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Interference of Cd^{2+} in functioning of the photosynthetic apparatus of higher plants

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Abstract

The actual opinions concerning the role of Cd^{2+} in inhibition of photosynthesis have been reviewed. The light phase of photosynthesis, particularly the site of Cd^{2+} action in the photosynthetic transport chain has been given the greatest attention. Cd^{2+}-induced inhibition of Photosystem II activity as the result of thylakoid membrane degradation has been discussed. The present studies on Cd^{2+}-inhibited dark reactions occurring in stroma has been analysed. Attention has been drawn to the fact that the results of studies *in vitro* are not always compatible with the changes found in the photosynthetic apparatus of higher plants growing in a Cd^{2+} containing medium.

Key words: acyl lipids, cadmium, photosynthesis, photosynthetic electron transport, photosystem I, photosystem II, thylakoid membrane

INTRODUCTION

Cadmium is one of the most toxic heavy metals in the contemporary environment and a prevalent metal in municipal and industrial effluents. Although Cd^{2+} is not known as an essential mineral nutrient for plants present in water and soil, it is readily taken up by the root system of many plant species, leading to toxicity symptoms such as growth reduction (Lamoreaux and Chaney 1977, Mahler et al. 1978, Jastrow and Koeppe 1980, Weigel and Jäger 1980, Rathore et al. 1981). A relatively high mobility of the metal in plant tissues induces impairement of cell metabolic processes (Miller et al. 1973, Huang et al. 1974, Li and Miles 1975, Strickland and Chaney 1979, Lee et al. 1976, Ernst 1980, Weigel

and Jäger 1980, Van Bruwaene et al. 1984, Weigel 1985a, b) as well as destruction of plant cells or organelles (Bittell et al. 1974, Simola 1977, Lamoreaux and Chaney 1978, Baszyński et al. 1980). The mechanism of Cd^{2+} toxicity has already been examined, using chloroplasts and mitochondria, intact plants, tissue homogenates and plant exudates (see Wagner 1979).

Photosynthetic processes of higher plants, being the main subject of our concern here, are particularly susceptible to Cd^{2+} (Carlson et al. 1975, Carlson and Bazzaz 1977, Jastrow and Koeppe 1980, Baszyński et al. 1980). Elevated levels of Cd^{2+} are known to inhibit photosynthesis in general and photosynthetic CO_2 fixation in particular (see Peterson and Alloway 1979). For example, according to Page et al. (1972), a 50% decrease in the yield was found in some field crops with tissue concentrations as low as 2-9 ppm Cd^{2+}. Other nonessential heavy metals of such a concentration are without effect on the crop yield (Hardiman and Jacoby 1984).

There may be many reasons for which Cd^{2+} inhibits the CO_2-fixation and they should be searched for in various phases of this process. One of the reasons of the inhibition of the whole plant net photosynthesis accompanied by reduced transpiration, as seen from the studies with detached leaves, has been attributed to Cd^{2+} induced closure of the stomata (Bazzaz et al. 1974a, b, Carlson et al. 1975, Lamoreaux and Chaney 1978). This aspect, however, will be deliberately omitted in further considerations of this paper, to deal more closely with Cd^{2+} interference in processes of photosynthesis at its molecular level.

THE EFFECT OF Cd^{2+} ON MEMBRANE-BOUND PHOTOCHEMICAL REACTIONS

So far, the studies on Cd^{2+} interference have been largely concerned with the light phase of photosynthesis. Most information concerning the effect of Cd^{2+} on photosynthetic electron transport comes from the studies in which Cd^{2+} solutions were fed to detached plant parts or added to isolated, broken or intact chloroplasts. Only in very few studies plants grown in the presence of the metal were used. It is noteworthy that the results obtained by both techniques, *in vitro* and *in vivo*, have not been always identical and unequivocal. It also seems that experiments *in vivo* provide data which reflect more validly the situation occurring in the natural environment.

Some experiments *in vitro* show that Cd^{2+} could directly affect photosynthetic reactions of chloroplasts: changes in the concentration and composition of pigments (Bazzaz and Govindjee 1974), inhibition of photo-

systems activity (Bazzaz and Govindjee 1974, Li and Miles 1975, Van Duijvendijk-Matteoli and Desmet 1975), inhibition of photophosphorylation (Lucero et al. 1976), and uncoupling of electron transport flow (Van Duijvendijk-Matteoli and Desmet 1975).

