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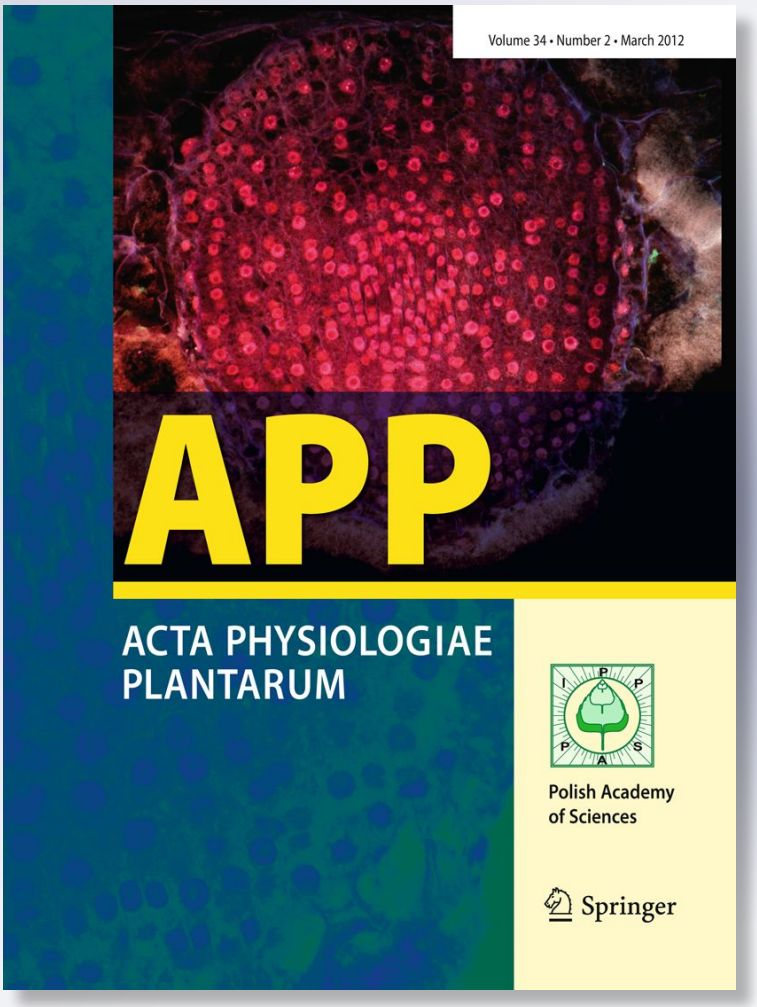

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ORIGINAL PAPER

Responses to excess iron in sweet potato: impacts on growth, enzyme activities, mineral concentrations, and anatomy

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Abstract This study aimed to evaluate the effects of different iron concentrations on growth characteristics, antioxidant enzyme activities, nutrient absorption, and anatomical changes in sweet potato (*Ipomoea batatas* L.). To accomplish this, seedlings from apical branches of plants that had already been established in the greenhouse were rooted in a hydroponic sponge and then transplanted into a hydroponic system intermittently for 2 weeks and irrigated with nutrient solutions containing iron (ferric-EDTA) at concentrations of 0.45, 0.9, 4.5, and 9.0 mmol L^{-1}. Height, leaf area, and total biomass were significantly reduced at iron concentrations of 4.5 and 9.0 mmol L^{-1}. The iron concentrations in the established leaves and those that developed after the solution supplementation increased significantly. The amounts of other nutrients were also affected, with manganese showing the most significant decrease. The activities of the antioxidant enzymes, superoxide dismutase, and ascorbate peroxidase increased in plants grown in the 9.0 mmol L^{-1} iron solution. At this concentration, however, the stomatal densities were reduced on the abaxial surfaces of the leaves, although the stomatal diameters increased. The ultrastructures of the radical cells showed mitochondrial impairment at high iron concentrations; however, the chloroplast structures remained unaffected.

Keywords *Ipomoea batatas* L. · Ferric-EDTA · Stress · Biomass · Nutrients · Stomata

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Introduction

Iron (Fe) is an essential nutrient for plant growth and development. The preferred form of iron for root absorption is Fe^{2+}, although it is also absorbed as Fe^{3+}-chelate (Briat et al. 2007). Iron is stored inside the cell in the chloroplasts, mitochondria, and vacuoles (Jeong and Guerinot 2009). Due to its ability to accept and donate electrons, it behaves as a cofactor for many enzymes involved in the respiratory chain, DNA biosynthesis, and nitrogen metabolism, making it essential to photosynthesis and chlorophyll biosynthesis (Jeong and Connolly 2009). Additionally, several enzymes involved in nitrogen and sulfur metabolism, such as nitrate reductase, nitrite reductase, sulfite reductase, and nitrogenase, use iron-containing prosthetic groups (Hänsch and Mendel 2009).

Homeostasis of this metal is essential for plant growth and development, because it has been shown to cause harm when present in both excessive and limiting amounts. One of the characteristic symptoms of iron deficiency is chlorosis, which is caused by decreased chlorophyll biosynthesis (Sharma 2007). Studies have shown that the same chemical properties that allow iron to act as an efficient catalyst and cofactor in cellular redox reactions also make it a potent toxin (Olaleye et al. 2009). Elevated concentrations lead to enhanced oxidative stress and the increased

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production of reactive oxygen species (ROS) (Robello and Galatro 2007).

