The antioxidative response of two tomato species with different drought tolerances as a result of drought and cadmium stress combinations

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ABSTRACT

The effects of drought, cadmium (Cd) and drought-Cd combinations on antioxidant compounds, antioxidant enzymes and shoot growth were investigated for drought tolerant [*Lycopersicon peruvianum* (L.) Mill.] and sensitive of (*Lycopersicon esculentum* Mill. cv. Lukullus) tomato species. Drought-Cd combinations significantly decreased shoot growth in both species ($P < 0.01$), drought stress also decreased shoot growth in drought sensitive *L. esculentum*. Cd was accumulated higher in the roots of drought sensitive *L. esculentum* than drought tolerant *L. peruvianum*. The chlorophyll contents decreased in all stress treatments in *L. esculentum* but did not change in *L. peruvianum*. Carotenoid contents significantly increased in all stress treatments in both species ($P < 0.01$). Significant increases in the contents of carotenoids in both species under stress conditions seemed to be associated with a protective role against reactive oxygen species (ROS). Ascorbate (ASC) content decreased during drought stress while increased under Cd stress. Catalase (CAT) and glutathione reductase (GR) activities significantly increased under drought stress in *L. peruvianum* while decreased in *L. esculentum* ($P < 0.001$). Ascorbate peroxidase (APX) activity decreased under all stress treatments in both species. Drought and Cd stresses increased superoxide dismutase (SOD) activity in both species. The present data did not show a relation between drought tolerance and levels of antioxidative defence system that was induced from Cd. However, there is a clear relationship between Cd uptake and drought tolerance of plants.

Keywords: ascorbate; cadmium; drought; carotenoids; catalase; glutathione reductase; ascorbate peroxidase; superoxide dismutase

Cadmium (Cd) is a wide spread pollutant; it can reach high levels in agricultural soils and can be easily assimilated by plants (Milone et al. 2003). Cd intake from food may be a potential health risk to humans. The content of Cd in the soil increases due to industrial use of Cd and Cd-contaminated fertilizers each year. Cd is not an essential nutrient for plants and it is extremely toxic, even at low concentrations (Vitoria et al. 2001, Milone et al. 2003). Cd is accumulated in the roots of most plant species. Only a small amount of Cd^{2+} is transported from the roots to leaves and its allocation in the shoot may vary considerably between different species (Larsson et al. 2002). Previous studies have shown that toxic concentrations of heavy metals such as iron, copper, zinc, nickel, manganese and cadmium cause oxidative stress which results in enzymatic and non-enzymatic anti-oxidative responses of plants (Ianelli et al. 2002, Tewari et al. 2002, Drazkiewicz et al. 2003). Ianelli et al. (2002) showed that an increase of superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT) and glutathione reductase (GR) activities was induced in all samples of roots, stolons and leaves of *Phragmites australis* by cadmium.

Drought is one of the most widespread environmental stresses and affects almost all the plant functions (Yamaguchi-Shinozaki et al. 2002). Drought stress and other physiological stresses cause oxidative injury. High antioxidant capacity or increased levels of antioxidants can prevent cell death and may correlate with stress tolerance (Van Der Mescht et al. 1998). The phenomenon of cross tolerance has been reported in plants under oxidative stress by Shaaltiel et al. (1988) and Malan et al. (1990). In accordance with these researchers, it was found that a plant tolerant to environmental pollutants such as SO_2, O_3, herbicides and heavy metals was also tolerant to natural stress conditions such as drought, low and high temperature, and high light.

Reactive oxygen species (ROS) are partially reduced forms of atmospheric oxygen. They typically result from the excitation of O_2 to form singlet oxygen ($^1O_2$) or from the transfer of one, two or three electrons to O_2, respectively, a superoxide radical (O^{2-}), hydrogen peroxide (H_2O_2) or a hydroxyl radi-

cal (OH). The cells are normally protected against ROS by the operation of an antioxidant defence system that is comprised of enzymic (SOD, CAT, GR, APX) and nonenzymic (ascorbate, α-tocopherol, carotenoids, glutathione) components (Van Der Mescht et al. 1998, Shigeoka et al. 2002, Tewari et al. 2002). The deleterious effects of ROS can be found in proteins and nucleic acids, chlorophyll and membrane function (Asada 1996).

