

REVIEW

Cd/Fe interaction in higher plants - its consequences for the photosynthetic apparatus

A. SIEDLECKA* and Z. KRUPA

*Department of Plant Physiology, Maria Curie-Skłodowska University,
Akademicka 19, 20-033 Lublin, Poland*

Abstract

Cadmium is one of the most dangerous environmental pollutants, affecting, among other things, plant mineral composition. It easily interacts with iron, one of the most important elements for plant growth and metabolism. This interaction, including modifying effects of lowered or excessive Fe supply on Cd-exposed plants and its consequences for the photosynthetic apparatus is reviewed. The influence of modified Fe and Cd supply on the uptake of both metals, their distribution, plant growth, and photosynthesis is also explained. Moderate Fe excess has a beneficial influence on Cd-treated plants, resulting in more intensive growth, photosynthetic pigments accumulation, and more efficient light phase of photosynthesis. Nutrient-medium Fe deficiency increases plant susceptibility to Cd. The main open questions of Cd/Fe interaction are: (1) the strong Fe-dependency of Cd mobility within the plant, and (2) photosynthetic dark phase adaptation to Cd stress.

Additional key words: Calvin cycle enzymes; chlorophyll; chloroplast structure; heavy metals; photosynthesis; photosystems; plant growth; uptake of mineral elements.

Introduction

Influence of heavy metals on plant metabolism has been studied for many years, mainly as effect of plant exposition to a single heavy metal. General relationships between heavy metals and mineral nutrition of plants grown in polluted environment are the most important factors modifying their toxicity (for review see Siedlecka 1995). Iron is one of the most important nutrient elements. A complicated but still

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*e-mail: asiedlec@biotop.umcs.lublin.pl, fax: (48-81) 537 51 02

Abbreviations: CA - carbonic anhydrase; Chl - chlorophyll; GAPDH - NADP-dependent glyceraldehyde-3-phosphate dehydrogenase; PS - photosystem; RuBPCO - ribulose-1,5-bisphosphate carboxylase/oxygenase.

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not fully elucidated regulation system is developed in plant cells to maintain Fe homeostasis (Marschner 1995). Heavy metals, such as for instance Cd, may interfere with this system, resulting in induced Fe deficiency despite satisfactory availability of Fe. This was documented in liquid nutrient-medium experiments as well as in the soil (Wallace *et al.* 1992, Siedlecka 1995). For Cd this effect is so strong that visible symptoms of Cd toxicity are almost the same as those of Fe deficiency. The present state of study on interaction between Cd and Fe is summarized in this review.

Interaction of Cd with Fe uptake and distribution

Iron, despite its common occurrence in the environment, is not easily available to plants due to its predominating insoluble forms in the soil. Higher plants have developed two strategies of Fe uptake (Guerinot and Yi 1994, Marschner 1995).

Strategy I is typical for all dicotyledonous and monocotyledonous plants, except *Gramineae*. In this strategy Fe^{3+} is reduced to Fe^{2+} before its uptake to the root (Fig. 1). This strategy consists of increased number of lateral roots, development of specific transfer cells, and three-step process of Fe uptake. The first step is release of protons, organic acids, and phenolic compounds to the soil, resulting in mobilization of Fe^{3+} ions from soil particles. The released ions are chelated by phenolic compounds to keep them in a solubilized form. The second step is reduction of Fe^{3+} to Fe^{2+} by root membrane reductases. They are constitutive root membrane proteins, but their activity in Fe-deficiency conditions increases so much that for many years they have been considered as inductive proteins. Root membrane reductases can reduce Fe^{3+} both in ionic form as well as Fe^{3+} ions chelated by phenolic compounds, or even Fe chelated by microbial siderophores. Some phenolic compounds, such as caffeic acid, at pH below 4.5 can also act as reducing agents. The last step in this strategy is transfer of Fe^{2+} through the membrane to the cytosol of root cells (Guerinot and Yi 1994, Marschner 1995, Schmidt *et al.* 1996).