ROS can be highly destructive because they seriously injure a variety of cellular components, including lipids, proteins, carbohydrates, and nucleic acids, leading to diverse morphological, biochemical, and physiological alterations (Fang et al. 2001). However, some plants can adapt to such stressful conditions by acquiring tolerance mechanisms. In the case of excess iron, one of the ways to limit damage is to stop the uncontrolled oxidation caused by antioxidant enzymes. The first enzyme that plays a defensive role against the damage caused by ROS is superoxide dismutase (SOD), which requires Fe, Mn, Cu, and Zn as metal cofactors. SOD is found in several cellular compartments and catalyzes the detoxification of $O_2^{\cdot -}$ to H_2O_2 and O_2 (Sinha and Saxena 2006). In addition to SOD, catalases (CAT) and peroxidases have been shown to participate in this protective mechanism (Costa et al. 2005).

Excess iron can also affect the absorption of other nutrients, such as calcium (Ca), magnesium (Mg), potassium (K), phosphorus (P), and also iron itself, due to the precipitation of iron oxide in plant roots (Zhang et al. 1999).

Studies on different plant species have shown anatomical and physiological alterations that depend on the growth conditions used (Melo et al. 2007; Adamski and Coelho 2008). Changes in stomatal behavior are also observed when plants are subjected to different stresses (Castro et al. 2005; Maranho et al. 2006).

Based on this information, the objective of the present study was to analyze the effect of different iron concentrations on morphological, physiological, enzymatic, and anatomical characteristics of sweet potato plants and to achieve a better understanding of the influence by excess iron on metabolism of this species.

Materials and methods

Sweet potato plants that were obtained from the roots of apical branches were transplanted to a hydroponics system and intermittently irrigated with a nutritional solution, as described by Hoagland and Arnon (1938), containing the following iron concentrations in the form of ferric-EDTA: 0.45 mmol L^{-1} (half of control concentration), 0.9 mmol L^{-1} (recommended level—control), 4.5 mmol L^{-1} (five times the control concentration), and 9.0 mmol L^{-1} (10 times the control concentration). The pH levels of the solutions were adjusted to 5.0, and they were each replenished every 3 days. Twenty plants per treatment were used, which remained under the treatment conditions for 15 days. After the treatment period, the plants were collected and evaluated for growth, nutrient concentrations in the leaves, antioxidant enzyme activities, and anatomical features.

The growth parameters that were evaluated included the branch lengths (cm), dry weights of the roots and shoots (g), and leaf areas (cm^2), which were estimated using a Li-Cor area meter, model LI-3100. The macro and micronutrients were determined from the dry masses of leaves that had already been established before the iron treatments (called "old leaves") and those that developed after the treatment applications (called "young leaves"), according to Tedesco et al. (1995).

The activities of the SOD, ascorbate peroxidase (APX), and CAT antioxidant enzymes were determined in young leaves at exactly 7 and 15 days after the treatments. Approximately, 0.2 g of fresh leaf tissue from each sample was ground in liquid N_2 with 20 % PVPP (polyvinylpolypyrrolidone) and homogenized in 1.5 mL of extraction buffer containing 100 mM potassium phosphate (pH 7.0), 0.1 mM EDTA, and 10 mM ascorbic acid. The homogenate was centrifuged at 13,000*g* for 10 min at 4 °C, and the supernatant was collected to determine the enzymatic activity.

SOD activity was determined, according to its ability to inhibit the photoreduction of nitroblue tetrazolium (NBT) (Giannopolitis and Ries 1977), in a reaction medium that was composed of 100 mM potassium phosphate (pH 7.8), 14 mM methionine, 0.1 μM EDTA, 75 μM NBT, and 2 μM riboflavin.

CAT activity was determined as described by Azevedo et al. (1998), with some modifications; activity was indicated by decreased absorbance measurements at 240 nm over a period of 2 min in a reaction medium (50 μL extract volume in total volume of 4 mL) containing 100 mM potassium phosphate buffer (pH 7.0) and 12.5 mM H_2O_2 that was incubated at 28 °C.

APX activity was evaluated according to Nakano and Asada (1981), by monitoring the oxidation rate of ascorbate at 290 nm. The incubation buffer was composed of 100 mM potassium phosphate (pH 7.0), 0.5 mM ascorbic acid, and 0.1 mM H_2O_2 (50 mL of extract volume in total volume of 4 mL).

For the ultrastructural analyses, the root and young leaf samples were fixed in Karnovsky solution (Karnovsky 1965), (2.5 % glutaraldehyde, 2.5 % formaldehyde, and 0.05 M cacodylate, pH 7.2) for 24 h. Then, the samples were washed in cacodylate buffer, post-fixed in a 2 % osmium tetroxide solution for 5 h, dehydrated in acetone solutions (25, 50, 75, 90, and 100 %), and subjected to a series of Spurr resin solutions in increasing concentrations that were diluted in acetone (30, 70, and 100 %). Sections were cut with an ultramicrotome (Reichert-Jung), set in 300-mesh copper grids, and contrasted with uranyl acetate (3 %) and lead acetate (3 %) for 3 min each. A Zeiss EM-109 transmission electron microscope was used to evaluate the specimens.

