In addition, PSI complexes contain a high amount of Fe in the form of Fe-S centres (12 Fe per PSI unit), which are structurally important for stabilization of the complexes (Amann *et al*. 2004). A decrease in the amount of LHCs may be due to Fe deficiency-induced loss of stabilizing Chls (Hoober *et al*. 2007), suppressed expression of *lhc* genes (Tziveleka *et al*. 1999, Fusco *et al*. 2005), and/or acclimation tendency towards a decreased antenna size (Timperio *et al*. 2007, Laganowsky *et al*. 2009). PSI supercomplexes are likely to represent NAD(P)H dehydrogenase-PSI(NDH-PSI) supercomplexes participating in cyclic electron flow (Peng *et al*. 2008, Xu *et al*. 2014). Thus, the higher proportion of PSI supercomplexes under Cd-induced Fe deficiency may be a sign of a higher contribution of cyclic electron flow to the excess light-energy-quenching processes (Basa *et al*. 2014). In the case of extremely Fe-deficient thylakoids, an increase in a proportion of the membrane-bound FNR was noticed (Benz *et al.* 2010) together with an increased abundance of ATP synthase and a higher stability of Cyt b_6f dimers (Basa *et al*. 2014). Iron deficiency enhanced the amount of Lhcb1 and Lhcb2 proteins of spinach leaves (Timperio *et al*. 2007) besides causing post-translational modifications of PsaH2 protein, which is involved in the binding of Lhcb proteins to PSI in *Arabidopsis* (Laganowsky *et al*. 2009) contributing to the light-harvesting efficiency of PSI participating in the cyclic flow of electrons. Basa *et al*. (2014) did not find a higher proportion of PSI supercomplexes or an increased abundance of membrane-bound FNR, ATP synthase, and higher stability of Cyt b_6f dimers in thylakoids of Cd-treated plants, which suggests that cyclic electron flow is not relevant as a protective mechanism under Cd stress. These authors correlated PSII organizational changes to Cd-induced Fe deficiency. However, PSII supercomplexes, differing in the amount of LHCII trimer and/or being in different oligomerization state, were the most sensitive to both Cd treatment and extreme Fe deficiency. This may be related to high sensitivity of Lhcb4 and Lhcb6 to the Fe deficiency (Timperio *et al*. 2007), since these connecting antennae are essential for the formation of super- and mega-complexes (Dekker and Boekema 2005). An *in vivo* study has demonstrated that Fe deficiency causes monomerization of PSI trimer and reduces the capacity for state transitions (Ivanov *et al*. 2006). Ivanov *et al*. (2007) showed that induction of CP43 during Fe deficiency is accompanied by a significant increase in the relative abundance of all carotenoids. The amount of CP43-less PSII core, considered as intermediate in the PSII regeneration cycle (Andersson and Aro 2001), is usually less reduced than that of the other PSII forms due to slow regeneration of PSII (Geiken *et al*. 1998). In moderately Fe-deficient thylakoids, however, the abundance of CP43-less PSII core is greater than in other PSII forms. An increase in the amount of PSII complex components, suggesting a higher rate of PSII repair, was also observed in *Brassica juncea* (Indian mustard), which is a hyperaccumulator both under Fe deficiency and Cd treatment (Qureshi *et al*. 2010). Therefore, plants grown even under moderate concentrations of Fe may have enough opportunity for repairing the damaged PSII, which is not otherwise possible under strong Fe deprivation or Cd stress. The most obvious change in the organization of complexes, *i.e*., increased Lhc monomer to trimer ratio in the thylakoids from stressed plants (Basa *et al*. 2014), was shown earlier in Cd-treated Indian mustard (Qureshi *et al*. 2010) and Fe-deficient sugar beet and spinach (Andaluz *et al*. 2006, Timperio *et al*. 2007). It has been demonstrated that light energy can be quenched more easily when absorbed by the monomeric Lhcs than by the trimeric form (Garab *et al*. 2002); this might be due to changed Lhcb isoforms, hence influencing the organization of both PSII supercomplexes (Damkjær *et al*. 2009) and LHCII (Caffarri *et al*. 2005). Transcriptome data of Fe-deficient barley plants showed that expression of two of the *lhcb1* genes was upregulated with a concomitant increase of monomeric Lhcb1 proteins (Saito *et al*. 2010). Distinct changes in Lhcbs were found in some other species, thus suggesting that acclimation may be species-specific (Andaluz *et al*. 2006, Timperio *et al*. 2007, Laganowsky *et al*. 2009).