ROS production is further enhanced when exposed to various abiotic stresses, such as drought (Van Heerden and Krüger 2002, Rubio et al. 2002), salt (Broetto et al. 2002, Hernandez and Almansa 2002), and low and high temperature (Pastori and Foyer 2002, Sairam et al. 1997/1998). These studies show that the activities of antioxidative enzymes are increased in response to biotic or abiotic stresses.

The antioxidative defence capacity of the cells is determined by the pool size of the antioxidants and protective pigments. A change in antioxidant contents may reflect the impact of environmental stresses on plant metabolism (Herbinger et al. 2002). As an antioxidant ascorbic acid has an important role in protecting against oxidative stress (Conklin 2001). Ascorbate (ASC) eliminates ROS through multiple mechanisms. ASC has the capacity to directly eliminate several different ROS including singlet oxygene, superoxide and hydroxyle radicals (Padh 1990). It also maintains the membrane-bound antioxidant α-tocopherol in the reduced state and indirectly eliminates H_2O_2 through the activity of APX. The function of the lipophilic antioxidant α-tocopherol is to protect membranes from oxidative damage. It is located primarily in thylakoid membranes and is therefore directly involved in the defence of chloroplast to oxidants. Antioxidant levels and the activities of ROS scavenging enzymes have been correlated with its tolerance to several different environmental stresses (Chaitanya et al. 2002, Tewari et al. 2002). The activities of antioxidant enzymes in plants under stress are usually regarded as an indicator of the tolerance of the genotypes against stress conditions.

This study was planned to determine the relation between tolerance to drought stress and cadmium toxicity. Cd was applied to induce the antioxidant defence system in two tomato species with different drought tolerances. The effects of drought, Cd and drought-Cd combinations on antioxidant enzyme activity and antioxidant compounds were investigated.

MATERIAL AND METHODS

Plant material and stress application. In this study, drought tolerant *Lycopersicon peruvianum* (L.) Mill. and drought sensitive *Lycopersicon esculentum* Mill. cv. Lukullus were used. The seeds were obtained from the Tomato Genetic Resource Center, Department of Vegetable Crops, University of California, Davis California, USA. Seeds were applied with 0.1 mol/l H_2SO_4 for 30 min and then surface sterilised with 3% sodium hypochloride for 10 min, rinsed in distilled water and imbibed for 24 h with aerated water. After imbibition, seeds were planted onto plastic pots. Plants were grown at 26/22°C (day/night) temperature on 65 ± 5% RH in a growth chamber with 480 μmol/m^2/s light (day/night 16/18 h). Drought stress and cadmium application were performed at the end of seven weeks. Cd application [100 mg/kg soil Cd^{2+} as Cd $(NO_3)_2$] and drought stress were simultaneously started. Seedlings grown under cadmium and drought stress for three weeks were harvested, and the lengths for their roots and shoots were measured.

Relative water contents (RWC). To determine RWC of plants, nine leaf discs were weighed (fresh weight, FW) immediately after harvesting from the plant. The same tissues were then placed in a redistilled water vial for 2 h at 25°C and then their turgid weights (TW) were calculated. The samples were then dried in an oven at 110°C for 24 h to obtain their dry weights (DW). RWC were calculated by the following equation:

$$RWC = (FW - DW)/(TW - DW).100$$

Cadmium analysis. The heavy metal content was determined by atomic absorption (Hitachi 180-80) after wet digestion of the dried root tissue in perchloric acid and nitric acid (1:3) as well as after dry ashing overnight at 400°C. The residues were disolved in nitric acid (0.1% v/v).

Extraction and analysis of pigments. The extraction of chlorophylls was carried out according to Porra et al. (1989). The leaves (0.5 g) were homogenised with 80% acetone. Chlorophyll *a* and *b*, chlorophyll *a*/*b* ratio and the total chlorophyll were measured. For carotenoid analysis, leaves were homogenised on acetone and 0.2 g Na_2SO_4. Then the extract was evaporated and residues were taken up to 2 ml chloroform and subjected to TLC. Carotenoids were monitored at 450 nm (Moore 1974).

Extraction and analysis of ascorbate. Leaves (1 g) were homogenised with 0.1 mol/l sodium acetate buffer (pH 3). Homogenate was centrifuged at 16 000 g for 5 min at 4°C and the supernatant was collected for analysis of ASC. Chromatography separation was performed by using a Agilent 1100 HPLC Analytical system. C18 column was used with 0.1 mol/l sodium acetate buffer (pH 5) as the mobile phase. ASC was carried out according to Schmieden and Wild (1994).