For the stomatal evaluations, leaves from the second or third branch nodes were fixed in 70 % alcohol, and paradermal cuts were manually made in the middle third of the leaves and cleared in a 5 % sodium hypochlorite solution. Then, each section was stained with a 0.05 % toluidine blue solution in 0.1 M phosphate buffer (Kraus and Arduin 1997) and mounted on microscope slides in 50 % glycerin. The stomatal densities on the abaxial and adaxial epidermises of the leaves were expressed as the number of stomata per mm^2, using a Zeiss Axiostar Plus optical microscope and Sony digital camera, model EX MPEG Movie, 3.3 Megapixels. The polar (length of guard cells) and equatorial (width of guard cells) diameters were determined, using the *Image Tool* measurement program for Windows, version 3.00.

Data related to the growth parameters, nutrient concentrations, stomatal densities, and sizes were subjected to an analysis of variance and Tukey's test with the probability set at 5 % to compare the means. Antioxidant enzyme activity data were also subjected an analysis of variance ($P \leq 0.5$); significant results were then subjected to a polynomial regression analysis (Machado and Conceição 2007). Model selection was based on statistical significance (F test) and the adjusted coefficient of determination (R^2).

Results

The exposures of sweet potato plants to Fe concentrations of 4.5 and 9.0 mmol L^{-1} caused typical iron-induced toxicity symptoms, such as the development of tanned coloring and lesions in older leaves. These symptoms were associated with decreases in the branch lengths, leaf areas, and dry weights of shoots and roots (Fig. 1).

Increased iron concentrations altered the concentrations of some of the nutrients in the leaves. There were significant increases observed in Fe concentrations and decreases in K, Ca, and Mg concentrations in the old leaves that were treated with 9.0 mmol L^{-1} Fe and decreases in the concentrations of Mg and Mn after the 4.5 and 9.0 mmol L^{-1} Fe treatments. In the young leaves (Table 1), the Fe and Ca concentrations increased, while that of Mn decreased at the higher iron concentration. The P concentrations were higher in leaves that were exposed to the 4.5 and 9.0 mmol L^{-1} Fe treatments.

In this study, the SOD response variable showed significant interaction between evaluation days and iron concentrations tested. After treatment for 15 days, SOD activity levels increased by 21.37 % in the plants exposed to the 4.5 mmol L^{-1} Fe treatment and 48.12 % in those exposed to the 9.0 mmol L^{-1} Fe treatment (Fig. 2a). For the CAT response variable, no significant interaction was found between evaluation days and iron concentrations tested (Fig. 2b). However, CAT activity increased by 25 % in the 4.5 mmol L^{-1} treatment and decreased by 5.83 % in the 9.0 mmol L^{-1} treatment compared to the control (0.9 mmol L^{-1}). An analysis of variance also showed significant interaction between evaluation days and iron concentrations tested for the APX activity variable (Fig. 2c).

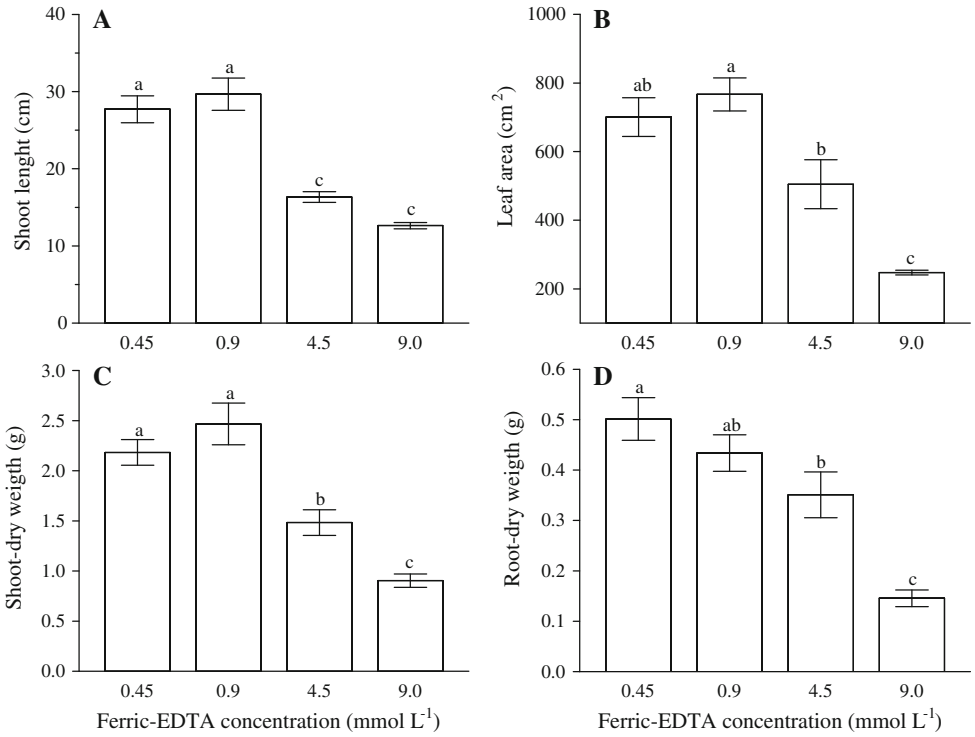

Fig. 1 Effect of ferric-EDTA concentration on sweet potato plant biomass: branch lengths (**a**), leaf area (**b**), shoot (**c**), and root (**d**). Means followed by the *same letter* do not differ by Tukey's test ($P < 0.05$) within each evaluated trait