Bazzaz and Govindjee (1974) using isolated maize chloroplasts in examinations of the effect of Cd^{2+} on photoreactions indicated the inhibition of PS II activity at the oxygen-evolving site of this system. The inhibitory effect of the metal on the electron transport has been also investigated by Van Duijvendijk-Matteoli and Desmet (1975) in broken spinach chloroplasts as measured by the oxygen uptake from the solution in Mehler reaction and by the induction of fluorescence. Using hydroxylamine and exogenous Mn to restore this activity they were able to show that Cd^{2+} is an inhibitor on the donor side of PS II at the water-splitting system. Similar results have been obtained by Hampp et al. (1976). They assumed that Cd^{2+} affects the electron flow between water oxidation and PS II. This site of Cd^{2+} action was questioned by Li and Miles (1975). According to their data the site of Cd^{2+} action is either at the primary electron donor or reaction center of the PS II reaction. However, a 25% loss of the total chlorophyll during Cd^{2+} treatment of isolated chloroplasts reported by Bazzaz and Govindjee (1974) and a 4.8% loss of the long-wave absorbing form of chlorophyll a during the treatment shown by Li and Miles (1975) have lead the latter authors to the conclusion that Cd^{2+} alters rather the reaction center chlorophyll of PS II.

Recently, the effect of Cd^{2+} on PS II activity was confirmed in the studies of Cd^{2+}-induced fluorescence properties at different stages of the greening processes in barley seedlings (Roynet et al. 1981). Moreover, these studies showed that Cd^{2+} effects the conformational state of the membranes, which suggests a relationship between the thylakoid structural organization and the Cd^{2+}-induced fluorescence changes. Thence the authors were inclined to assume that the inhibition of the electron flow by Cd^{2+} could be due to thylakoid membrane perturbations rather than to a direct effect on the water-splitting system. Investigating later the Cd^{2+} inhibition characteristics by prompt and delayed fluorescence and by flash oxygen yield measurements, Roynet and Lannoye (1984) suggested that Cd^{2+} inhibits the charge stabilization steps on the oxidizing side of PS II. They also confirmed some inhibition of oxygen evolving capacity in the presence of Cd^{2+}.

PS II activity decrease as the result of disorganization of the photosynthetic apparatus was suggested earlier in the *in vivo* studies on the photochemical activity of photosystems of Cd^{2+}-treated tomato plants (Baszyński et al. 1980).

Although most of the data of studies *in vitro* point to an inhibitory effect of Cd^{2+} on PS II, the exact site of its action remains unresolved.

To test the possibilities that Cd^{2+} blocks the electron transport of PS I in isolated chloroplasts, Li and Miles (1975) measured the methyl viologen reduction in the presence of DAB and showed that Cd^{2+} inhibition is limited to PS II only. PS I was fully functional when a PS I electron donor was provided. An isolated opinion is represented by De Filippis

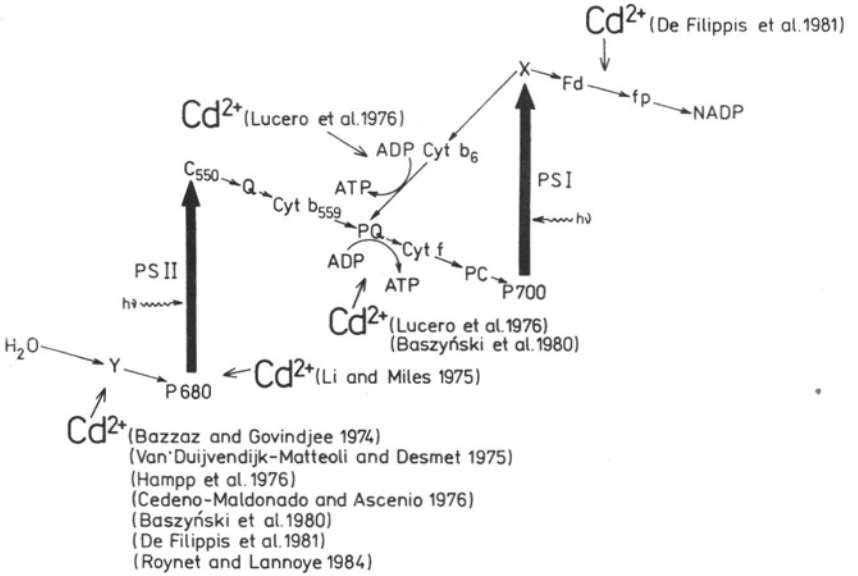

Fig. 1. The possible site for Cd^{2+} action in photosynthetic electron transport chain

