Received: 25 September 2017 | Revised: 6 March 2018 | Accepted: 14 March 2018

DOI: 10.1002/fes3.131

ORIGINAL RESEARCH

WILEY Food and Energy Security Open Access

New insights about cadmium impacts on tomato: Plant acclimation, nutritional changes, fruit quality and yield

Marcia E. A. Carvalho[1] | **Fernando A. Piotto**[1] | **Salete A. Gaziola**[1] | **Angelo P. Jacomino**[2] | **Marijke Jozefczak**[3] | **Ann Cuypers**[3] | **Ricardo A. Azevedo**[1]

[1]Departamento de Genética, Escola Superior de Agricultura "Luiz de Queiroz"/Universidade de São Paulo (Esalq/USP), Piracicaba, Brazil

[2]Departamento de Produção Vegetal, Escola Superior de Agricultura "Luiz De Queiroz"/Universidade de São Paulo (Esalq/USP), Piracicaba, Brazil

[3]Centre for Environmental Sciences, Hasselt University, Diepenbeek, Belgium

Correspondence
Ricardo A. Azevedo, Departamento de Genética, Escola Superior de Agricultura "Luiz de Queiroz"/Universidade de São Paulo, Piracicaba, Brazil.
Email: raa@usp.br

Funding information
Fundação de Amparo a Pesquisa do Estado de São Paulo, Grant/Award Number: 2009/54676-0 and 2013/15217-5; Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 303749/2016-4 and 476096/2013-8

Abstract

Tomato is an important crop worldwide. Cadmium (Cd) concentrations in fruits depend on tomato genotype. This work aimed to study the relation among Cd accumulation, tolerance mechanisms, and fruit features in two tomato cultivars with contrasting tolerance to Cd stress. Tolerant (Yoshimatsu) and sensitive (Tropic Two Orders) plants were grown in control and contaminated soils (0.04 and 3.77 mg/kg Cd, respectively) from the seedling stage to fruit production. Both cultivars were able to acclimatize to Cd exposure, probably through mechanisms associated with reductions in the magnesium status. Cadmium concentrations varied according to the following descending order: roots = leaf blades > (peduncle + sepals) > stem = fruits. However, the tolerant cultivar accumulated more Cd than did the sensitive one. Although Cd reached the fruits from the first to the fourth bunches, peduncle and sepals may act as a barrier to Cd entrance in tomato pulp and peel. The Cd-induced changes in the fruit mineral profile varied according to plant cultivar, organ, tomato tissue, and bunch position. Moreover, plant yield was not affected by the Cd stress, which was able to improve fruit size and weight in the tolerant cultivar. In conclusion, new insights about the Cd-induced effects on tomato development and fruit attributes were provided by growing plants in soil, which is the media generally used to cultivate this crop, rather than hydroponics. It was shown that tomato cultivars with contrasting tolerance to Cd toxicity can reach sexual maturity and produce fruits with no yield losses, despite impacts on development from long-term Cd exposure. This study also revealed the role of floral receptacle and its related structures in limiting, even partially, Cd translocation to the fruits. Furthermore, Yoshimatsu's capacity to produce bigger and heavier fruits, in plants under Cd exposure, may probably be associated with enhanced Cd accumulation.

KEYWORDS

cadmium, environmental contamination, food security, heavy metals, *Solanum lycopersicum*

1 | INTRODUCTION

Tomato (*Solanum lycopersicum* L.) consumption increases every year due to the fruit attractiveness (many colors, shapes, sizes, and flavors), multiple utilizations (from in natura consumption to processed sauces), and production of therapeutic compounds (Bergougnoux, 2014; FAOSTAT, 2016). However, tomato fruits are a potential pathway for cadmium (Cd) entrance into the food chain (Gratão et al., 2012; Hussain, Saeed, Khan, Javid, & Fatima, 2015; Hussain et al., 2017; Kumar, Edelstein, Cardarelli, Ferri, & Colla, 2015), hence affecting human health by triggering infertility (Alaee, Talaiekhozani, Rezaei, Alaee, & Yousefian, 2014), causing kidney and bone diseases, and increasing cancer risk (Järup & Åkesson, 2009; Nair, Degheselle, Smeets, Van Kerkhove, & Cuypers, 2013). The threshold for Cd concentration in vegetables is set at 0.05 mg/kg (Commission of the European Communities, 2014), but tomato fruits can contain almost twice this limit (Hussain et al., 2015), even when plants are grown in soil with Cd concentrations accepted by the CETESB (i.e., below 3.6 mg/kg, CETESB, 2014).

