CADMIUM-INDUCED OXIDATIVE STRESS IN POTATO TUBER

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(Received: November 22, 1996. Accepted: May 13, 1997)

ABSTRACT

Short-term treatment of tuber discs of potato (*Solanum tuberosum* L.) with cadmium chloride elevated the concentration of active oxygen species ($\cdot\text{O}_2^-$, H_2O_2) and activated the antioxidative system. Two cultivars, Bintje and Bzura, susceptible and tolerant, respectively, to cadmium were examined. In more tolerant, control tissues the activity of ascorbic acid peroxidase (AAP) and catalase (CAT) was higher than in the sensitive ones. During first hours of stress, the inhibition of superoxide dismutase (SOD), CAT and AAP was observed and it comes from inactivation of enzymes by cadmium ions. A subsequent activity increase of the enzymes aroused earlier in tolerant tissues. It seems therefore, that tolerant tissues possess a more efficient antioxidative system.

KEY WORDS: active oxygen species, ascorbic acid peroxidase, cadmium, catalase, *Solanum tuberosum* L., superoxide dismutase.

INTRODUCTION

Environmental factors, both abiotic and biotic, induce oxidative stress by increasing the synthesis of active oxygen species (AOS) ($\cdot\text{O}_2^-$, H_2O_2 , $\text{OH}\cdot$) in plant cells (Scandalios, 1993). A balance between the synthesis of AOS and their detoxication is maintained by an antioxidative system of cell (Monk et al., 1989). This system includes numerous enzymes and small molecules. Among the enzymes, the most important are: SOD, which scavenges $\cdot\text{O}_2^-$, as well as AAP and CAT which remove H_2O_2 . The non-enzymatic elements of system include antioxidants such as ascorbic acid, cysteine, glutathione, α -tocopherol and β -carotene.

Tuber parenchyma of potato cultivar Bzura – more tolerant to cadmium – had higher concentration of cysteine, glutathione and ascorbic acid than the tissues of the susceptible cultivar (Stroiński and Bandurska, 1996). Additionally, in the former material, after treatment with Cd^{+2} ions, an earlier increase in concentrations of the total, acid-soluble thiols and phytochelatins was noticed.

In some cases, the efficiency of some elements of the antioxidative defense system can determine, to some extent, the tolerance of cell to several stress factors (Bowler et al., 1992; Dalton, 1995), whereas in other cases such the relationship was not noticed. For example, several contrasting observations have been made on how SODs activities are involved in plant protection against air pollution stress. The SOD activity was higher in several plants more tolerant to oxidative stress induced by SO_2 , or NO_2 , or O_3 , or high light intensity, or low temperature (Jäger et al., 1980; Tanaka et al., 1988; Huttunen

and Heiska, 1988; Sen Gupta et al., 1991; Dalton, 1995) but in several others plants these factors either did not change or decreased the activity of this enzyme (Matters and Scandalios, 1987; Hausladen et al., 1990; Wingsle et al., 1992; Wingsle and Hällgren, 1993). Analysis of transgenic plants with overexpression of SOD showed that this effect may either be associated with greater resistance to oxidative stress (Bowler et al., 1991; Perl et al., 1993; Sen Gupta et al., 1993) or not (Tepperman and Dunsmuir, 1990; Pitcher et al., 1991). Similar contrasting effects with SOD activity were noticed for plants treated with some heavy metals. An increase of this enzyme activity in several plants, following the treatment with Cu, or Mn, or Al, or Pb, or Cd was observed (del Rio et al., 1985; Cakmak and Horst, 1991; Chongpraditnun et al., 1992; Przymusiński et al., 1995) and only in *Phaseolus vulgaris* seedlings treated with cadmium SOD activity was observed to decrease (Somashekaraiah et al., 1992).

The aim of this study was to investigate the influence of Cd^{+2} ions on the level of $\cdot\text{O}_2^-$ and H_2O_2 and activities of SOD, AAP and CAT in cadmium tolerant and non-tolerant tissues of potato tuber. In our earlier experiments the higher resistant cultivar in long-term cadmium-treatment exhibited smaller growth inhibition, higher cadmium dilution in the tissues, minor changes in macro- and ultrastructure, as well as in the Zn and Mn contents (Stroiński et al., 1990a, b). At the same time however, in these two kinds of tissues cadmium induced changes in polyamines levels (Stroiński and Szczotka, 1989; Stroiński, 1995a; Stroiński, 1997), in peroxidase activity (Stroiński, 1995b) and in membrane permeability (Stroiński and Floryszak-Wieczorek, 1990, 1993) were different.