Table 1. Effects of drought, Cd and drought-Cd combinations on the shoot length (cm) in drought tolerant *L. peruvianum* and drought sensitive *L. esculentum*

	L. peruvianum	*L. esculentum*
Control	93.8 ± 18.2 ac	111.6 ± 5.2 a
Drought	92.0 ± 03.8 bcd	75.3 ± 4.4 d
Cd	92.5 ± 14.4 bcd	104.6 ± 4.0 ab
Drought + Cd	81.1 ± 09.9 cd	85.1 ± 3.1 cd

Values are the means ± *SD* of three replicates

Table 2. Accumulation of Cd (mg/kg dry weight) in roots of drought tolerant *L. peruvianum* and drought sensitive *L. esculentum*

	L. peruvianum	*L. esculentum*
Control	45 ± 06 c	45 ± 06 c
Drought	45 ± 06 c	45 ± 06 c
Cd	190 ± 10 ab	230 ± 20 a
Drought + Cd	50 ± 20 c	130 ± 10 b

Values are the means ± *SD* of three replicates

Enzyme extraction and assays. Fresh leaves (1 g) were homogenized in 5 ml of 0.1 mol/l potassium phosphate buffer (pH 6.8) containing 0.025% (w/v) triton x-100 and 0.1 mmol/l EDTA. The homogenate was centrifuged at 15 000 g for 20 min at 4°C and the supernatant was immediately used for the following enzyme assays. Total SOD activity was assayed by monitoring the inhibition of photochemical reaction of nitro blue tetrazolium (NBT) according to the method of Beyer and Fridowich (1987). One unit of SOD activity was defined as the amount of enzyme that was required to cause 50% inhibition of the reduction of NBT as monitored at 560 nm. CAT activity was assayed by measuring the rate of decomposition of H_2O_2 at 240 nm, as described by Aebi (1983). GR activity was measured by following the change in 340 nm as oxidized glutathione (GSSG)-dependent oxidation of NADPH, according to the method of Carlberg and Mannervik (1985). To determine APX activity, fresh leaf tissue (1 g) was homogenized in 15 ml of extraction medium containing 200 mmol/l HEPES, 2 mmol/l EDTA, 5 mmol/l $MgCl_2$, and 4 mmol/l sodium ascorbate. The crude extract was centrifuged at 16 000 g for 5 min at 4°C, and the supernatant was used for the measurements. The reaction mixture contained 50 mmol/l potassium phosphate buffer (pH 7), 500 μmol/l ascorbate, 1 mmol/l H_2O_2 and extract. A fall in absorbance at 290 nm was measured as ascorbate was oxidized. APX activity (unit/g FW) was calculated using an extinction coefficient of 2.8 mmol/l/cm for ascorbate at 290 nm (Vanaker et al. 1998, Bonnet et al. 2000).

Statistical evaluation. At least duplicate measurements of three replicates were used to determine the effects of four independent variables (control, drought, Cd and drought-Cd combination) on antioxidative response and growth. Data were evaluated by analysis of variance (ANOVA) using the Statistica for Windows software package. The least significant difference (*LSD*) test was applied to compare mean values.

RESULTS

The comparison with control plants, in the *L. peruvianum* shoot growth remained unchanged with drought and Cd (Table 1). The drought-Cd combination significantly decreased the shoot growth in both genotypes ($P < 0.01$). The shoot length of *L. esculentum* significantly decreased under drought and drought-Cd combination. While the shoot growth of the drought sensitive tomato species, *L. esculentum*, was negatively effected from drought and drought-Cd combinations, it was not affected from Cd treatment. The leaf relative water content (RWC) was not changed during drought in tolerant *L. peruvianum*, while it decreased in *L. esculentum*. Cd treatments decreased the RWC in *L. peruvianum* but in combination with drought and Cd we found higher values of RWC (Figure 1). The Cd contents in the roots of both species exposed to Cd were significantly higher ($P < 0.001$) than in drought-Cd treated plants (Table 2). Furthermore, it can be seen that there is a higher Cd accumulation