Strategy II is typical only for *Gramineae*. Specific chelating compounds, phytosiderophores, are synthesized in the root cells and used for chelating of Fe in the soil (Fig. 1, Ma and Nomoto 1996). The whole complex of Fe-phytosiderophore is transported through the cell membrane, and Fe^{3+} is reduced to Fe^{2+} inside root cells (Marschner 1995, Ma and Nomoto 1996). This strategy is more effective than the first one and *Gramineae* are less sensitive to Fe-deficiency than other plants (Marschner 1995). Phytosiderophores, such as mugenic acid and its derivatives, are synthesized from the non-protein amino acid, nicotianamine. This amino acid acts as a chelating agent in plants of both strategies and is used for xylem and phloem Fe transport, Fe storage in leaves, and regulation of the balance between so-called "active" and "non-active" Fe pools in leaves (Pich and Scholz 1993, Herbiik *et al.* 1996).

Toxic influence of Cd on strategy I plants leads to decreased activity of root cell membrane reductases and their insufficient activation under Fe-deficiency (Fig. 1, Alcántara *et al.* 1994). This, together with decrease in root development and damage of root membrane, results in induction of Fe deficiency among Cd-exposed plants.

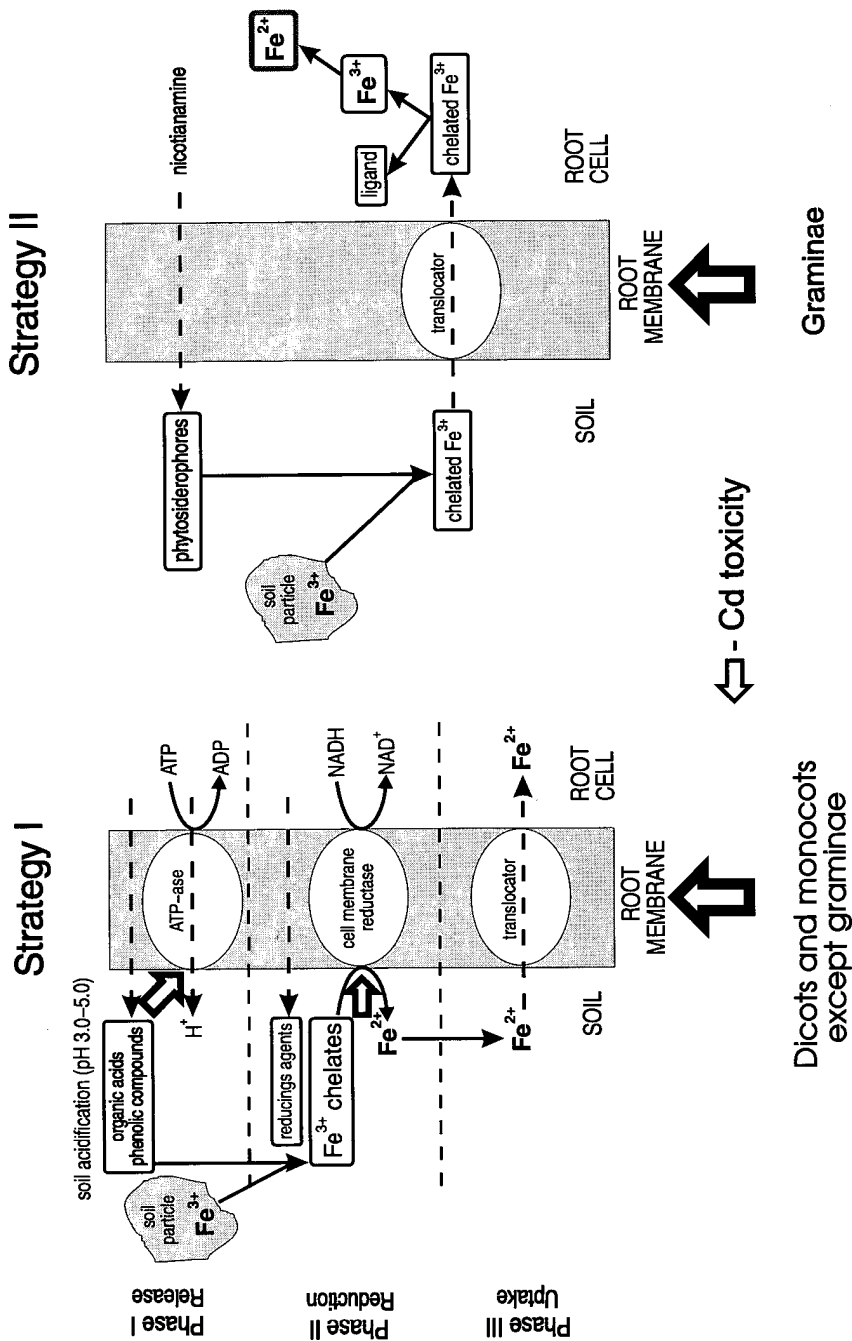


Fig. 1. Two strategies of Fe uptake by higher plants. White open arrows show the possibilities of Cd influence (specific proteins and/or root membrane as a whole). See text for more explanations.

