Cadmium against Higher Plant Photosynthesis – a Variety of Effects and Where Do They Possibly Come From?

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The complexity of *in vivo* toxic effects of Cd on higher plants makes almost impossible an accurate distinction between direct and indirect mechanisms of its action on the photosynthetic apparatus. We, therefore, postulate that multiple Cd effects on plant physiological and metabolic processes may finally be focused on photosynthesis. This would also explain the phenomenon that only a small fraction of Cd entering chloroplasts may cause such disastrous changes in their structure and function. In return, the inhibition of photosynthesis affects numerous metabolic pathways dependent on the primary carbon metabolism.

Introduction

The studies on the effects of Cd on photosynthesis have risen the question about the mechanisms of its toxicity towards this crucial metabolic pathway in plants. The photosynthetic apparatus appears to be especially sensitive to Cd. On average, about 75% of Cd entering the plant is in one way or another bound in the root system (Jastrow and Koeppe, 1980; Krupa and Baszyński, 1995, and references therein). There are many mechanisms involved in the detoxication process giving such high efficiency of this phenomenon (Verkleij and Schat, 1990; Shier, 1994). According to available data up to 11% of total Cd content in plants can be found in stems, and about 15%, depending on plant species and the ability to detoxicate this heavy metal, enters the leaves (Jastrow and Koeppe, 1980). Only 0.6–1.4% of this amount can be finally found in chloroplasts (Weigel and Jäger, 1980; Krupa and Baszyński, 1995; Leita *et al.*, 1996). This fact might be surprising in the light of the data mentioned above. How to explain that only a very small fraction of all Cd entering leaf tissues is located in these organelles? Very recently, Chardonnens *et al.* (1998) reported that in leaves of both Cd tolerant and sensitive ecotypes of *Silene vulgaris* the highest metal concentration was found in lower epidermis, whilst mesophyll cells were the region of its relatively lowest accumulation.

The analysis of an average Cd accumulation within the mesophyll cells reveals that about 48% is located in the cell wall, 39% in the cytoplasm and vacuole and only 13% in chloroplasts and mitochondria (Ernst, 1980). Although the contents of Cd in chloroplast stroma and thylakoids are not known, we may suppose that they must be much lower since in many cases metal may form deposits on the outer surface of the chloroplast envelope (Cumming and Taylor, 1990). Therefore, facing the above data on metal accumulation in specific plant organs and organelles one may ask for the reasons of such high susceptibility of photosynthesis to Cd.

The principles of *in vitro* and *in vivo* studies on Cd effects on photosynthesis

It was first in 1949 when Macdowall observed a strong inhibition of photosystem II activity by Hg and Cu in isolated chloroplasts, and no effect of Ni, Co and Zn (Macdowall, 1949). And then, after many years of a lag phase the studies on the effects of heavy metals, including Cd, have emerged again in the early seventies. The research on the inhibitory effects of Cd and other heavy metals on the photosynthetic apparatus was at that time mostly concentrated on thylakoid membranes and the components of photosynthetic electron transport, located mainly within these membranes. Although all those experiments have brought numerous valuable data, they were mostly concentrated on *in vitro* studies, *i.e.* isolated cells, protoplasts or chloroplasts and their fragments like thylakoids.

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The major disadvantage of such studies is that the time of the metal action must be very short due to very poor object vitality, usually counted in hours. Thus, to achieve distinct inhibitory effects enormously high metal concentrations were used, up to 1000 times higher than those for *in vivo* studies. Moreover, one must realize that the *in vitro* system lacks the whole organism responses to this stressful situation, therefore observed phenomena are of rather simple and direct nature. Although the results of *in vivo* experiments on the whole plant level are much more complicated to explain because of rather indirect effects of Cd on the photosynthetic apparatus, mostly due to the complexity of treated system, they have certain advantages over *in vitro* studies. First of all, much lower metal concentrations are used, then the treatment can be prolonged to days and/or weeks. This laboratory situation is, therefore, much closer to naturally Cd-polluted environment than *in vitro* ones. However, we must keep in mind that the full picture can only be obtained after careful analysis of the results of both experimental approaches to the problem of Cd toxicity towards the photosynthetic apparatus of higher plants.