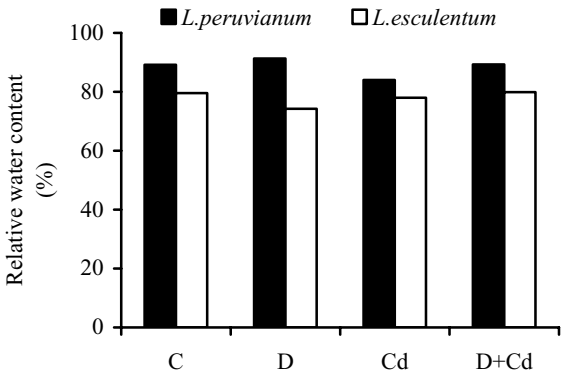

Figure 1. Effects of drought (D), Cd and drought-Cd (D+Cd) combinations on relative water content in drought tolerant *L. peruvianum* and drought sensitive *L. esculentum* (control – C)

Table 3. Effects of drought, Cd and drought-Cd combinations on the concentration of chlorophylls (mg/g fresh weight) in drought tolerant *L. peruvianum* and drought sensitive *L. esculentum*

		Chlorophyll *a*	Chlorophyll *b*	Chlorophyll *a*/*b* ratio	Total chlorophyll	Carotenoids/ chlorophyll ratio
L. peruvianum	control	0.86 ± 0.03 e	0.33 ± 0.01 c	2.6 ± 0.0 b	1.2 ± 0.05 d	0.07 ± 0.02
	drought	0.94 ± 0.01 de	0.40 ± 0.02 c	2.3 ± 0.1 cd	1.3 ± 0.04 d	0.14 ± 0.01
	Cd	0.96 ± 0.01 cde	0.37 ± 0.03 c	2.6 ± 0.2 b	1.3 ± 0.04 d	0.16 ± 0.01
	drought + Cd	1.06 ± 0.04 c	0.37 ± 0.02 c	2.8 ± 0.2 a	1.4 ± 0.06 c	0.16 ± 0.01
L. esculentum	control	1.42 ± 0.05 a	0.81 ± 0.02 a	1.8 ± 0.0 e	2.2 ± 0.08 a	0.03 ± 0.01
	drought	1.26 ± 0.04 b	0.69 ± 0.06 b	1.8 ± 0.1 e	2.0 ± 0.11 b	0.08 ± 0.02
	Cd	1.32 ± 0.15 ab	0.61 ± 0.12 b	2.2 ± 0.2 d	1.9 ± 0.28 b	0.12 ± 0.02
	drought + Cd	1.00 ± 0.03 cd	0.41 ± 0.09 c	2.4 ± 0.1 bc	1.4 ± 0.04 c	0.18 ± 0.02

Values are the means ± *SD* of three replicates

in the roots of the drought sensitive *L. esculentum* than in the tolerant *L. peruvianum* ($P < 0.001$).

Chlorophyll contents were not affected by the stress treatments in *L. peruvianum* (Table 3). In *L. esculentum* loss of total chlorophyll elevated to 36% under drought and Cd stress combinations ($P < 0.01$). The differences between both species in chlorophyll contents were significant ($P < 0.001$). In *L. peruvianum*, chlorophyll *a*/*b* ratio had decreased under drought stress. Chlorophyll *a*/*b* ratio increased under Cd and drought-Cd combinations in *L. esculentum*.

Significant increases in the content of total carotenoids were observed in both species in all stress treatments but the maximum carotenoid concentrations were found mainly in drought-Cd combination ($P < 0.01$) (Figure 2). In all stress treatments, there was a significant increase in carotenoids per unit of chlorophyll. The concentration of ascorbic acid (ASC) decreased during drought and drought-Cd combination ($P < 0.01$) but there was no change with Cd in both species (Figure 2).

Compared with the controls, in *L. peruvianum* exposed to drought and Cd, and *L. esculentum* exposed to drought and drought-Cd combination