et al. (1981b), who, on the basis of observations with *Euglena* obtained under quasi *in vivo* conditions, assume two sites of Cd^{2+} inhibition in the photosynthetic electron transport chain. Besides the commonly recognized site associated with PS II the second site of action is distinguished which appears to be localized at the reducing side of PS I. The main inhibition site of electron flow around PS I should be NADP-oxidoreductase involved in the photoreduction of NADP. It is a sulphydryl requiring enzyme, and Cd^{2+} being a powerful sulphydryl antagonist could inhibit its activity (Vallea and Ulmer 1972).

The synthesis of ATP, the second product of the light phase of photosynthesis is also affected by Cd^{2+}. In isolated broken chloroplasts Cd^{2+} inhibits cyclic and non-cyclic phosphorylation (Lucero et al. 1976).

According to our knowledge of the relationship between the structure and function in thylakoid membranes one can suppose that Cd^{2+} may effect the structure of the membrane disorganizing its architecture. However, the studies *in vitro* have not brought any data in this regard. Occasional studies of plants growing on Cd^{2+}-containing medium point to changes in

chloroplast organization. Cd^{2+} causes first of all a significant decrease in chlorophyll content (Czuba and Armrod 1973, Imai and Siegel 1973, Baszyński et al. 1980, Callegari and Lannoye 1981, De Filippis et al. 1981a). This decrease depends on the age of leaves; younger leaves are less tolerant of Cd^{2+} concentration (Buczek 1984). A decrease of

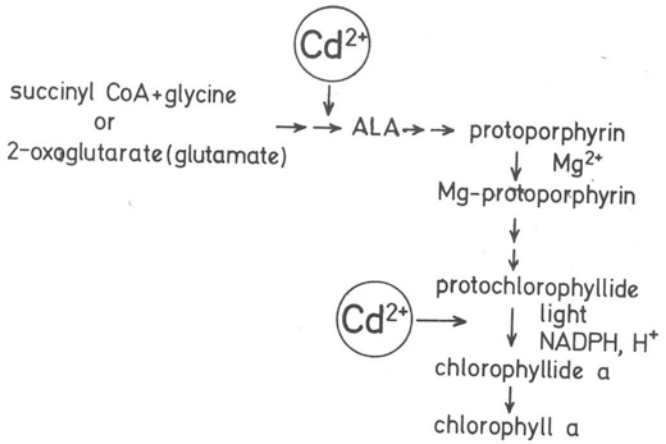

Fig. 2. The site for Cd^{2+} action in the pathway of chlorophyll biosynthesis

chlorophyll content in leaves may result from inhibition of this pigment biosynthesis or its enzymatic degradation. There is no precise evidence of Cd^{2+}-induced decomposition of the pigment. However, Stobart et al. (1985) have recently shown that Cd^{2+} inhibits the biosynthesis of chlorophyll on the level of the formation of the photoactive protochlorophyllide reductase complex and of the synthesis of 5-aminolaevulinic acid. This finding suggests that the inhibition of chlorophyll biosynthesis could represent a primary event in the toxicity of Cd^{2+} for plant growth (Stobart et al. 1985). It is also in agreement with the statement of Baszyński et al. (1980) that *in vivo* Cd^{2+} lowered the chlorophyll concentration in tomato plants before affecting photosynthesis.

The electron micrographs of chloroplasts of the tomato treated with Cd^{2+} show very significant changes in relation to control plants (Fig. 3). They concern the occurrence of plastoglobules which give evidence of the lipids release from thylakoid membranes and disorganization of the inner structure mainly that of grana stacks (Baszyński et al. 1980). The chloroplasts of Cd^{2+}-treated plants are also distinctly smaller. This observation is confirmed by measurements of the volume of chloroplasts and their number per surface unit of the leaf of several plant species studied (Dudka et al. 1983, Kłobus and Buczek 1985, Stacko and Tukendorf, unpublished). Degradation of the inner structure of chloroplasts due to the long-term action of Cd^{2+} on tomato plants is similar to senescence response. One

Table 1

Acyl lipid content of thylakoid membranes isolated from chloroplasts of control and Cd^{2+}-treated tomato plants. Values represent the mean ± SE of three replicates (Krupa and Baszyński, unpublished)