The age of plants exposed to Cd treatment is also of crucial importance. The effects of Cd on plant as a whole and photosynthesis as such differ very substantially due to the stage of growth. In very young seedlings being in intial growth stage and treated shortly with Cd we can only observe retarded growth with no spectacular effects of the metal on the photosynthetic apparatus. In young plants subjected to short-term (days) treatment with Cd, despite the retarded growth, a decrease in plastid pigments and rather indirect inhibition of photosynthetic electron transport can be observed (Skórzyńska-Polit and Baszyński, 1995, 1997). Under such experimental conditions Cd also interacts with the uptake of essential nutritional elements like for instance Fe, Ca, P, Mg, Mn and many others (Siedlecka, 1995, and references therein; Hernández *et al.*, 1996; Yang *et al.*, 1996). If plants are older and treated with Cd for weeks then the most important effect of metal toxicity is the strong interaction with essential elements with all consecutive consequences for plant growth and metabolism. The observed degradation of the photosynthetic apparatus reflects the premature senescence processes initiated by Cd (Krupa and Baszyński, 1995). Some of these phenomena will be discussed in more details in the following chapters.

Cd *versus* photosynthetic electron transport

The results of *in vitro* and *in vivo* experiments on the effects of Cd on isolated chloroplasts or thylakoid membranes are summarized in Fig. 1. There are several steps in the photosynthetic electron transport chain found to be affected directly or indirectly by Cd (Krupa and Baszyński, 1995; Prasad, 1995, 1996, and references therein). One of the most crucial chlorophyll-protein complexes – light-harvesting chlorophyll *a/b* protein complex II (LHCII), the major light harvesting antenna in photosynthesis, was shown to be disturbed by Cd in at least two aspects of its structure and function. First, the oligomeric structure of this complex, which is of primary importance for the efficient collection of light energy, is indirectly affected by Cd. Metal causes a decrease in the level of *trans*-Δ^3-hexadecenoic fatty acid, specifically bound in *sn-2* position of the chloroplastic phosphatidylglycerol (PG) molecules (Krupa, 1988). The level of this fatty acid has been proven to be correlated with oligomerization of LHCII (Krupa,

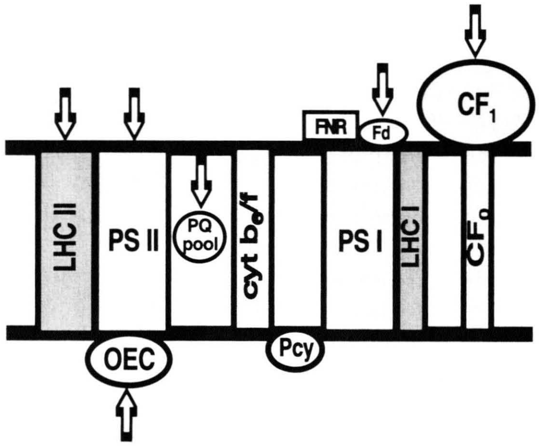

Fig. 1. The toxicity of Cd towards components of the photosynthetic electron transport. Arrows indicate sites of the metal action. CF_0, proton channel complex; CF_1, chloroplast ATP synthase complex; cyt b_6/f, cytochrome b_6/f complex; Fd, ferredoxin; FNR, ferredoxin-NADP oxidoreductase; LHCI, light-harvesting complex of photosystem I; LHCII, light-harvesting complex of photosystem II; OEC, oxygen-evolving complex; Pcy, plastocyanin; PQ, plastoquinone; PSI, photosystem I; PSII, photosystem II.

1988; Krupa *et al.*, 1992b). Degradation of LHCII oligomeric structure leads to less efficient light energy utilization and decreased rate of photosynthetic electron transport. Also other authors reported that Cd interacts *in vitro* with the subunits of this complex leading to its conformational changes (Ahmed and Tajmir-Riahi, 1993). Moreover, we must consider the fact that LHCII comprises up to 70% of the total chlorophyll content in thylakoid membranes. Thus, the inhibitory effects of Cd on certain steps of chlorophyll synthesis must also be reflected in this complex. Besides Stobart's studies (1985) revealing that Cd may affect both the formation of δ-aminolevulinic acid (ALA) and the photoreduction of protochlorophyllide, it was also Böddi *et al.* (1995) who has observed the inhibition of the latter step of chlorophyll synthesis. The opposite conclusion was drawn by Horváth *et al.* (1996) from the studies on the effects of Cd on the formation of the photosynthetic apparatus during greening of barley leaves. According to them, Cd acts mainly by disturbing the integration of chlorophyll into stable chlorophyll-protein complexes of the thylakoid membranes rather than affecting chlorophyll synthesis itself.