Table 1 Nutrient amounts per sweet potato leaf dry mass from plants grown in nutrient solution with different ferric-EDTA concentrations

	Treatments (mmol L^{-1} ferric-EDTA)							
	Old leaves				Young leaves			
	0.45	0.9	4.5	9.0	0.45	0.9	4.5	9.0
Macronutrients (g kg^{-1} dry mass)								
N	39.09a	43.96a	39.58a	30.71a	41.85a	54.04a	48.64a	47.12a
P	7.40ab	6.19b	7.15ab	7.59a	6.92a	6.07a	9.30b	10.68b
K	73.97a	64.70ab	69.82a	55.50b	81.50a	77.31a	74.92a	76.65a
Ca	25.50a	23.40a	22.84a	19.40b	15.50ab	12.60b	13.51b	16.78a
Mg	6.49b	7.26a	5.90c	4.29d	4.99a	4.80ab	4.50ab	4.16b
Micronutrients (mg kg^{-1} dry mass)								
Cu	13.61a	11.7a	9.18a	10.70a	15.80a	18.05a	15.83a	16.15a
Zn	56.48a	48.45ab	48.40ab	44.02b	48.70a	42.36a	26.85a	42.64a
Fe	118.90a	199.20a	207.00a	349.10b	108.10a	108.13a	144.30a	186.90b
Mn	321.90a	388.02a	152.50b	67.22b	159.20a	191.00a	83.70b	37.74b

Means followed by the same letter do not differ by Tukey's test ($P < 0.05$) within each leaf type

Increased enzyme activities were observed in concordance with increased iron concentrations during both assessment periods; the treatment with the highest concentration (9.0 mmol L^{-1}) increased activities by 84.16 and 38.81 % after 7 and 15 days of application, respectively.

The addition of a solution containing a high concentration of iron to the nutrient medium (9.0 mmol L^{-1}) caused decreases in the stomatal densities on the abaxial sides of the leaves (Fig. 3). However, this variable remained consistent on the adaxial sides of the same leaves (Table 2). The diameters (polar and equatorial) of the stomata on the abaxial sides of the leaves increased when they were treated with higher concentrations of iron (4.5 and 9.0 mmol L^{-1}), while the equatorial adaxial diameters remained unaltered. The treatment with the lowest iron concentration (0.45 mmol L^{-1}) produced the greatest polar adaxial diameters (Table 2).

The images generated by the transmission electron microscopy of the cortex cells in the sweet potato roots (Fig. 4) following the 0.45 and 0.9 mmol L^{-1} Fe treatments showed mitochondria with typical structures (smooth outer membranes and highly folded internal structures called ridges) near the cellular peripheries (Fig. 4a, b, e). However, for the high iron concentration treatments (4.5 and 9.0 mmol L^{-1} Fe), dark spots that probably consisted of precipitated iron (ferritin) were found in large quantities in the cells and the mitochondrial membranes were not visible (Fig. 4c, d, f).

Pertaining to the ultrastructure of the mesophyll cells (Fig. 5), we observed that the plant chloroplasts from all of the Fe treatments were ellipsoidal with starch grains and typical grana and stroma arrangements (Fig. 5a–f). However, electron-dense spots that could be indicative of ferritin accumulation were also observed in the chloroplast stroma of plants treated with 9.0 mmol L^{-1} Fe (Fig. 5d).

Discussion

The reductions in growth and lesions on older leaves and the concomitant higher concentrations of ferric-EDTA that occurred in the plant tissues may be interrelated (Table 1). For the 9.0 mmol L^{-1} treated plants, the Fe concentration in the old leaves was 349.1 mg kg^{-1} dry weight. In rice plants, values of between 300 and 500 mg kg^{-1} are considered to be critical levels for indicating toxicity (Dobermann and Fairhurst 2000), although according to Pugh et al. (2002), the critical levels for most plants would be above 500 mg kg^{-1} dry weight. These data may suggest that there is variation among species and growing conditions. Although plants that were exposed to the 9.0 mmol L^{-1} Fe treatment also exhibited significantly higher iron levels in their dry young leaf biomasses (186.9 mg kg^{-1} dry mass), this amount was lower than that observed in old leaves (Table 1). According to Sinha and Saxena (2006), the roots are the main accumulation sites of excess iron in *Bacopa monnieri*, whereas only minor amounts of iron are translocated to the shoots, and the excess of Fe in roots of rice hinder the development of border cells and cause thickening of root cap cell walls (Zang et al. 2011). Such changes may have resulted in the marked reduction observed in the roots of plants exposed to higher Fe concentration (Fig. 1d). Thus, the data from our study may also indicate a possible control mechanism associated with the transport of this element among leaves at different stages of development.