It is hypothesized that the organizational changes in the LHC antennae in sugar beet under both Cd stress and Fe deficiency could cause reduction in the proportion of absorbed energy reaching the reaction centre, thus

limiting the degradation of photosynthetic components caused by photoinhibitory processes. Carotenoid content and composition also contribute to the protection of photosynthetic apparatus against excess light, particularly in severely Fe-deficient plants, where high amounts of zeaxanthin accumulate in the thylakoids (Morales *et al*. 1990, Quílez *et al*. 1992). In the Chl *b* and xanthophyll-biosynthesis mutants, xanthophylls were either bound loosely to the complexes or occurred as free pigments (Dall'Osto *et al*. 2010). The dynamics among the various biochemical, molecular, and proteomic players ultimately decides the stability of the thylakoids and contributes to the overall photosynthetic efficiency of the chloroplast. However, it cannot be denied that during Cd stress, occurrence of partial Fe deficiency might help in reducing the production of ROS that concomitantly helps in acclimation through reorganization or repairing of thylakoid complexes. Thus, it can be concluded that repairing of thylakoids/MPCs takes place at the cost of the rate of photosynthesis and production output of chloroplasts and reduces biomass accumulation and crop yield.

Preferred methodologies to study MPCs

During the last several years, proteomics, with the assistance of spectrometry and bioinformatics, has changed the traditional way of research. X-ray crystallographic analysis has been in use for decades to determine the 3D structure of proteins, which essentially needs purified proteins in their crystallized form. This analysis would impart more information about the structure, topology, and orientation of MPCs in the membrane. In order to identify each protein and individual protein complexes, intact protein assemblies (made of multiple protein subunits) need to be isolated first. For this purpose, a newer technique, called blue-native polyacrylamide gel electrophoresis (BN-PAGE or BNP), was introduced. Initially, Schägger and von Jagow (1991) separated MPCs in enzymatically active form in mitochondria extracted from a variety of samples, and then Huang *et al.* (1994) resolved the chloroplast Cyt b_6f complex, using this technique. Later, a series of innovations in proteomics, including shotgun proteomics and mass spectrometry, facilitated chloroplast studies (Wu *et al*. 2003). By employing the BNP technique, isolated chloroplasts are burst to extract the MPCs-harboring intact thylakoids, which are then treated with appropriate amounts and strength of mild nondenaturing detergents so that the multiprotein assemblies are separated on native gels without any disintegration. Once each MPC is separated on concentration-gradient gel, in-gel reduction, alkylation, and sodium dodecylsulphate (SDS)-based ionization are achieved for dissociation of each protein subunit by placing each MPC band from BNP on top of SDS-PAGE. Every MPC obtained using BNP resolves into spots in vertical fashion, corresponding to the number of proteins present in the MPC. The resolved proteins on the gel are then stained and visualized using appropriate stain. Every spot on the gel is labeled for reference and attribution of its name after its identification through peptide mass fingerprinting (PMF), using a mass spectrometer (Eubel *et al*. 2005).

Further, for protein targeting in MPCs, immuno-proteomics is a method of choice (Kikuchi *et al*. 2011). For post-translational modifications of proteins, the more efficient and high throughput techniques may include the BNP and iTRAQ (isobaric tag for relative and absolute quantitation)-assisted protein identification (Xie *et al*. 2011). The signals (peak timings/peptide retention time) generated for a protein digested by specific protease are unique, hence serving as a fingerprint, which can be matched with the information stored in public databases. Besides matching PMF, bioinformatics can be used for further analysis of identified proteins, such as prediction of 3D structure, motif analysis, ligand binding, retrieval of cDNA sequence, and gene information. The protein that fails to match might be a unique and novel protein, which can be further characterized. Genome-sequence information is vital for accuracy of protein sequence with almost absolute matching of proteins against the genome of the same organism.