The numerous studies on the effects of Cd on the photosystem II (PSII) have proven it to be especially sensitive to the metal, both on its donor and acceptor side (Clijsters and Van Assche, 1985; Van Assche and Clijsters, 1990; Krupa and Baszyński, 1995; Prasad, 1995, 1996, and references therein). Oxygen evolving complex (OEC), donating electrons from the thylakoid lumen straight to the PSII reaction centre, was postulated as the primary target of Cd toxicity. Both the destruction of OEC and the interaction with ions like Mn^{2+}, Ca^{2+} and Cl^{-}, neccessary for its proper function, have been considered as mechanisms of this toxicity (Maksymiec and Baszyński, 1988; Skórzyńska and Baszyński, 1993). Also the PSII reaction centre with all its redox components may be affected by Cd (Baszyński *et al.*, 1980; Barua and Jana, 1986; Becceril *et al.*, 1988; Atal *et al.*, 1991; Tukendorf and Baszyński, 1991). However, these data were mostly obtained from *in vitro* studies on isolated chloroplasts, thylakoids or purified PSII particles and cannot be directly discussed in terms of whole plant level. The total plastoquinone (PQ) pool is also decreased by Cd, thus certainly leading to less efficient transport of electrons to the photosystem I (PSI) (Baszyński *et al.*, 1980). This photosystem, being for long time considered as relatively resistant to Cd, has also appeared to be affected by the metal, although in a rather indirect way. Siedlecka and Baszyński (1993) showed that in Cd-treated maize seedlings the inhibition of electron flow *via* PSI is due to Cd-induced Fe deficiency, and thus, significantly diminished level and activity of ferredoxin (Fd).

Since there are almost no reports on direct influence of Cd on the photophosphorylation components in thylakoid membranes, except that of Teige *et al.* (1990), we may only speculate that the inhibition of the electron flow must have an indirect impact on this process as well.

Toxicity of Cd towards dark reactions of photosynthesis

In 1985 Weigel, after presenting his results on *in vitro* effects of Cd on photosynthetic reactions in isolated mesophyll protoplasts, has concluded that: "... *the present results leave little doubt that Cd acts on the photosynthetic apparatus mainly at the level of dark reactions but not on membrane bound, primary photochemical reactions*" (Weigel, 1985). A few years later a similar conclusion has been drawn from chlorophyll *a* fluorescence studies, carried out *in vivo* on bean plants (Krupa *et al.*, 1992a, 1993). Therefore, can we really ascribe all the inhibitory effects of Cd to the photosynthetic carbon reduction cycle, considering observed changes in the primary photochemical reactions and electron transport as a secondary effects?

As it has been already shown both in case of Cd, as of many other heavy metals, all three key steps of the Calvin cycle – carboxylation, reduction and regeneration, are heavily affected (Krupa and Baszyński, 1995; Prasad, 1995, 1996, and references therein). Without any doubt, the most sensitive step of the enzymatic phase of photosynthesis is the carboxylation of the primary acceptor of CO_2 – ribulose-1,5-bisphosphate (RuBP) as well as phosphoenolpyruvate (PEP). Both enzymes controlling these reactions in C_3 and C_4 plants – Rubisco and PEP carboxylase, are inhibited by Cd (Krupa and Baszyński, 1995; Prasad, 1995, and references therein). It is actually considered that Cd may affect Rubisco function and structure in several ways, depending on the metal concentration in the nutrient medium, plant growth stage and eventually plant suceptibility to heavy metal. The nature of this inhibition is not fully elucidated yet, although there are some suppositions presented very recently by Siedlecka *et al.* (1998). Fig. 2 shows that Cd may decrease enzyme activity by damaging its protein structure, may replace Mg^{2+} ions being neccessary cofactors of the carboxylation reaction, or may even cause shift towards oxygenation properties of Rubisco. Very high concentrations of Cd may also lead to an irreversible disconnection of small and large subunits of the enzyme causing its full inhibition. The latter was observed only in *in vitro* experiments (Stiborova, 1988; Malik *et al.*, 1992). The list of enzymes involved in the primary carbon metabolism and affected by Cd comprises also of 3-phosphoglyceric acid kinase, glyceraldehyde-3-phosphate dehydrogenase, ribulose-5-phosphate kinase, fructose-1,6-bisphosphatase, aldolase, fructose-6-phosphate, 2-kinase and very recently investigated bean chloroplast carbonic anhydrase (Krupa and Baszyński, 1995, and references therein; Siedlecka *et al.*, 1997, 1998).

It is, therefore, clear that the dark phase of photosynthesis is very heavily affected by Cd. Thus, we may now come back to the question asked at the beginning of this chapter. What is the primary and the secondary target of Cd toxicity towards photosynthesis – electron transport or enzymatic reactions? As shown recently in our laboratory, the Calvin cycle is the primary target, although the plant growth stage must be also considered. In older plants treated with Cd for longer periods of time the substantial direct effects of heavy metal on the components of photosynthetic electron transport are observed (Siedlecka and Krupa, 1996b; Skórzyńska-Polit *et al.*, 1995; Skórzyńska-Polit and Baszyński 1995, 1997; Krupa and Moniak, 1998). In general, our previous hypothesis is supported that the primary target of heavy metal toxicity, including Cd, might be the enzymatic phase of photosynthesis, which in return may slow down the reactions of the light phase, either by down-regulation or by feedback inhibition due to inefficient consumption of ATP and NADPH, thus the maintenance of a high proton gradient across the thylakoid membrane (Krupa *et al.*, 1993).