In general, the amount of Cd translocated to the fruits is proportional to its concentration in the growth media (Gratão et al., 2012; Hussain et al., 2017; Kumar et al., 2015). The problem arose due to anthropogenic activities that strongly increased metal content in arable lands, augmenting Cd concentrations that range from 0.01 to 0.8 mg/kg in natural areas to 1,500 mg/kg in contaminated areas (Kabata-Pendias, 2011). The environmental pollution occurs mainly near urban and industrial centers where a range of vegetables is commonly grown. The major source of soil Cd is atmospheric deposition from metal smelters and phosphorous (P) fertilizers, and also a substantial amount is released through mining, metal-based pesticides, industrial waste, and battery production (Kabata-Pendias, 2011). Therefore, many countries implemented environmental legislations concerning Cd concentrations in edible portions of crops (Commission of the European Communities, 2014), as well as in agricultural soils (CETESB, 2014) where plants uptake this metal.

In soil, most of the Cd (55%–90%) is presented as a free metal ion that is readily available to plants, being absorbed through roots and translocated to shoots after a short period of exposure (Gratão et al., 2015; Kabata-Pendias, 2011; Pompeu et al., 2017). Physicochemical characteristics of the soil, such as pH, texture, and organic matter content, affect Cd availability for plant absorption, which is particularly enhanced under acidic conditions (Castaldi & Melis, 2004; Kabata-Pendias, 2011; Kibria, Osman, & Ahmed, 2006; Manciulea & Ramsey, 2006; Melo, Alleoni, Carvalho, & Azevedo, 2011; Nogueirol, Monteiro, Gratão, Silva, & Azevedo, 2016). Furthermore, soil microorganisms may influence Cd uptake as well as its effects on tomato plants (1) by changing availability of nutrients that, in addition to be necessary to the plant development, may compete with Cd in sites for absorption and/or translocation, (2) by modifying hormonal balance in plants, and (3) by modulating the production of reactive oxygen species, which are important signaling molecules (Cuypers et al., 2016; Dourado et al., 2013; Madhaiyan, Poonguzhali, & Sa, 2007; Sebastian & Prasad, 2016a). In addition, similar to nutrients (Alvarenga, 2013), the uptake of nonessential elements may be enhanced in plants that were grown in hydroponic systems in comparison to soil. Therefore, studies about Cd translocation and accumulation in crops must be carried out in the growth media in which each species is usually cultivated.

Once within the plant, Cd triggers oxidative stress, disturbs nutrient uptake and distribution, impairs photosynthesis, triggers chromosomal aberrations, and decreases yield (Bayçu, Gevrek-Kürüm, et al., 2017; Bayçu, Rognes, et al., 2017; Carvalho et al., 2018; Gallego et al., 2012; Gratão, Polle, Lea, & Azevedo, 2005; Gratão et al., 2012; Hédiji et al., 2015; Sebastian & Prasad, 2016a,b). Multiple studies have shown great damages in cell systems due to the overproduction of reactive oxygen and nitrogen species (the so-called ROS and RNS, respectively) as a consequence of plant exposure to heavy metals (Alves et al., 2017; Branco-Neves et al., 2017; Cuypers et al., 2016; Fidalgo, Freitas, Ferreira, Pessoa, & Teixeira, 2011; Fidalgo et al., 2013; Gallego et al., 2012; Iannone, Groppa, & Benavides, 2015). To a certain extent, plants can cope with the heavy metal-induced oxidative stress by employing enzymatic and nonenzymatic antioxidant machineries, which encompass the modulation of superoxide dismutase (SOD, EC 1.15.1.1), catalase (CAT, EC 1.11.1.6), ascorbate peroxidase (APX, EC 1.11.1.11) activities, among other enzymes, as well as the synthesis of amino acids, soluble sugars, glutathione, and their derivates (Cuypers et al., 2016; Gallego et al., 2012; Jozefczak, Remans, Vangronsveld, & Cuypers, 2012; Méndez, Pena, Benavides, & Gallego, 2016; Štolfa, Pfeiffer, Špoljarić, Teklić, & Lončarić, 2015).

Long-term exposure to Cd, however, generally impacts crop production by decreasing the weight and number of fruits, which is frequently coupled to reductions in the number of flowers and fruit setting rate (Hédiji et al., 2010, 2015; Hussain et al., 2017). Moreover, Cd accumulation in fruits triggers stem-end yellowing in tomatoes (Kumar et al., 2015), causing visual damages that may reduce their commercial value. Interestingly, Cd accumulation and its effects on fruit quality, yield, and even progeny fitness depend on tomato cultivars (Carvalho et al., 2018; Gratão et al., 2012; Hussain et al., 2015; Kumar et al., 2015), indicating a degree of tolerance/sensitivity to this metal. In this context, the use of tomato cultivars with contrasting sensitivity to Cd exposure can be a valuable tool to identify the relation among tolerance mechanisms, Cd accumulation, and fruit quality and yield. For this purpose, the tolerant and sensitive tomato cultivars Yoshimatsu and Tropic Two Orders, respectively, were grown in soil rather than hydroponics, which is the most frequent system employed by researchers, in order to approach the reality of tomato cultivation and, consequently, to obtain information about the actual Cd concentration and its effects on plant development and fruit parameters after a long-term exposure to this toxic metal.