Agenda of future research

Iron-sulphur (Fe–S) clusters are cofactors of proteins that function in vital processes including photosynthesis, respiration, sulphur and nitrogen assimilation, amino acid and purine metabolism, DNA repair and translation *etc*. (Balk and Pilon 2011). In fact, it is essential to focus not only on Fe but also on S metabolism, because Fe–S clusters are most commonly liganded to proteins *via* sulfhydryl groups of cysteine side chains (Lill 2009). Study of clusters, such as the 2Fe-2S, 4Fe-4S-ferredoxin-type (coordinated by four cysteine residues) and the 2Fe-2S-Rieske-type cluster (liganded by 2 Cys and 2 His residues), may widen our knowledge related to facts associated with sulphur, another important nutrient, besides Fe. We propose a model that helps locate the major sites that might face the risk of Cd effect during synthesis of MPCs (Fig. 2). It would be of great interest to study the impact of Cd on protein trafficking, mainly of those proteins that are supposed to be imported to chloroplasts and interact with other proteins involved in the formation of MPCs. We suggest several potential

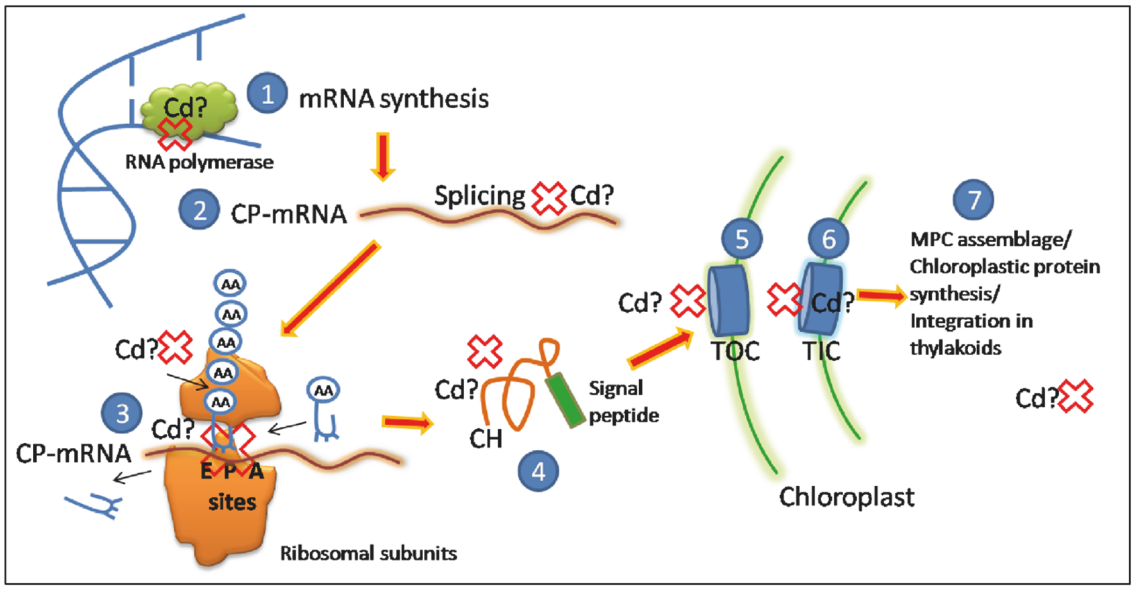

Fig. 2. Possible targets of Cd interaction (*red crosses*) at different stages of proteins to be imported into chloroplast (CP) and incorporated as a subunit of multiprotein-pigment complexes (MPCs). 1. During CP-RNA synthesis. 2. Binding with CP-mRNA. 3. Failure of mRNA binding to ribosome and inhibition of ribosomal activity. 4. Binding to and distortion of CP-peptide/protein or molecular chaperone (CH). 5. Binding to translocons at outer chloroplast (TOC) membrane. 6. Binding to translocons at inner chloroplast (TIC) membrane. 7. MPCs protein metabolism in chloroplast and thylakoids.

targets of Cd interaction at different stages of proteins to be imported to the chloroplast (CP herein) and incorporated as a subunit of multiprotein-pigment complexes. Cd may affect a single or multiple target(s) during CP-RNA synthesis that may include inhibition of transcription factor/RNA polymerase or binding with CP-mRNA (during immature or mature stages) to cause failure of mRNA binding to ribosome or inhibition of interaction between ribosomal subunits, binding to and distortion of CP-peptide/protein or molecular chaperone (CH), binding to translocons at the outer chloroplast (TOC) membrane, or binding to translocons at the inner chloroplast (TIC) membrane. However, impact of Cd on MPC assemblage or upregulation of proteases, which degrade MPC components, cannot be ruled out. As demonstrated in Fig. 1, number of important MPC proteins is of chloroplastic origin and supposed to be affected by Cd and Fe deficiency.

Studies based on mutants, specifically, point-mutants with loss of residues binding to Fe-S, will considerably enrich our understanding of interaction between Cd, Fe, and components (proteins, lipids, and pigments) of photosystem(s). This would certainly help to locate the main target of Cd at the photosystem level.

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