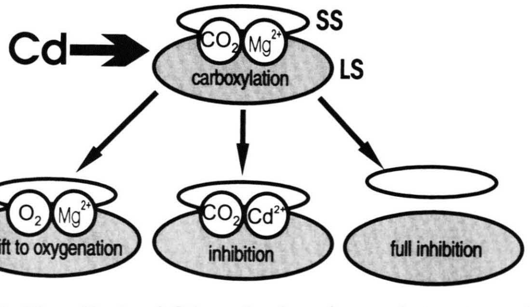

Fig. 2. The effects of Cd on the function and structure of ribulose-bisphosphate carboxylase/oxygenase (Rubisco). LS, large subunits of Rubisco; SS, small subunits of Rubisco (after Siedlecka *et al.* 1998).

Direct or indirect mechanisms of Cd toxicity for the photosynthetic apparatus?

Before we shall try to answer this question we must realize all the complexity of the higher plant. Cd, as well as other heavy metals, affects higher plant organism on many levels of its organization and function. There are no single, isolated reactions or pathways or processes being totally independent from each other. A simple and obvious example is shown in Fig. 3. The portion of total higher plant metabolism that aquires carbon atoms from atmospheric CO_2 and incorporates them into the organism is photosynthesis. It converts atmospheric CO_2 and the sunlight energy into organic compounds with the release of O_2. These compounds are then "burned" in cellular respiration, converting them and O_2 into CO_2 and chemical energy (ATP). Therefore, any disturbance in one of these interrelated processes affects the other one. One may easily conclude that the

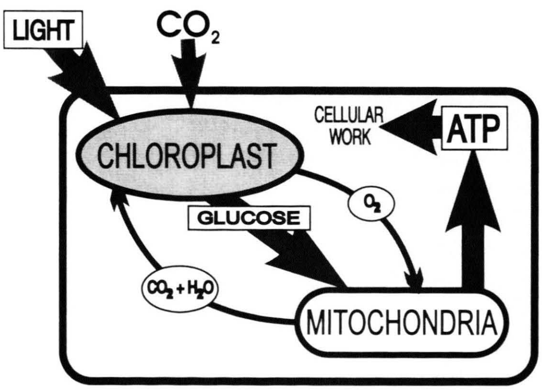

Fig. 3. An example of the intercellular relationships between key metabolic processes.

more general physiological or metabolic function is affected by heavy metal the wider is the response of anatomical structures, cell compartments or processes within the higher plant.

In the opinion of many authors water stress and abnormalities observed in plant gas exchange are the primary reasons for all other disturbances caused by Cd (Barceló and Poschenrieder, 1990; Costa and Morel, 1994; Costa *et al.*, 1994; Leita *et al.*, 1995). We cannot forget that also plant hormones, regulating most of its physiological and metabolic processes, are influenced by Cd as well as many phenomena related to plant gene expression and translation (Moya *et al.*, 1995; Shah and Dubey, 1995; Hollenbach *et al.*, 1997).

As we have already mentioned in the previous chapters, there are also strong indications that Cd initiates the premature senescence of plants. One of striking visual symptoms is the degradation of the lamellar structure of chloroplasts in Cd-treated plants with all the consequences for the structure and function of photosynthetic electron transport (Baszyński *et al.*, 1980; Krupa *et al.*, 1987; Barceló *et al.*, 1988; Ghoshroy and Nadakavukaren, 1990).

The most visible symptom of Cd toxicity is leaf chlorosis. There are two major reasons of chlorosis, both already mentioned in earlier chapters. One is inhibition of chlorophyll synthesis and the other – interaction between Cd and Fe (Siedlecka and Krupa, 1996a). Cd-induced Fe deficiency may also affect photosynthetic electron transport and the Calvin cycle activity (Siedlecka and Baszyński, 1993; Siedlecka *et al.*, 1996, 1997).

The complexity and diversity of *in vivo* toxic effects of Cd on higher plant makes an accurate distinction between direct and indirect mechanism of its action almost impossible. We, therefore, postulate, that in fact we deal with multiple effects which are finally focused on the photosynthetic apparatus. On the other hand, photosynthesis being absolutely crucial for the functioning of plant, may in return affect all other physiological and metabolic processes.

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