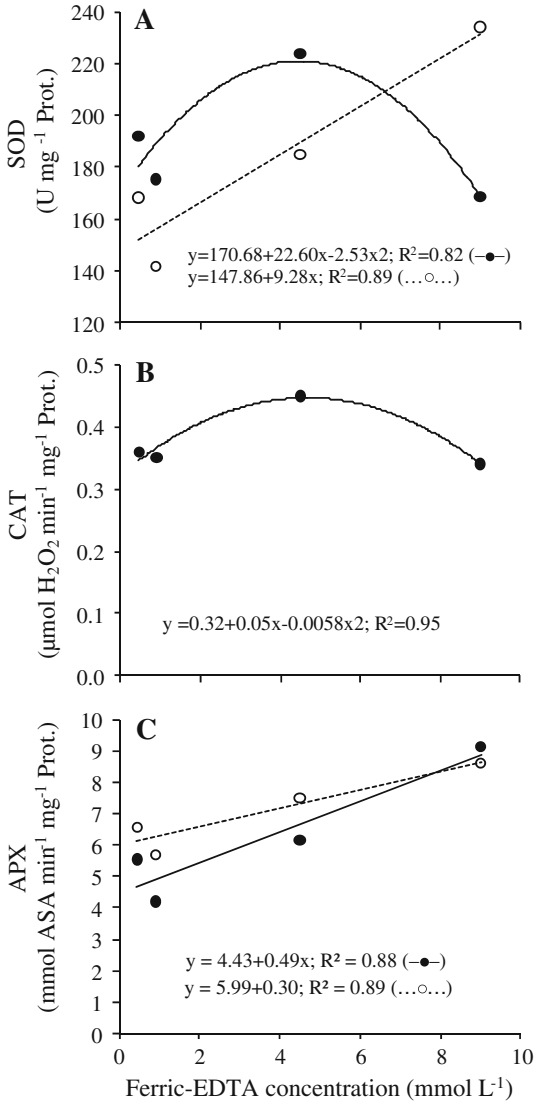

Fig. 2 Enzyme activities in sweet potato leaves grown in nutrient solutions with different ferric-EDTA concentrations at 7 (*continuous line with filled circles*) and 15 days (*dotted line with open circles*) following the onset of treatments. **a** Superoxide dismutase (SOD); **b** catalase (CAT); and **c** ascorbate peroxidase (APX)

Some plants exhibit resistance or adaptation mechanisms that can overcome the effects of stress caused by excess Fe. One such mechanism is Fe^{2+} oxidation in the rhizosphere, which forms plaques that can prevent its excessive absorption (Dobermann and Fairhurst 2000). The plaques have chemical and physical properties that are similar to the iron oxides found in soil and allow them to be able to adsorb other ions (Liu et al. 2007). In this study, we observed a significant reduction in some nutrients in the shoot dry masses of the plants that contained the highest Fe concentrations, indicating a possible influence of the iron oxide barrier on nutrient absorption. Additionally, Fe and Mn compete for the same physiological binding site (Baser and Somani 1982), which may have inhibited Mn absorption and its translocation to the shoot. According to Krüeger et al. (2002), a Fe^{2+} binding and transport protein was identified in the phloem of *Ricinus communis* that could also bind to Cu^{2+}, Zn^{2+}, and Mn^{2+} metals. There were no statistical differences observed in the Cu and Zn concentrations in the leaves of the sweet potatoes that were exposed to differing Fe concentrations, indicating that the transport of these metals remained unaltered.

The tolerance mechanisms of leaf tissues in response to high iron levels, such as the induction of the antioxidant system, have been suggested to be important factors in various species that are exposed to high Fe levels, because this nutrient is capable of generating ROS, especially the hydroxyl radical (OH·), by binding to various small chelators (Stein et al. 2009). Thus, the synchronized actions of the antioxidant enzymes are essential for ROS removal. SOD dismutase two superoxide radicals ($O_2^{\cdot -}$) to molecular oxygen (O_2) and hydrogen peroxide (H_2O_2) and is considered to be the first enzyme in plant antioxidant defense (Sinha and Saxena 2006). In this experiment, 15 days after the application of the treatments, the high Fe doses significantly stimulated SOD activity in the sweet potato leaves, suggesting that the enzyme plays an important role in protecting against oxidative stress (Fig. 2a). However, H_2O_2 is also toxic to the cell and must be detoxified. This process is carried out by CAT and/or peroxidase (APX). CAT and APX belong to two different classes of housekeeping enzymes and have different affinities to H_2O_2, with APX acting in the µM range and CAT in the mM range. Thus, while APX would be responsible for refined ROS modulation for signaling, CAT would be responsible for removal of excess ROS that accumulated during stress (Mittler 2002).

According to Chatterjee et al. (2006), CAT synthesis is blocked when substrate amounts are limited, which corroborates with the results obtained in our study showing that the highest iron concentration (9.0 mmol L^{-1}) leads to decreased CAT activity, probably due to decreased H_2O_2 levels caused by increased APX activity (Fig. 2b, c). Thus, it can be inferred that there were variations in the H_2O_2 concentrations in the sweet potato plants exposed to the highest iron concentration (9.0 mmol L^{-1}) and therefore variation in the activities of CAT and APX. The synchronized actions of SOD, CAT, and APX may have contributed to the reduction of Fe stress in the sweet potato leaves. Previous studies showed that iron-tolerant rice variety presented most intensive activity of the protective enzymes, such as SOD, CAT, and peroxidase (Zhang et al. 2011).