It may be one of the most important aspects of Cd toxicity (Terry 1981, Thys *et al.* 1991, Siedlecka and Baszyński 1993, Siedlecka 1995).

The influence of excessive Fe doses on Cd-treated plants showing strategy I of Fe uptake has yet been unknown. When Fe-deficient plants were transferred to a medium with enhanced Fe-supply, two phases in plant membrane Fe^{3+} reductase response were observed. After the initial increase in its activity and rapid Fe uptake, the second phase was characterized by decrease in reductase activity. The final activity was adjusted to the final Fe supply (Schmidt *et al.* 1996). Some indirect results were obtained for plants cultivated under Cd/Fe interaction. The extent of Cd influence on Fe accumulation in roots depended on external Fe supply. In a nutrient medium deficient in Fe, the significance of Cd influence decreased with increased deficiency of Fe. However, in the presence of Cd in the nutrient medium the uptake of Fe was markedly decreased (Siedlecka and Krupa 1996a). Cadmium interference with Fe translocation from roots to leaves is one of the most important aspects of Cd/Fe interaction. In the presence of Cd in nutrient medium this translocation decreased significantly, resulting in Fe deficiency in shoots (Wallace *et al.* 1992, Fodor *et al.* 1996, Siedlecka and Krupa 1996a). The strategy II-plants are less sensitive to Cd toxicity than those of strategy I (Marschner 1995).

Nonetheless, Fe can also influence the Cd uptake and translocation from roots to shoots. Under Cd stress, plants develop at least one of the three known ways of heavy metal immobilization in roots (Brune *et al.* 1995, Leita *et al.* 1996): transformation into metabolically non-active compounds, *e.g.*, by chelating with non-protein amino acids; accumulation of toxic ions in the cell wall or vacuole; precipitation in the form of insoluble salts or chelating with citric acid, phytochelatines, homophytochelatines.

The ways of Fe interaction with these mechanisms have not been investigated yet, but in experiments with bean plants the nutrient-medium Fe deficiency resulted in increased translocation of Cd to leaves (Siedlecka and Krupa 1996a). Cadmium immobilization in roots was enhanced at excessive Fe supply (Thys *et al.* 1991, Siedlecka and Krupa 1996a).

Cd/Fe interaction *versus* leaf and chloroplast structure

Each plant organ, due to membrane selectivity and mechanisms of heavy metals immobilization, is a barrier to Cd movement from the soil to the chloroplasts. Only a small part from the total pool of Cd accumulated by plant can reach the leaf, and again only a part of it can enter chloroplasts (Fig. 2, Krupa and Baszyński 1995). Nevertheless, this slight amount of Cd develops many direct and indirect effects which, added together, result in a strong inhibition of photosynthesis. This phenomenon is known as the "enhancement effect" or the "effect of multiplication" (Krupa and Baszyński 1995). Leaf growth inhibition, acceleration of senescence processes, disturbances in stomatal movements (closing of stomata or blocking their movement at the permanent opening state), increase in activity of peroxidases, ribonucleases, and deoxyribonucleases belong to the common symptoms of Cd toxicity (Fig. 3, Barceló and Poschenrieder 1990, Greger and Johansson 1992, Costa

and Morel 1994, Krupa and Baszyński 1995, Siedlecka 1995). Hence, the heavy metal influence on plants depends largely on their growth stage: at the early stage of development plants respond mainly by growth inhibition, while older plants respond by acceleration of the senescence processes (Sheoran *et al.* 1990, Sieghardt 1990,