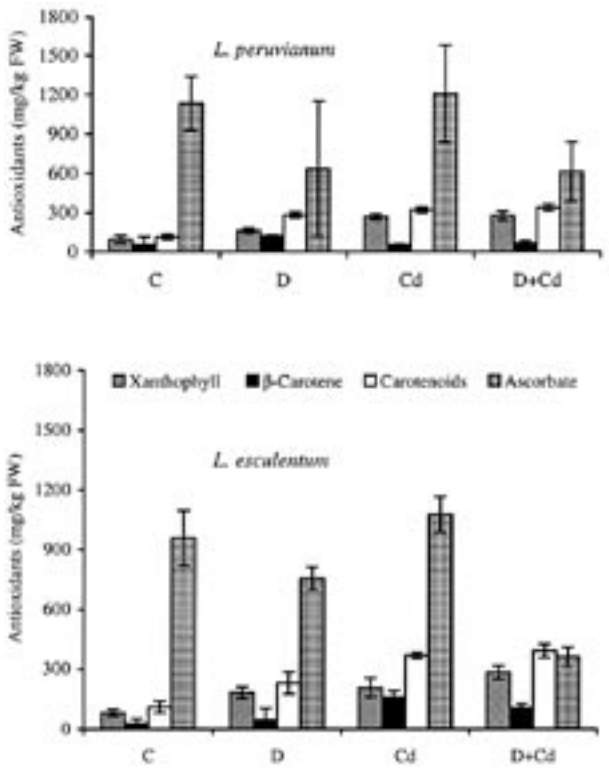

Figure 2. Effects of drought, Cd and drought-Cd combinations on antioxidant contents in leaves of drought tolerant *L. peruvianum* and drought sensitive *L. esculentum*; values are the means ± *SD* of three replicates

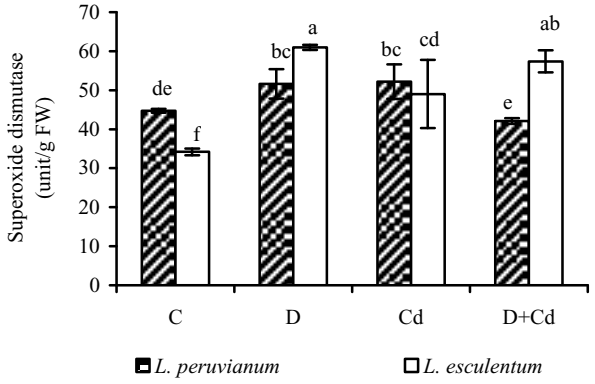

Figure 3. Effects of drought, Cd and drought-Cd combinations on superoxide dismutase activity in leaves of drought tolerant *L. peruvianum* and drought sensitive *L. esculentum*; values are the means ± *SD* of three replicates

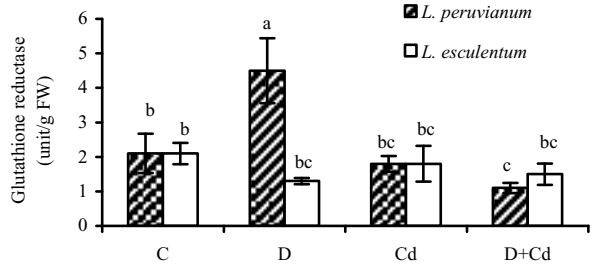

Figure 4. Effects of drought, Cd and drought-Cd combinations on glutathione reductase activity in leaves of drought tolerant *L. peruvianum* and drought sensitive *L. esculentum*; values are the means ± *SD* of three replicates

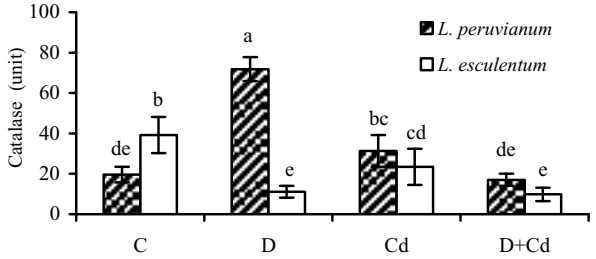

Figure 6. Effects of drought, Cd and drought-Cd combinations on catalase activity in leaves of drought tolerant *L. peruvianum* and drought sensitive *L. esculentum*; values are the means ± *SD* of three replicates

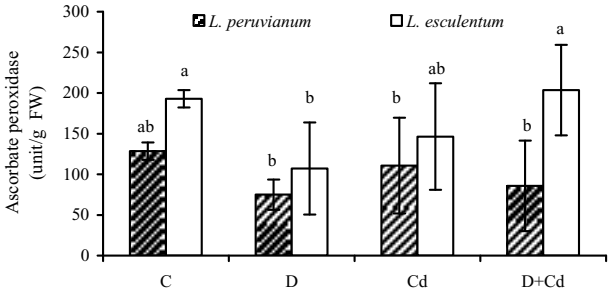

Figure 5. Effects of drought, Cd and drought-Cd combinations on ascorbate peroxidase activity in leaves of drought tolerant *L. peruvianum* and drought sensitive *L. esculentum*; values are the means ± *SD* of three replicates

significantly increased SOD activity ($P < 0.001$). While in drought-Cd combinations SOD activity decreased in *L. peruvianum*, this enzyme activity in *L. esculentum* decreased in Cd stress (Figure 3). GR activity significantly increased in drought tolerant *L. peruvianum* during drought ($P < 0.001$) (Figure 4). In sensitive *L. esculentum*, all of stress treatments inhibited GR activity. Cd and drought-Cd combinations decreased the GR activity in both species.