MATERIALS AND METHODS

Experiments were carried out using tubers of two potato cultivars, Bintje and Bzura, respectively susceptible and tolerant to cadmium (Stroiński et al., 1990a, b). Tubers were superficially sterilized by immersing in 0.1% solution of sodium hypochlorite for 5 minutes. Discs (18 diameter x 4 mm thick) were excised from medulla of tubers and prior to treatment were aged for 20-24 hrs at 20 °C in the dark. After that the discs were infiltrated with CdCl_2 solutions (0.01 and 1mM) or H_2O , under two vacuum impulses for 1 min, then washed with distilled water, and incubated in a moist chamber at 20 °C in the dark. $\cdot\text{O}_2^-$ generation was determined from the amount of reduced cytochrome c, calculated from the increase in absorbance at 550 nm ($E=21.1 \text{ mM}^{-1} \text{ cm}^{-1}$), as described by Doke (1983). Other determinations were performed in discs, frozen in liquid nitrogen. Content of H_2O_2 was determined as described Becana et al. (1986). SOD (EC 1.15. 1.1) activity was measured by means the nitro-blue tetrazolium - KO_2 system (Henry et al., 1976). One unit of SOD is defined as the amount of enzyme required to bring about 50% inhibition of the rate of NBT reduction measured at 560 nm. AAP (EC 1.11. 1.7) activity was estimated according to Nakano and Asada (1981) by monitoring the rate of ascorbate oxidation at 290 nm ($E=2.8 \text{ mM}^{-1} \text{ cm}^{-1}$). Catalase (EC 1.11. 1.6) activity was determined by measuring the rate of H_2O_2 conversion to O_2 at room temperature, using an oxygen electrode (Oxytec, RE K1-1), in 2 ml solution containing 100 mM phosphate buffer pH 7.4, 10 -50 μg of extract protein. The reaction was initiated by adding H_2O_2 to give the final concentration of 20 mM. Total protein concentrations were measured according to Goa (1953). To determine Cd content, the potato tissues were wet ashed by the use of an acid mixture (36% HCl : 20% HClO_4 : H_2O = 2: 1: 1 v/v) and the element was determined by means of flame atomic absorption spectrometry (Perkin-Elmer, USA).

RESULTS

Concentrations of $\cdot\text{O}_2^-$ and H_2O_2

Short-term treatment of potato discs with CdCl_2 increased the concentrations of $\cdot\text{O}_2^-$ (Fig. 1) and H_2O_2 (Fig. 2) very fast. A higher level of this active oxygen species sustained for 48 hrs in both kind of materials. By comparing H_2O_2 concentration in the control materials of the two potato cultivars, it was found that it was higher in the more tolerant tissues. At higher concentrations of cadmium, a rapid increase of H_2O_2 levels in both materials, but then in the more tolerant material a fast decrease to the control level in 8 hr of experiment were observed. In the susceptible material, the increased level of H_2O_2 remained the same up to 72 hr of the experiment.

SOD activity

The effect of cadmium on SOD activity in the studied samples is presented in Fig. 3. Characteristic inhibition effects of enzyme activity were observed. On the basis of the comparison of these effects in two kinds of tissues it was found, that the inhibition appeared faster and sustained longer in the susceptible tissues.

When CdCl_2 was added to crude extracts from potato tuber tissues, the decrease of SOD activity was observed (Fig. 6). At 60 μM CdCl_2 concentration 45% inhibition of activity in extract of susceptible tissue and 30% inhibition of activity in extract of tolerance tissue were noticed.

Fig. 1. Reduction of extracellular cytochrome c by potato tuber tissue discs treated with CdCl_2 ($\text{Cd}1=0.01\text{mM}$; $\text{Cd}2=1\text{mM}$). Concentration of Cd in tissues in Cd1 experiment yield 12 $\mu\text{g/g}$ fw in tissues of cv Bintje, and 6 $\mu\text{g/g}$ fw in tissues of cv. Bzura. In Cd2 experiment these values yield respectively 63 and 61 $\mu\text{g/g}$ fw. Each value is a mean $\pm$ SE of three experiments.