Acyl lipids	Thylakoid membranes	Lipid content, μmol/μmol Chl	%
Monogalactosyl-diacylglycerol	control	1.858 ± 0.036	100
	Cd^{2+}-treated	1.337 ± 0.103	72
Digalactosyl-diacylglycerol	control	0.827 ± 0.061	100
	Cd^{2+}-treated	0.669 ± 0.017	81
Sulfoquinovosyl-diacylglycerol	control	0.297 ± 0.034	100
	Cd^{2+}-treated	0.249 ± 0.002	84
Phosphatidyl-glycerol	control	0.323 ± 0.005	100
	Cd^{2+}-treated	0.246 ± 0.024	76
Phosphytidyl-choline	control	0.117 ± 0.008	100
	Cd^{2+}-treated	0.077 ± 0.003	66
Total	control	3.422	100
	Cd^{2+}-treated	2.578	75
Trans Δ^3-hexadecenoic acid present in phosphatidylglycerol, mol%			
	control	22.7 ± 4.1	
	Cd^{2+}-treated	15.9 ± 2.1	

of the recently noted symptoms of senescing processes induced by Cd^{2+} treatment of plants could be degradation of acyl lipids in thylakoid membranes. Such changes in acyl lipid composition during ageing of isolated chloroplasts were demonstrated earlier (Siegenthaler and Rawyler 1977). On the other hand PS II activity in Cd^{2+}-treated plants decreases considerably at almost unchanged PS I activity. At the same time inhibition of non-cyclic phosphorylation is observed, but cyclic phosphorylation is unaffected (Baszyński et al. 1980). Thus the question arises whether PS II activity decrease is caused by decomposition of lipids in thylakoid membranes. The chloroplasts of Cd^{2+}-treated plants show a distinct decrease in the content of all acyl lipids occurring in them, to a different extent in each of them (Table 1). There seems to be no doubt that the decomposition of acyl lipids results in the impairement of the membrane functions sustained by these lipids, including PS II activity.

Among the lipids responsible for the impairement of PS II activity, the loss of which is observed under Cd^{2+} treatment, two deserve a special attention. One is supposed to be phosphatidylcholine which, in the opinion