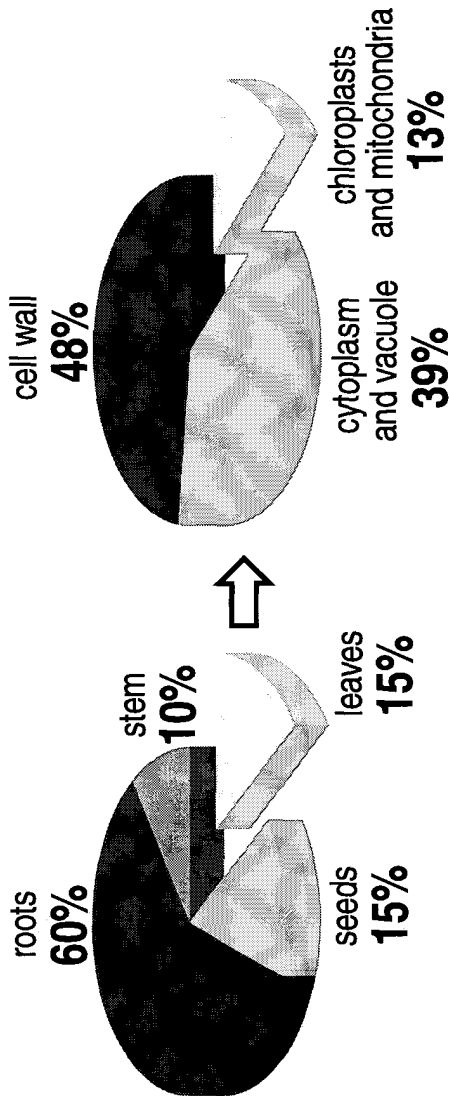


Fig. 2. Cadmium distribution in the higher plant (values from Ernst 1980, Jastrow and Koeppel 1980, Krupa and Baszyński 1995, Siedlecka and Krupa 1996b).

Krupa and Baszyński 1995, Skórzyńska-Polit *et al.* 1995). Similar relationships were also observed in the influence of toxic Fe concentrations (Guerinot and Yi 1994, Kampfenkel *et al.* 1995). Chlorophyll (Chl) synthesis and incorporation into Chl-protein complexes are diminished in the presence of Cd (Böddi *et al.* 1995, Horváth *et al.* 1996).

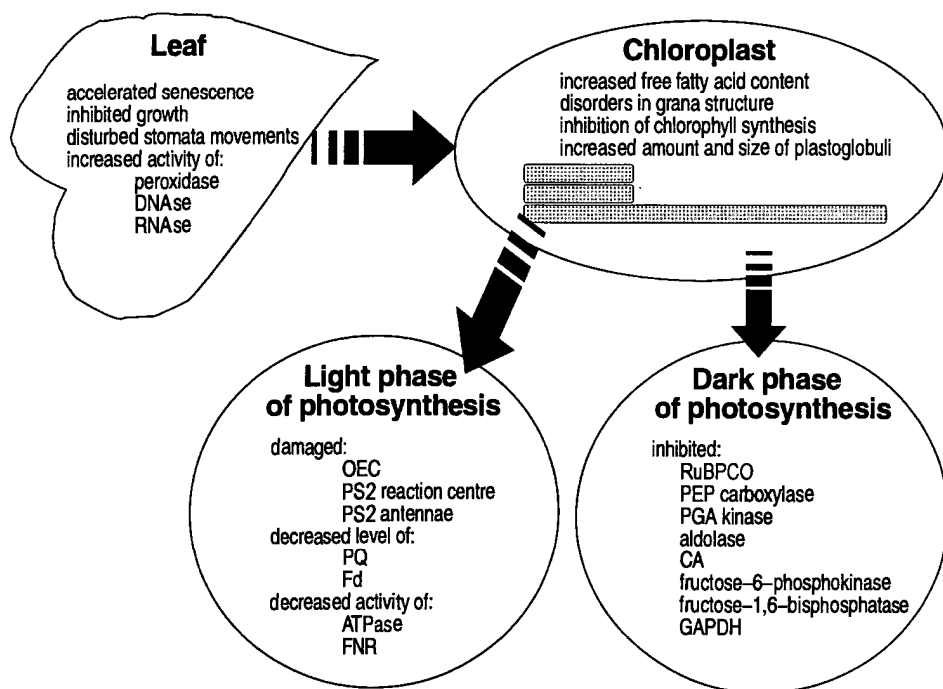


Fig. 3. Physiological and metabolic processes of higher plants influenced by Cd. CA - carbonic anhydrase; Fd - ferredoxin; FNR - ferredoxin-NADP reductase; GAPDH - glyceraldehyde phosphate dehydrogenase; OEC - oxygen evolving complex; PEP - phosphoenolpyruvate; PGA - 3-phosphoglycerate; PQ - plastoquinone; RuBPCO - ribulose-1,5-bisphosphate carboxylase/oxygenase. See text for details.