CAT activity

Comparison of CAT activity in the control tissues of both cultivars showed that in tolerant tissues this activity is two times higher (Fig. 4) and during senescence of tissues the difference in that CAT activity was observed up to 30 hr of this process. The presence of cadmium in the susceptible tissues

Fig. 2. Influence of cadmium on H_2O_2 concentration in potato tuber tissues discs. Details as for Fig. 1.

did not affect the activity of this enzyme up to 30 hr of this experiment, and then this activity was noted to rise. The same treatment of tolerant tissues resulted in a small decrease in CAT activity in the first few hours of the experiment, and then after 10 hrs this activity of enzyme was reported to grow up.

When CdCl_2 was added to crude extracts from potato tuber tissues, the decrease of CAT activity was observed (Fig. 6). At 60 μM CdCl_2 concentration 22% inhibition of activity in extract of susceptible tissue and 34% inhibition of activity in extract of tolerance tissue were noticed.

AAP activity

When comparing AAP activity in the control tissues of both cultivars, it was noticed that in the tolerant tissues this activity was much higher (Fig. 5). After treating these tissues with CdCl_2 , a fast decrease in AAP activity was noticed, yet this effect in a tolerant material was smaller and disappeared more quickly.

Addition of CdCl_2 to crude extracts from tissues resulted in inhibition of AAP. 27% inhibition in extract of tolerant tissue and 42% one in extract of susceptible material were found at 60 μM CdCl_2 concentration (Fig. 6).

DISCUSSION

An essential problem for the aerobic organisms is effective removal of the toxic oxygen species produced during normal metabolic activity or as a result of action of various exogenous environmental stress factors, such as heat, chilling, drought, water-logging, intense light, and pollutants including, in light of this study, cadmium. After treating parenchyma tissues of potato tuber with cadmium ions at higher concentration, fast increase of concentrations of O_2^- and H_2O_2 was noticed (Figs 1 and 2). These effects were very similar for tissues revealing different tolerance to these metal ions, but in more tolerant discs the H_2O_2 level decreased very fast to the level in control material. The balance between production of active oxygen species and their detoxication was maintained by antioxidative system of cell (Monk et al., 1989b; Scandalios, 1993) possessing many, various enzymatic and nonenzymatic elements.

SOD is considered as a key enzymatic antioxidant, and numerous studies indicated, that this element in the system is activated in response to different stress factors (Bowler et al., 1992; Scandalios, 1993; Przymusiński et al., 1995). In this study, such simple relation was not observed. During the first hours, after treating the tissues with Cd^{2+} , the inhibition effect of SOD was appeared (Fig. 3). This inhibition effect comes probably from the inactivation of SOD as metalloenzyme by cadmium (Fig. 6). As follows from the comparison of the results for tolerant and susceptible tissues, for the former the effect was smaller and subsided more quickly. This observation and a similarly increased level O_2^- in both materials noticed during 30 hrs of stress application (Fig. 1) indicate, that changes of SOD activity do not account for the different tolerance of these tissues. In few plants, the increase of this enzyme activity caused by a long time period, at least 48 hrs, of treatment with heavy metals was observed (del Rio et al., 1985; Cakmak and Horst, 1991; Chongpraditnun et al., 1992; Przymusiński et al., 1995) but these experiments could not characterize an earlier events of direct metal influence on the enzyme. In *Phaseolus vulgaris* seedlings treated with cadmium for 3 and 6 days the decrease of SOD activity was observed (Somasekaraiah et al., 1992). In some cases, the transgenic plants with over production of SOD exhibited an enhanced tolerance (Bowler et al., 1992; Perl et al., 1993; Sen Gupta et al., 1993; Van Camp et al., 1994), but in others they did not (Tepperman and Dunsmuir, 1990; Pitcher et al., 1991). It seems, that SOD activity is not always the most important for the tolerance of the plant cell to oxidative stress.

In the plant cell, H_2O_2 is metabolized by the CAT family and by the peroxidases (Foyer et al., 1994). CAT is limited in its effectiveness by its poor affinity to H_2O_2 and its primary localization in peroxisomes. However, in many cases, the resistance to the environmentally induced oxidative stresses was

Fig. 3. Influence of cadmium on SOD activity in potato tuber tissues discs. Details as for Fig. 1.