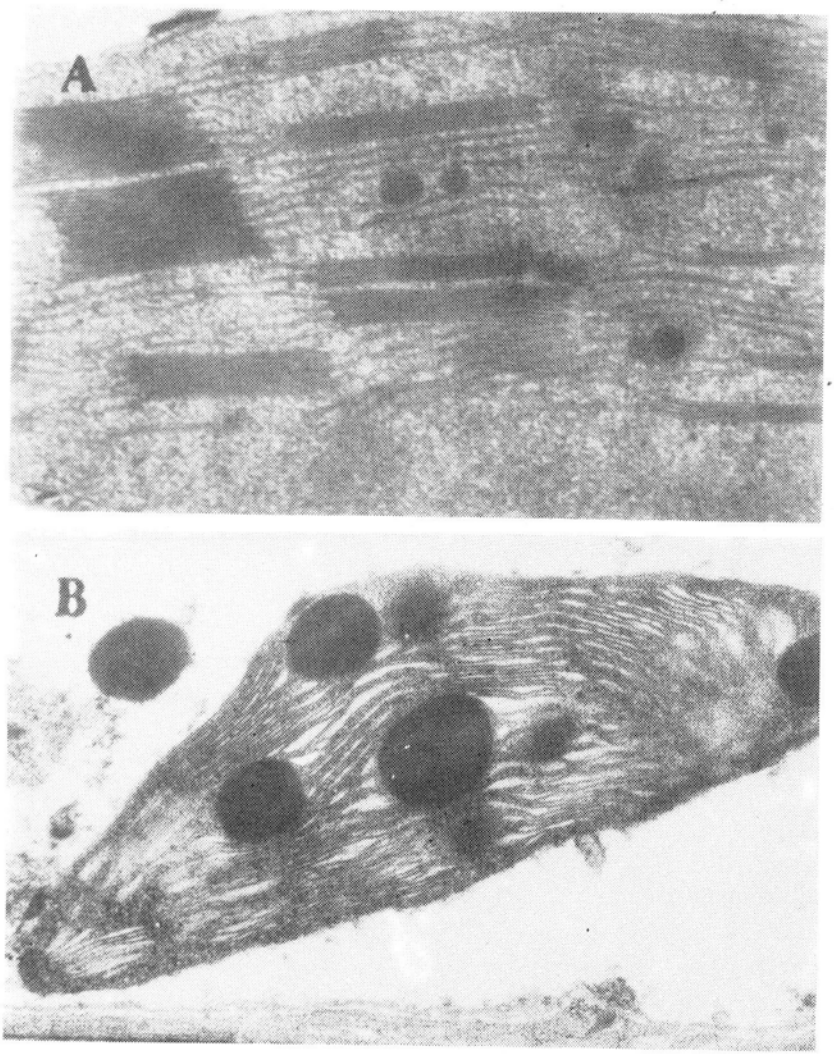

Fig. 3. Electron micrographs of the chloroplasts of Cd^{2} -treated tomato plants. 40000×. A — control chloroplast from full nutrient leaves. B — chloroplast of Cd^{2} -treated plants (Baszyński et al. 1980)

of many investigators, is associated with the PS II complex (Siegenthaler 1982, Krupa 1984, Radunz 1984). According to Rawyler and Siegenthaler (1981a) the presence of an intact pool of phosphatidylcholine in the inner layer of the membrane is essential for maximal PS II activity. Also Gounaris et al. (1983) demonstrated that this lipid stimulates O_2 evolution in an oxygen-evolving PS II preparation.

The other lipid may be phosphatidylglycerol, the loss of which in thylakoid membranes of Cd^{2+}-treated plants is also very high. This supposition is

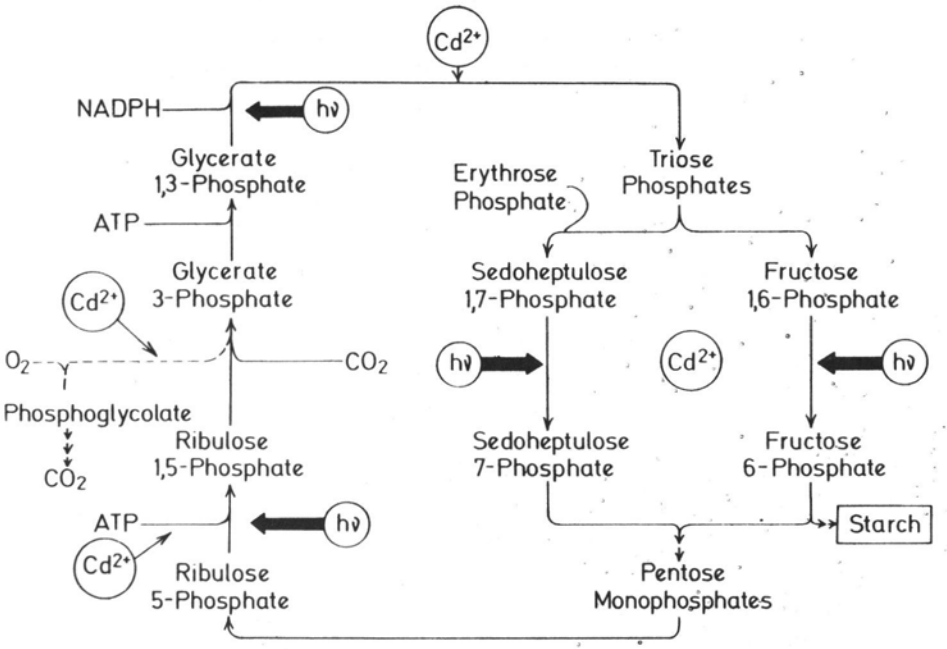

Fig. 4. The possible inhibitory sites of Cd^{2+} on Calvin cycle

based on the hypothesis suggesting that phosphatidylglycerol could play a role in grana stacking (Dubacq and Tremolières 1983). A good correlation between the amount of appressed thylakoids and the synthesis of phosphatidylglycerol molecules containing trans-Δ^3-hexadecenoic acid has often been observed (see Dubacq and Tremolières 1983). This acid present in phosphatidylglycerol is probably linked to the formation of grana stacks (Tremolières et al. 1982). The disappearence of grana stacks in chloroplasts of Cd^{2+}-treated plants and the following decrease in PS II activity (Baszyński et al. 1980) may thus be the result of the decrease in phosphatidylglycerol content and of the release outside the lamellae of almost 1/3 of trans-Δ^3--hexadecenoic acid present in control plants. It was also shown recently that phosphatidylglycerol — component of lipid environment of the PS II complex — has a dramatic effect on its electron transport capacities (Murphy

et al. 1984). On the basis of investigations on thylakoid membranes treated with phospholipase Rawyler and Siegenthaler (1981b) suggest another possible physiological role of phosphatidylglycerol as an element which may regulate the rate of PS I electron transport.