Sweet potato leaves are characteristically amphistomatic and have paracytic stomata (Menezes et al. 2003). Studies have shown that water stress (Melo et al. 2007), photoperiods (Castro et al. 2005), and organic and mineral

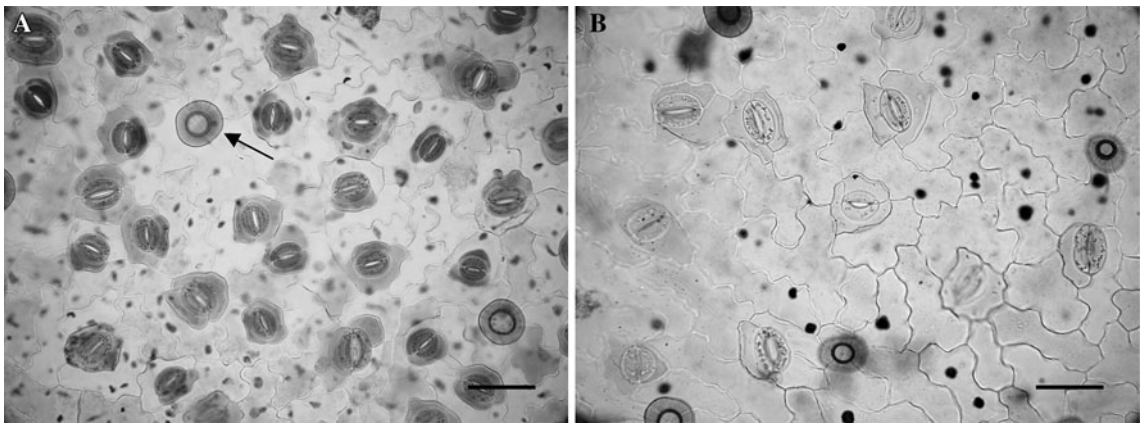

Fig. 3 Paradermic sections of abaxial epidermis from sweet potato leaves in relation to ferric-EDTA concentration in nutrient solution. **a** 0.9 mmol L^{-1} Fe (control); **b** 9.0 mmol L^{-1} Fe (10× control concentration). The *arrow* indicates glandular trichomes. *Bar* 50 µm

Table 2 Stomatal density and diameter (mean ± SEM) in sweet potato leaves in relation to ferric-EDTA concentration in nutrient solution

Evaluated characteristics	Treatments (mmol L^{-1} Fe)			
	0.45	0.9	4.5	9.0
Adaxial epidermis				
SD (no/mm^2)	8.50 ± 1.1a	7.90 ± 0.7a	8.60 ± 0.5a	7.10 ± 0.8a
SPD (µm)	34.70 ± 0.5a	32.00 ± 0.6b	33.10 ± 0.4ab	32.20 ± 0.7b
SED (µm)	24.70 ± 0.3a	24.20 ± 0.2a	23.90 ± 0.2a	25.00 ± 0.3a
Abaxial epidermis				
SD (no/mm^2)	24.00 ± 1.5a	24.20 ± 1.8a	22.30 ± 1.3a	13.70 ± 1.3b
SPD (µm)	30.70 ± 1.1a	32.70 ± 0.6a	35.90 ± 0.6b	35.90 ± 0.6b
SED (µm)	23.20 ± 0.3a	23.30 ± 0.2a	24.90 ± 0.4b	26.70 ± 0.5c

Means followed by the same letter do not differ by Tukey's test ($P < 0.05$)

SD stomatal density, *SPD* stomatal polar diameter, and *SED* stomatal equatorial diameter

fertilizers (Rosolem and Leite 2007; Corrêa et al. 2009) can cause alterations in stomatal densities. In the sweet potato, a reduction in the number of stomata per mm^2 was observed on the abaxial epidermis, which generally has a higher concentration of stomata, as the iron dosage increased (Table 2; Fig. 3). It has been reported that stomatal density is also inversely correlated with guard cell length (Galmes et al. 2007). In the present study, the abaxial stomata of plants that were exposed to the 4.5 and 9.0 mmol L^{-1} Fe treatments showed larger polar and equatorial diameters (Table 2), indicating a possible inverse relationship between density and stomatal diameter. Thus, the presence of high iron concentrations during leaf growth may have caused biochemical alterations that influenced normal tissue and stomatal development. Considering the fact that it is necessary for some plants to adapt to certain physical and physiological stress conditions, lower stomatal densities may have been offset, at least in part, by the increased stomatal diameters.

Similar to the chloroplasts, the mitochondria require large amounts of iron (necessary cofactor in the electron transport chain and for the formation of Fe–S clusters) and must maintain homeostasis by storing excess iron to prevent ROS formation (Jeong and Guerinot 2009). In sweet potato plants, the 4.5 and 9.0 mmol L^{-1} EDTA-iron concentrations that were used may be toxic to mitochondria, and in the present study, it was shown that the mitochondrial ultrastructures were completely altered (Fig. 4d, f). The excess iron may have enhanced free radical formation and the resulting degradation of the root cellular components, mainly the mitochondria, leading to impaired respiratory metabolism and, consequently, plant growth (Fig. 1).

According to Souza-Santos et al. (2001), excess iron can induce lipid peroxidation, altering membrane structures and permeabilities. Increased SOD and APX activities were observed (Fig. 2a, c) due to the higher ROS production that occurred following the highest iron concentration treatment, because the oxidative stress in the roots may have been more severe and, thus, the ROS were not efficiently detoxified, leading to membrane degradation. This fact may have contributed to the ultrastructural alterations found in the sweet potato roots (Fig. 4).