The highest APX activity was found in *L. esculentum* ($P < 0.01$) as compared with *L. peruvianum*. Drought and Cd stresses decreased APX activity in both species. In *L. esculentum* APX activity remained unchange in drought-Cd combination (Figure 5). Drought induced a significant increase in the activity of CAT in leaves of *L. peruvianum*, whereas in those of *L. esculentum*, CAT activity decreased under stress conditions ($P < 0.001$), compared with control (Figure 6). Cd induced a small increase in the activity of CAT in *L. peruvianum*. In stress combinations, CAT activity remained unchanged in *L. peruvianum*, while the lower CAT activity was found during drought and drought-Cd combinations in *L. esculentum*.

DISCUSSION

Drought stress and other physiological stresses cause oxidative injury, high antioxidant capacity or increased levels of antioxidants can prevent cell death and may correlate with stress tolerance (Van Der Mescht et al. 1998). Mechanisms that reduce oxidative injury may play a secondary role during drought tolerance.

Cd accumulation in drought tolerant *L. peruvianum* was lower than drought sensitive *L. esculentum*. Drought significantly reduced Cd accumulation in both tomatoes, particularly drought tolerant *L. peruvianum* did not uptake it. This result indicates that drought tolerance could prevent Cd uptake because of low water level in the soil. These findings show that Cd^{2+} uptake might be related to the rate of water uptake from the soil.

The decrease of chlorophyll *a/b* ratio in drought tolerant *L. peruvianum* might show better protection of PSII against drought stress. However, low chlorophyll *b* content under Cd application may be a result of the sensitivity of PSII to Cd stress. An increase in carotenoids/chlorophyll ratio might be of a protective value as carotenoids are known to be potent quenchers of ROS, particularly singlet oxygen (Tewari et al. 2002, Caretto et al. 2002, Chaitanya et al. 2002).

Decreasing chlorophyll contents in *L. esculentum* during drought-Cd combination were accompanied by a sharp decrease in the ASC content. Ascorbate is the major water-soluble antioxidant, which protects plant cells against ROS and oxidative damage (Herbinger et al. 2002). In the present study, ascorbate content decreased under drought stress and drought-Cd combinations in both species. This result seems to contradict the postulated need for higher antioxidative defence capacity. However, a drought-induced decrease in carbon fixation through stomatal closure may limit ascorbate synthesis, which is directly connected to carbon metabolism (Herbinger et al. 2002). The decrease of ASC may be due to various factors such as slower

synthesis, faster utilisation, or a decreased reduction rate of oxidation products (Borraccino et al. 1994). A similar relationship between ASC and chlorophyll has been suggested by Borraccino et al. (1994) and Herbinger et al. (2002).

Both drought and Cd stresses resulted in decreases APX activity and ASC in both species. Decreased APX activity would decrease the demand for ascorbate regeneration mediated through decreased GR activity especially in *L. esculentum*. GR activity is regarded as the rate limiting enzyme in the ascorbate-glutathione cycle (Van Heerden and Krüger 2002). GR activity significantly increased in drought tolerant *L. peruvianum* under drought stress. This finding contradicts that of Van Der Mescht et al. (1998), who reported that there were no correlations between GR activity and the response to drought stress. Drazkiewicz et al. (2003) demonstrated APX activity decreased at high Cu concentrations. In contrast, APX increased under drought stress in potato (Van Der Mescht et al. 1998). But Schickler and Caspi (1999) reported that this enzyme remained unchanged in Cd treatment.