Accordingly, there arises the question whether Cd^{2+} affects lipid and/or fatty acid biosynthesis. For the time being this question has remained unanswered. The disappearing grana and the increase of the number of plastoglobules observed in the electron micrographs rather account for the effect of Cd^{2+} on hydrolysis of lipids. As yet, the activity of lipases in leaves of Cd^{2+}-treated plants has not been determined. Were the decrease in lipid content in thylakoid membranes of Cd^{2+}-treated plants not caused by inhibition of lipid biosynthesis but by degradation processes, the release of fatty acids could be also taken into consideration. The low PS II activity in Cd^{2+}-treated plants could probably depend on these acids which might appear due to the degradation of chloroplast lipids. In the experiments with isolated chloroplasts, unsaturated fatty acids inhibited photosynthetic electron transport (Krogmann and Jagendorf 1959). Although electron flow activities through both photosystems were affected by free fatty acids, those of PS II were far more sensitive than those of PS I (Siegenthaler and Rawyler 1977). One can ask whether the decrease in lipid content in the membranes of Cd^{2+}-treated plants is quantitatively related to the release of unsaturated fatty acids from the membrane and whether these amounts are sufficient to account for the decrease of PS II activity. It was shown by Siegenthaler (1973) and Venediktov and Krivosheyeva (1983) that the effective concentration range of unsaturated fatty acids for 50% PS II inhibition was a fatty acid/chlorophyll molar ratio of about 1.0. From calculations of the data obtained in experiments with Cd^{2+}-treated plants it emerges that the amount of these acids exceeds this ratio and may contribute to such decrease of PS II activity observed in these plants. Siegenthaler (1974) reported that the inhibition site of unsaturated fatty acids is located on the oxidizing side of PS II, which is the same as that of Cd^{2+} inhibitory action shown previously *in vitro* as well as *in vivo* experiments (Bazzaz and Govindjee 1974, Van Duijvendijk-Matteoli and Desmet 1975, Baszyński et al. 1980).

At present there is not available an experimental confirmation of free fatty acids involvement in PS II activity decrease caused by Cd^{2+} action *in vivo*. However, such a possibility has been confirmed *in vitro*. The protection of bovine serum albumin against the inhibitory effect of Cd^{2+} on PS II activity showed that fatty acids released from the thylakoid membranes incubated with Cd^{2+} are the main agents inducing this inhibition (Krupa and Baszyński 1985). Incomplete restoration of PS II activity in the presence of bovine serum albumin indicates a possible damage of the membrane structure due to Cd^{2+} treatment, which could also be the reason

of PS II activity inhibition but to a much lesser extent. However, the role of unsaturated fatty acids in the decrease of PS II activity of chloroplasts isolated from plants growing on Cd^{2+}-containing medium cannot be judged without a closer examination. Changes of the chloroplast structure caused by Cd^{2+} action *in vivo* are, as it was mentioned above, similar to those observed in ageing organellae, but loss of activity of chloroplasts during senescence is not caused by liberation of free unsaturated fatty acids as reported by Köckritz et al. (1984). It seems that in the light of the present studies it can be concluded that the decrease in PS II activity observed in chloroplasts of Cd^{2+}-treated plants results from structural and functional alteration of the thylakoid membranes because of the decomposition of the lipid environment of PS II. Changes in the polypeptides composition of thylakoid membranes caused by Cd^{2+} need a separate discussion but the present very few observations do not permit to express an opinion on them.