The dark spots observed in leaf and root cells of plants exposed to high Fe concentration (9.0 mmol L^{-1}) and contrasted with uranyl acetate and lead acetate (Figs. 4, 5)

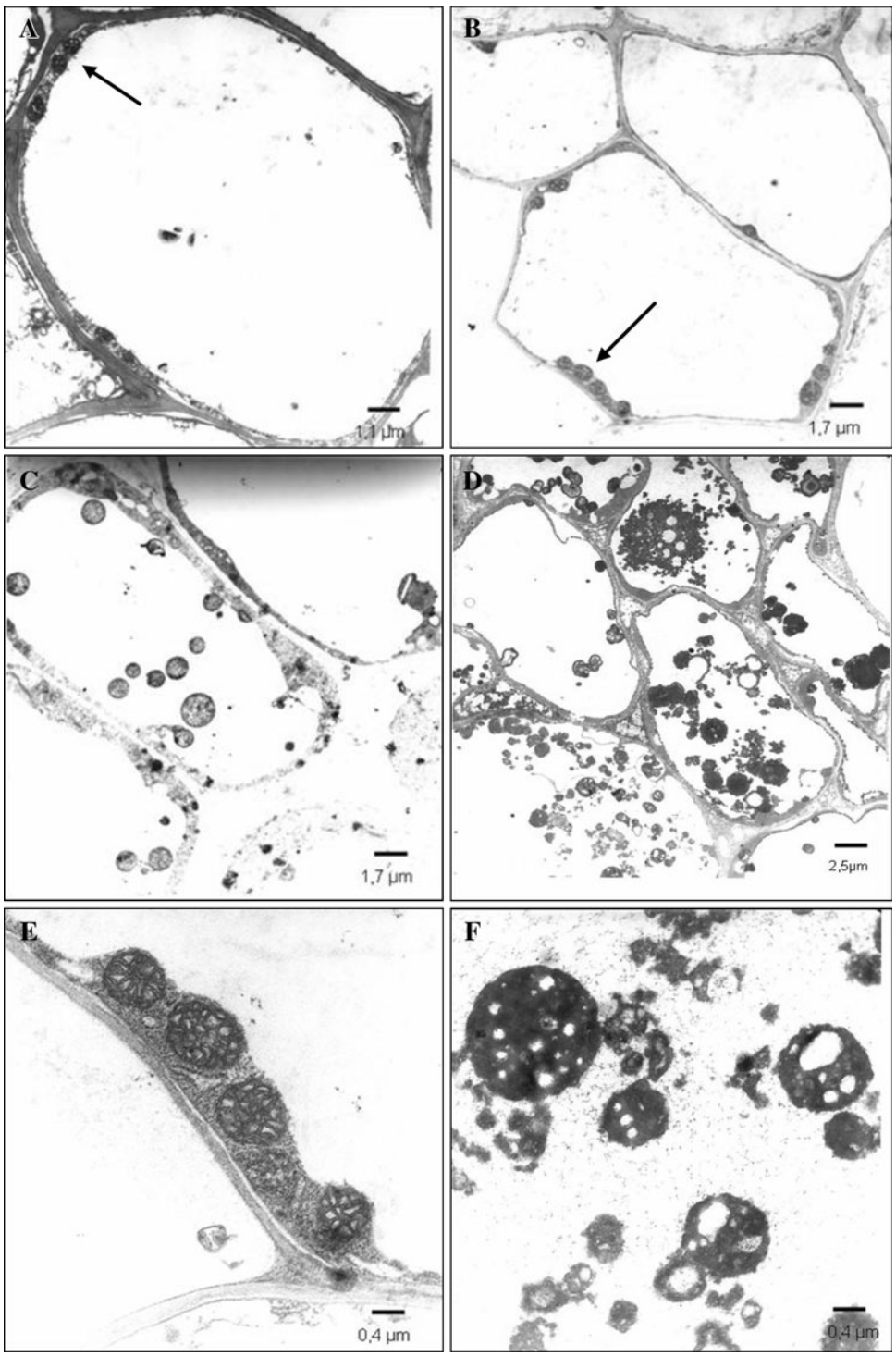

Fig. 4 Transmission electron micrograph of cortex cells in roots of sweet potato plants exposed to different ferric-EDTA concentrations. **a** 0.45 mmol L^{-1}; **b**, **e** 0.9 mmol L^{-1}; **c** 4.5 mmol L^{-1}; **d**, **f** 9.0 mmol L^{-1}. *Arrows* indicate mitochondria

are probably Fe-containing nonheme protein (ferritin) or products of its degradation (phytosiderin), as observed by Paramonova et al. (2007) in *Mesembryanthemum crystallinum* under stress conditions. Ferritins are proteins that are present in plants and function to sequester excess iron absorbed by the cells (Duy et al. 2007; Amils et al. 2007), preventing free radical formation via the Fenton reaction. According to Zancani et al. (2004), the ferritins in leaves, both crystalline and non-crystalline, are mainly located in the mitochondria and chloroplasts. The ferritin protein is important for the protection against oxidative stress mediated by iron. Ravet et al. (2009) recently demonstrated that ferritins are essential for protecting cells and that their absence leads to reduced growth and defects in