Both Cd and drought stress induced an increase in the activity of SOD in leaves of *L. peruvianum* and *L. esculentum*. But this increase was higher in drought sensitive *L. esculentum* than drought tolerant *L. peruvianum*. It means that the increase of SOD activity could reflect an increase in ROS production which could be associated with the rise of mitochondrial and chloroplastic activity occurring during drought and Cd stress. Similarly, in *Phragmites australis* leaves, 50 μmol/l $CdSO_4$ caused an increase of SOD enzymes activity (Iannelli et al. 2002). Milone et al. (2003) showed that in Cd-treated wheat leaves, SOD activity decreased to about 50% of the control value. Increases in SOD activity have also been reported due to the excess supply of some other heavy metals. For example, Tewari et al. (2002) indicated that the increased activities of antioxidative enzymes in response to excess of cobalt are suggesting a strong induction of oxidative stress. The highest GR activity was found in droughted *L. peruvianum*. Similar effects on GR activities of drought stress were observed in the soybean (Riekert van Heerden and Krüger 2002) and wheat (Keleş and Öncel 2002). Cd and drought-Cd combinations decreased GR activity in both tomatoes species. Cd treatment reduced this enzyme activity in the *Alyssum* species (Schickler and Caspi 1999). The decrease in GR activity at high concentrations of Cd may be the result of a direct reaction to metal with sulfhydryl groups, interferring with the glutathione cycle.

Drought stress significantly increased CAT activity in tolerant *L. peruvianum*, which was decreased in sensitive *L. esculentum*. Also a similar effect was observed under Cd stress. A direct correlation was shown between applied Cd concentration and increased CAT activity in the tissues, so that high concentrations of $CdCl_2$ caused an increase in CAT activity (Vitoria et al. 2001). Thus Cd concentration in the present study may be low due to a greater increase in CAT activity. Vitoria et al. (2001) reported that $CdCl_2$ induced an increase in CAT activity in radish plants. CAT is only present in peroxisomes, but it is indispensable for ROS detoxification during stress when high levels of ROS are produced. The balance between SOD, APX or CAT activities in cells is crucial for determining the steady-state level of superoxide radicals and H_2O_2. This balance, together with the sequestering of metal ions, is thought to be important to prevent the formation of highly toxic hydroxyl radical via the metal-dependent Haber-Weiss or Fenton reactions (Mittler 2002).

In conclusion, the present data shows that there is a clear relationship between Cd uptake and the drought tolerance of plants. Drought tolerant species can uptake the lower amounts of Cd from the soil, thus it can avoid the harmful effects of Cd. Both drought and Cd stresses accelerated the generation of reactive oxygen intermediates and induced the antioxidative defence system. However, the results of this study did not show a direct relationship between levels of ascorbate and carotenoids as antioxidants involved in a defence system that is induced with drought tolerance and Cd.

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ABSTRAKT

Antioxidační odezva u dvou druhů rajčat s rozdílnou tolerancí vůči suchu jako výsledek stresové kombinace sucha a kadmia

Byl sledován vliv sucha, kadmia (Cd) a kombinace sucho + kadmium na obsah antioxidačních látek, aktivitu antioxidačních enzymů a růst nadzemní části rajčat druhu tolerantního [*Lycopersicon peruvianum* (L.) Mill.] a senzitivního (*Lycopersicon esculentum* Mill. cv. Lukullus) vůči suchu. Kombinace sucho + Cd významně snížila růst nadzemní části u obou druhů, stres suchem rovněž snížil růst nadzemní části u senzitivního *L. esculentum*. Cd se akumulovalo více v kořenech senzitivního *L. esculentum* než u vůči suchu tolerantního *L. peruvianum*. Zdá se, že významný nárůst obsahu karotenoidů u obou druhů za podmínek stresu lze dát do souvislosti s ochrannou rolí vůči reaktivním kyslíkovým formám (ROS). Obsah chlorofylu se snížil u všech stresových variant u *L. esculentum*, avšak nezměnil se u *L. peruvianum*. Obsah karotenoidů se významně zvýšil u všech stresových variant u obou druhů. Obsah askorbové kyseliny (ASC) se snížil u variant se stresem vyvolaným zvýšeným suchem, avšak u stresu vyvolaného Cd se zvýšil. Aktivita katalázy (CAT) a glutationreduktázy (GR) výrazně vzrostla u *L. peruvianum* za stresu vyvolaného suchem, zatímco u *L. esculentum* se snížila. Aktivita askorbátperoxidázy (APX) se snížila u všech variant za použití stresu u obou druhů. Rovněž sucho a Cd-stres zvýšily aktivitu superoxiddismutázy (SOD) u obou druhů. Nalezené výsledky neprokázaly vztah mezi tolerancí vůči suchu a hladinou antioxidačního obranného systému vyvolanou působením Cd.

Klíčová slova: askorbát; kadmium; sucho; karotenoidy; kataláza; glutationreduktáza; askorbátperoxidáza; superoxiddismutáza

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