Fig. 4. Influence of cadmium on CAT activity in potato tuber tissues discs. Details as for Fig. 1.

associated with a high activity of CAT (Scandalios, 1993). Potato tuber parenchyma tissues more tolerant to cadmium showed constitutively higher CAT activity, and its synthesis is induced faster by cadmium ions treatment relative to the susceptible tissues (Fig. 4) and this explains a faster removal of H_2O_2 from this tissue (Fig. 2). Addition of cadmium ions directly to extracts from both kinds of tissues resulted in decrease of the CAT activity, greater in extract from tolerant one (Fig. 6). It appeared that the estimated CAT activity in tissues is the sum of inactivation process and induction of CAT synthesis. Additionally, this indicated that activity of the induction process had to increase faster in the tolerant tissue.

AAP scavenges H_2O_2 with ascorbic acid as an electron donor in the cytoplasm, in the chloroplast (Asada, 1992), in the vacuole (Barcelo et al., 1991) and in the apoplast (Takahama and Oniki, 1992). AAP activity increased in response to several stress factors (Bowler et al., 1992). In our experiment, cadmium treatment of tissues unexpectedly decreased AAP activity during the first hours of observation. In more tolerant tissues, the inhibition effect was smaller and faded faster than in the susceptible material (Fig. 5). AAP as metalloenzyme can be inactivated by cadmium, which was confirmed by experiments with isolated enzyme (Fig. 6).

Among the nonenzymatic antioxidants, ascorbic acid, cysteine and glutathione are very important for the redox status

Fig. 5. Influence of cadmium on AAP activity in potato tuber tissues discs. Details as for Fig. 1.

of plant cell (Liczmański, 1988; Monk and Davies, 1989a). In more tolerant control tissues of potato tuber, the concentrations of cysteine, glutathione and ascorbic acid were higher than in the susceptible ones (Stroiński and Bandurska, 1996). Additionally, in this material under cadmium stress condition an earlier increase in concentration of total, acid-soluble thiols and phytochelatin was observed. This tissue possessed elevated constitutive levels of some enzymatic and nonenzymatic antioxidants and it seems that they play main role in the its relative higher tolerance to cadmium.

The mechanism of plant resistance to oxidative stress seems to be depended on several components of antioxidative system, which importance for efficiency of antioxidative system can be different for different plant – oxidative stimuli systems.

Fig. 6. Influence of cadmium chloride on AAP, CAT and SOD activities in crude extracts from potato tuber discs. CdCl_2 was added to crude extracts to give the final concentration from 0.6 to 600 μM . The samples were preincubated for 30 minutes at 20 °C before estimation of enzyme activities. Each value is a mean $\pm$ SE of three experiments.

ACKNOWLEDGEMENT

We thank M. Zieleziska for technical assistance. This study was supported in part by KBN (6P204 059 06).

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STRES OKSYDACYJNY W BULWACH ZIEMNIAKA INDUKOWANY PRZEZ KADM

STRESZCZENIE

Krótkotrwałe traktowanie krążków z bulwy ziemniaka (*Solanum tuberosum* L.) chlorkiem kadmu powoduje wzrost stężenia aktywnych form tlenu oraz uaktywnienie systemu antyoksydacyjnego. W badaniach użyto dwie odmiany ziemniaka, Bintje i Bzura, odpowiednio wrażliwą i odporną na działanie kadmu. Aktywności peroksydazy kwasu askorbinowego (PKA) i katalazy (KAT) w tkankach kontrolnych odmiany odpornej były większe niż w tkankach wrażliwych. W pierwszych godzinach stresu odnotowano spadek aktywności dismutazy nadadtlenkowej, PKA i KAT wywołany prawdopodobnie przez inaktywację enzymów przez jony kadmu. Późniejszy wzrost aktywności tych enzymów następował wcześniej w tkankach odpornych. Wydaje się, że tkanki odporne posiadają bardziej sprawny system antyoksydacyjny.

SŁOWA KLUCZOWE: aktywne formy tlenu, dismutaza nadadtlenkowa, kadm, katalaza, peroksydaza kwasu askorbinowego, *Solanum tuberosum* L.