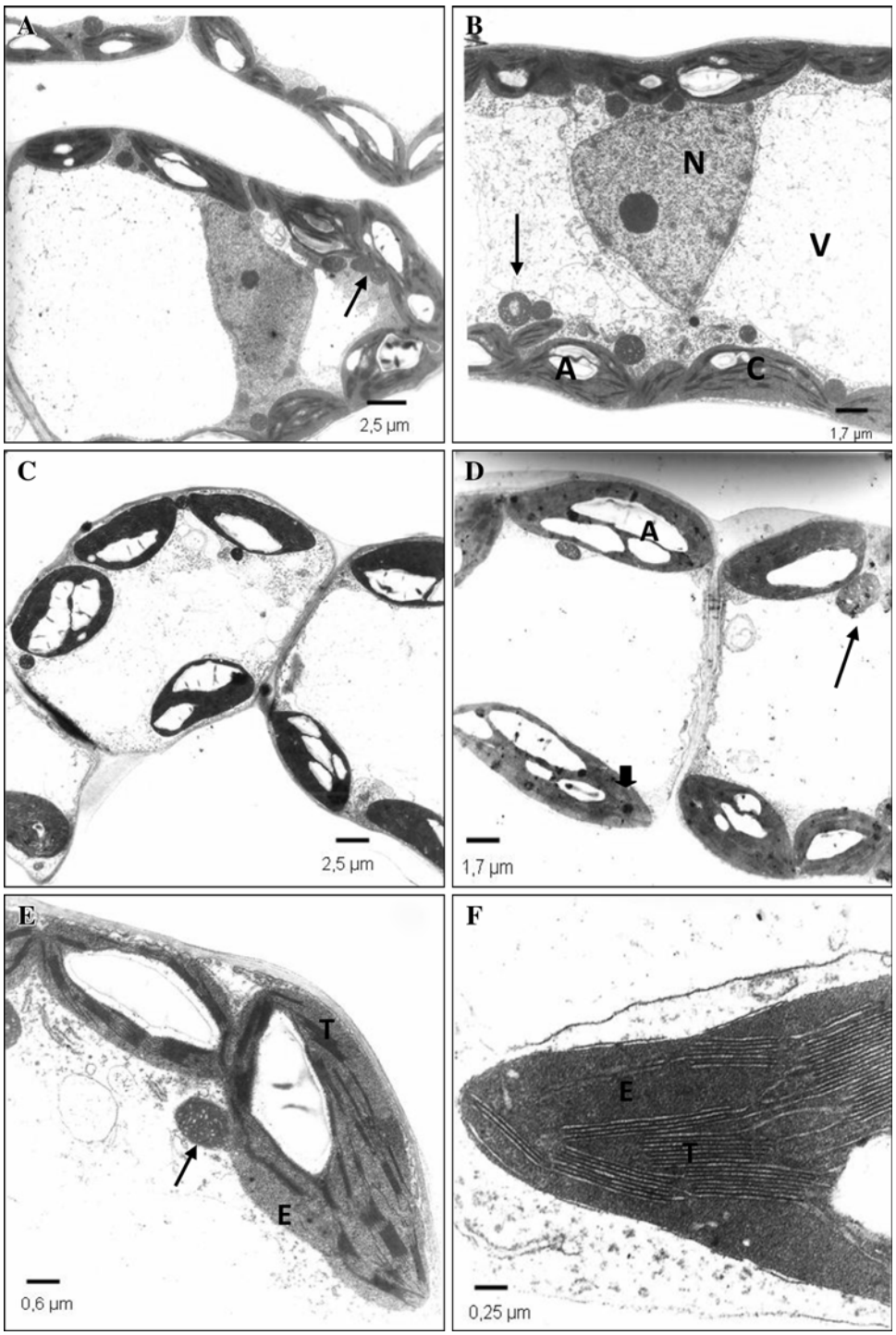

Fig. 5 Transmission electron micrograph of chloroplasts in plants exposed to different ferric-EDTA concentrations. **a** 0.45 mmol L^{-1}; **b**, **e** 0.9 mmol L^{-1}; **c** 4.5 mmol L^{-1}; **d**, **f** 9.0 mmol L^{-1}. The *arrows* indicate mitochondria and the *thick arrow* indicates possible accumulation of the ferritin protein. *C* chloroplast, *A* starch grain, *N* nucleus, *V* vacuole, *E* stroma, and *T* thylakoid

reproductive development, presumably due to the toxicity that results from the excess iron. In addition, the chlorophyll concentrations were higher when the sweet potato plants were exposed to high iron concentrations (9.0 mmol L^{-1}), and the JIP test parameters, which describe absorption and light energy use efficiency (Tsimilli-Michael and Strasser 2008), were intensified in these plants, indicating improved efficiencies in the capture, absorption, and use of light energy (Adamski et al. 2011). Thus, these results indicate that sweet potato plants that are exposed to high iron concentrations show no signs of toxicity in leaves that develop after the treatment application, which may jeopardize chloroplast ultrastructures and photosynthetic light reactions.

Our results suggest that excess iron significantly reduces the development of all parts of the sweet potato plant,

especially the roots, which experience ultrastructural alterations in their cells and severe structural damage to their mitochondria. Additionally, the accumulation of ferritin or products of its degradation was also observed. Moreover, while iron is localized primarily in leaf chlorophyllous cells, increasing its concentration in this organ does not substantially alter the chloroplast ultrastructure.

Author contribution Janete M. Adamski conducted the experiment, and did the data collection, writing, and literature search; Rodrigo Danieloski conducted the experiment and performed data collection; Sidnei Deuner performed the analyses of enzyme activity SOD, APX, and CAT, and data interpretation; Eugênia J. B. Braga performed data interpretation, writing, and literature search; Luis A. S. de Castro performed ultrastructural analyses; José A. Peters performed study design, data interpretation, writing, and literature search.

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