Under Cd/Fe interaction, the increase in susceptibility of young bean plants to Cd under Fe-deficiency was considered after observation of severe inhibition of growth and decrease in Chl accumulation. Detoxificatory influence of a double Fe dose on Cd-treated bean plants resulted in increased leaf size and pigment accumulation. Nonetheless, synergism between high Fe excess and high Cd concentrations resulted in severe leaf growth inhibition (Siedlecka and Krupa 1996a,b).

Chloroplasts are most sensitive both to Cd-stress and nutrient-medium Fe deficiency or Fe excess (Platt-Aloia *et al.* 1983, Terry and Abadía 1986, Barceló *et al.* 1988, Kampfenkel *et al.* 1995, Stoyanova and Tschakalova 1997). Only about 1 % of the total Cd accumulated by a plant is located in chloroplasts, but it causes severe

disturbances in their structure and function (Ghoshroy and Nadakavukaren 1990, Siedlecka and Krupa 1996b). Direct and/or indirect influence of Cd is observed as increased pool of free fatty acids in thylakoid membranes, disturbances in grana structure, increase in size or amount of plastoglobuli, damages in light-harvesting antennae of PS2, PS2 reaction centre, and oxygen evolving complex, decrease in the amounts of plastoquinone and ferredoxin, and decrease in the activity of ferredoxin:NADP oxidoreductase and ATPase (Fig. 3, Baszyński 1986, Krupa *et al.* 1987, 1993, Barceló *et al.* 1988, Becerril *et al.* 1988, Krupa 1988, Maksymiec and Baszyński 1988, Sheoran *et al.* 1990, Siedlecka and Baszyński 1993, Costa and Morel 1994, Skórzyńska-Polit *et al.* 1995).

For young bean plants investigated in Cd/Fe interaction experiment some modifications in leaf Cd distribution were observed. With the increase in Fe availability for roots the Cd mobility within the plant decreased, resulting in decrease in chloroplast-located Cd (Siedlecka and Krupa 1996b).

Cd/Fe interaction and the light phase of photosynthesis

Cd-induced Fe deficiency has been well documented for Cd-treated plants. The photosynthetic electron transport chain might be limited by decreased availability of Fe because of many of its Fe-containing constituents. Until now this relationship has been directly confirmed for ferredoxin (Siedlecka and Baszyński 1993). Nevertheless, as mentioned above, the effect of multiplication in Cd toxicity for the photosynthetic apparatus results in inhibition of the whole photosynthetic electron transport chain. In *in vivo* experiments, ATP accumulation was observed due to its limited use in further steps of photosynthesis at non-disturbed synthesis, both for blue-green algae and higher plants (Pawlik *et al.* 1993, Siedlecka *et al.* 1997). For bean plants this phenomenon was confirmed by Chl *a* fluorescence measurements showing increased pH gradient in thylakoids (Krupa *et al.* 1992, 1993, Krupa and Siedlecka 1995, Siedlecka *et al.* 1997). In *in vitro* experiments, PS2 was more sensitive to Cd toxicity than PS1 (for review see Baszyński 1986, Krupa and Baszyński 1995), but in experiments with chloroplasts isolated from *in vivo* Cd-treated plants the activity of both photosystems as well as photosynthetic O₂ evolution were inhibited to a similar extent (Siedlecka and Krupa 1996b). The comparison between direct measurements of the activity of the photosystems and Chl *a* fluorescence values obtained for bean plants under Cd/Fe interaction showed that Cd influence on PS2 and PS1 activities markedly depended on Fe supply. Under nutrient-medium Fe deficiency, the activity of both photosystems decreased and plants were more sensitive to Cd-toxicity. Enhanced Fe supply, despite being a limiting factor for the photosynthesis of control plants, had a beneficial influence on Cd-treated plants (Siedlecka and Krupa 1996b). However, the results of fluorescence measurements suggested that the observed changes in the light phase of photosynthesis were rather of indirect nature due to inhibited activity of the Calvin cycle (Krupa *et al.* 1992, 1993, Krupa and Siedlecka 1995, Siedlecka and Krupa 1996b).