THE EFFECT OF Cd^{2+} ON DARK REACTIONS OF PHOTOSYNTHESIS

Reduced PS II activity and non-cyclic phosphorylation rates in chloroplasts of Cd^{2+}-treated plants (Baszyński et al. 1980) decrease the photosynthetic NADP and ATP production which may be the cause of Cd^{2+}-induced photosynthetic CO_2-fixation inhibition. However, the involvement of dark reactions in the inhibitory effect of Cd^{2+} cannot be excluded. The possibility of Cd^{2+} action on the photosynthetic apparatus at the level of dark reaction was indicated by the inhibition of CO_2-fixation by isolated spinach chloroplasts at lower Cd^{2+} concentrations than those reported for the inhibition of electron transport (Hampp et al. 1976, Cedeno-Maldonado and Ascenio 1976). Recently Weigel (1985a, b) provided evidence that electron transport reactions are not involved in Cd^{2+}-induced inhibition of photosynthesis. Weigel's studies, however, were carried out on mesophyll protoplasts or isolated intact chloroplasts exposed to Cd^{2+}, and further studies are needed to elucidate whether his findings are also valid in regard to long-term exposure of whole plants to Cd^{2+}. Protoplasts are close to the *in vivo* situation but are nevertheless independent, e.g. of limitations caused by increased stomatal resistance.

Weigel (1985a) measuring 77K chlorophyll fluorescence emission spectra in the absence and presence of Cd^{2+} as well as light induced electrochromic pigment absorption changes around 518 nm, obtained results showing that electron transport at PS II and PS I was not affected by the metal ions. Also in isolated intact chloroplasts neither electron transport at PS II nor the whole chain of the electron transport as measured by methyl viologen-dependent O_2 uptake were significantly impaired by Cd^{2+} (Weigel 1985b). During these measurements CO_2-fixation was almost totally inhibited by the metal as measured by CO_2 dependent O_2-evolution of both protoplasts and intact chloroplasts. A closer information about the location of

Cd^{2+} inhibition within the Calvin cycle is provided by studies on steady state concentrations of ^{14}C-labeled Calvin cycle intermediates (Weigel 1985b). These results imply that Cd^{2+} inhibits photosynthesis by interaction with different sites of the Calvin cycle. Cd^{2+}-induced alteration of RuBP carboxylase/oxygenase activity may be one of the reasons for inhibition. The increase of the relative level of ^{14}C-labeled glycolate suggests the shift of enzyme activity more towards its oxygenase function. This is also accounted for by a smaller 3-phosphoglycerate sensitivity to Cd^{2+} than the overall CO_2-fixation. Weigel does not also exclude the participation of RuBP carboxylase in the inhibition of photosynthesis. Its participation is indicated by the increase of the level of ^{14}C-labeled glycolate and concomitant decrease and increase of the relative levels of ^{14}C-labeled 3-phosphoglycerate and RuBP. This assumption is contrary to the fact found earlier that light activation of RuBP carboxylase in isolated protoplasts is not affected by Cd^{2+} (Weigel 1985a). A strong inhibition of phosphoenolopyruvate carboxylase in C_4 plants by low concentration of Cd^{2+} was recently reported (Iglesias and Andreo 1984).

The regenerative phase of the cycle may be another site of Cd^{2+} inhibition. This supposition is based on the increase of the relative levels of ^{14}C-labeled triosephosphate and fructose-1,6-bisphosphate. That Cd^{2+} might also inhibit enzymes taking part in the reaction sequence pyruvate--phosphoenolopyruvate-oxalate-malate is suggested by a relative increase of ^{14}C-labeled pyruvate and decrease of malate.

Although the inhibition sites of dark reactions by Cd^{2+} have not been known completely, the discovery that inhibition of photosynthetic CO_2-fixation is determined above all by the reactions occurring in chloroplast stroma is not depreciated. Despite the lack of evidence at present that a similar inhibition mechanism occurs in chloroplasts of plants cultivated on Cd^{2+} containing medium, such a possibility should be taken into account. Future studies are expected to bring an answer to this question.

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Ingerencja Cd^{2+} w funkcjonowanie aparatu fotosyntetycznego roślin wyższych

Streszczenie

Przedstawiono współczesne poglądy dotyczące roli Cd^{2+} w inhibowaniu procesu fotosyntezy. Główną uwagę poświęcono świetlnej fazie fotosyntezy a zwłaszcza miejscu działania Cd^{2+} w łańcuchu fotosyntetycznego transportu elektronów. Przedyskutowano indukowane Cd^{2+} hamowanie aktywności II układu fotosyntezy jako wyniku degradacji błon tylakoidowych. Omówiono dotychczasowe badania nad rolą Cd^{2+} w hamowaniu reakcji ciemnych zachodzących w stromie. Zwrócono uwagę na fakt, iż wyniki badań *in vitro* nie zawsze wyjaśniają zmiany zachodzące w aparacie fotosyntetycznym roślin wyższych uprawianych na podłożu zawierającym Cd^{2+}.