Cd/Fe interaction and the enzymes of the dark phase of photosynthesis

Since the experiments of Weigel (1985a,b), suggesting the Calvin cycle as the primary target of Cd toxicity, enzymes connected with the dark phase of photosynthesis have often been studied. In many *in vitro* and *in vivo* experiments disturbances in saccharide metabolism were observed (Vassilev *et al.* 1997) that were due to Cd-dependent inhibition of enzymes such as RuBPCO, phosphoenolpyruvate carboxylase, glyceraldehyde-3-phosphate kinase, aldolase, fructose-6-phosphate kinase, fructose-1,6-bisphosphatase, and carbonic anhydrase (Fig. 3, Lee *et al.* 1976, Weigel 1985a,b, Stiborová 1988, Greger 1989, Greger and Ögren 1991, Greger and Bertell 1992, Malik *et al.* 1992, Krupa and Baszyński 1995). The nutrient-medium Fe-deficiency also decreased RuBPCO activity and depleted the carboxylation process, while Fe excess stimulated photorespiration (Kampfenkel *et al.* 1995, Winder and Nishio 1995).

Heavy metals affect the activity of these enzymes by complicated mechanisms of direct inhibition or activation or by indirect effect on the regulatory mechanisms (van Assche and Clijsters 1990). In leaves of bean plants, Cd and non-physiological Fe concentrations (deficiency or excess) in the growth medium resulted in decrease in RuBPCO activity (Siedlecka *et al.* 1997). As reviewed by Portis (1992), limited RuBPCO activity may be counteracted by RuBPCO activation system. Its operation is expressed by increased RuBPCO activation state (% of enzyme protein active *in vivo*) and enhanced CO₂ availability resulting from elevated carbonic anhydrase (CA) activity. Increase in the ATP/ADP ratio may also be a part of this mechanism. All elements of this system may cooperate or operate separately (Portis 1992). At low Cd concentration one of these elements - increase in CA activity - was sufficient to maintain full RuBPCO activity, but only at optimum Fe supply (Siedlecka *et al.* 1997). At high Cd concentrations as well as at non-optimum Fe doses, CA activity decreased and other elements of the RuBPCO activation system predominated. Unfortunately, they were not efficient enough to counteract the stress limitations and the RuBPCO activity decreased (Siedlecka *et al.* 1997). Thus, CA-dependent mechanism of RuBPCO activation may belong to the most efficient ones, but its operation is restricted by Fe nutrition status and high Cd concentrations.

Concluding remarks

Cd/Fe interaction significantly affects plant growth and development. Nutrient-medium Fe deficiency results in decreased Fe content in roots and leaves, and also in increased uptake and accumulation of Cd. Moderate Fe excess beneficially influences Cd-treated plants, their growth, Chl accumulation, and the light phase of photosynthesis, but a strong Fe excess, toxic itself, enhances Cd toxicity. Nonetheless, the influence of different Cd and Fe availability on plant growth and metabolism cannot be considered only as the changes in content of both metals in the plant tissue. These mechanisms are much more complicated, and many aspects of

their operation still remain unexplained. At least two interesting aspects of Cd/Fe interaction need further investigations:

(1) The influence of Fe on Cd uptake and distribution within plant: Cd immobilization in roots decreases with decreased Fe content in nutrient medium. This results in increased Cd toxicity towards photosynthesis. Mechanisms of Fe-dependent Cd immobilization in roots are unknown at present. It is even difficult to speculate which one of Cd immobilization systems is affected: phytochelatin, non-protein amino acids, chelating by cell wall components, or any other possible way. Moreover, not only Cd transport to leaves, but also its translocation to chloroplasts is diminished by increasing Fe supply.

(2) The particular sensitivity of the photosynthetic dark phase to Cd/Fe interaction. At optimum Fe content in nutrient medium and moderate Cd stress the unique mechanism of CA-connected maintaining of RuBPCO activity is very efficient. However, it is still unknown why this mechanism, in which Zn-containing enzyme (CA) seems to play a key role, is so dependent on Fe status in plant? Nutrient-medium Fe deficiency is a limiting factor for RuBPCO and CA activities and, although Cd-dependent CA-activation mechanism may operate, it is ineffective in maintaining depleted RuBPCO activity. Surprisingly, even the moderate Fe excess, so beneficial for the growth and light phase of photosynthesis in Cd-treated plants, decreases RuBPCO and CA activities and blocks CA-dependent mechanism of plant adaptation to Cd stress. Particular sensitivity of dark phase to heavy metal stress, well documented now, is not a satisfying explanation for this phenomenon.

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