2 | MATERIALS AND METHODS

2.1 | Plant material and growth conditions

Seeds of tomato *Solanum lycopersicum* cvs. Yoshimatsu (Cd tolerant) and Tropic Two Orders (Cd sensitive) were chemically scarified by stirring in 2% HCl (v:v) for 15 min in order to standardize germination. Subsequently, seeds were sown in polystyrene trays filled with thin exfoliated vermiculite, which were irrigated four times a day. After seedling emergence, daily application of macro- and micronutrients (Peters Professional 20-20-20 at 1 g/L) was initiated in order to maintain suitable seedling development. After 1 week, this concentration was increased to 1.5 g/L, which was used until the 29-day-old seedlings were transplanted to 20 dm^3 pots filled with natural soil containing intrinsically low Cd concentration (0.04 mg/kg, Table S1). The control soil was the own natural soil with low Cd concentration. In order to reach levels similar to the maximum allowed for agricultural purposes (3.6 mg/kg soil, CETESB, 2014), a $CdCl_2$ solution was added to the natural soil containing low Cd concentration, so increasing the amount of available Cd from 0.04 to 3.77 mg/kg (Table S1). Next, the Cd-contaminated soil was mixed, and incubated for 15 days. The chemical and physical properties of control and contaminated soils, which were analyzed before the onset of experiments, are presented in Table S1. In total, four treatments were tested, that is, (1) tolerant cultivar in control soil, (2) tolerant cultivar in Cd-contaminated soil, (3) sensitive cultivar in control soil, and (4) sensitive cultivar in Cd-contaminated soil. Fungicides, pesticides, and fertilizers were applied to all plants, as recommended for tomato crop management. During the entire trial (since seed sowing), plants were cultivated in a greenhouse. From June to December 2015, plants were grown in control and contaminated soils (i.e., totalizing 131 days under Cd exposure) until the fruits of the four first bunches became mature, completely red. The monthly temperature and humidity were recorded, as provided by the meteorological station of Esalq/USP (Table S2).

2.2 | Plant biometry and chlorophyll content

The plant height, from the root–stem transition region to the onset of the apical meristem, was evaluated with millimeter measuring tape in all replications, before the apex removal (i.e., apical pruning). In the end of the biological cycle, three replications of each treatment were used to determine the leaflet area from the seven youngest and fully expanded leaves, which were detached from the plants and measured in an area meter (LI-COR®, LI-3100). Samples of leaflets and stems were kept in paper bags and dried in an oven (65 ± 2°C) until constant weight for dry mass determination. The specific leaf area (leaflet area/leaflet dry weight) was also calculated. Chlorophyll content was indirectly evaluated using a Soil Plant Analysis Development (SPAD) chlorophyll meter (Konica Minolta, SPAD-502 model), through two measurements in the biggest terminal leaflets of the two youngest and fully expanded leaves in each experimental unit.

2.3 | Production and quality parameters

The number of flowers and mature fruits, from the first to the third bunch, was recorded. Fruit diameter and height were evaluated by using a digital pachymeter, and the weight was determined through a digital scale. Subsequently, fruits were washed with water and gently dried with paper sheets. Only fruits from the first bunch were used for the determination of fruit firmness, pH, color, total soluble solids (SS), titratable acidity (TA), and SS/TA ratio, which indicates ripening and palatability (Araújo, Aroucha, Nascimento, Ferreira, & Lopes, 2016). The fruit firmness (N) was evaluated by using a penetrometer with a 5 mm tip (Sammar 85261.0472 TR model) by two measurements in fruit's opposite sides, in which the peel was removed. For the determination of fruit external color [L^* (luminosity), C^* (saturation), a^*, b^* and h (tonality angles)], two assessments in fruit's opposite sides were performed by using the colorimeter Minolta CR-300 (Minolta 2017).

The pulps of two fruits (without peel and after removal of the placenta with seeds) were squeezed with gauze to obtain tomato juice that was used to estimate the SS through a digital refractometer (Atago PR-101, Palette). Two measurements per replication were performed in order to obtain the mean value, which was expressed as ºBrix. The pH of the fruit juice was measured with a digital pH meter (Mettler Toledo, Seven Easy model) upon dilution of 5 g tomato juice into 45 ml distilled–deionized water. Next, the potentiometric titration was evaluated by adding 0.1 N NaOH to reach pH 8.1. The percentage of citric acid was calculated based on the NaOH volume by using the following formula (Carvalho, Mantovani, Carvalho, & Moraes, 1999):

$$\%\ \text{citric acid} = \frac{64 \times \text{NaOH} \times \text{N}}{\text{ws} \times 10},$$

where: NaOH = volume of NaOH (ml); N = normality of NaOH; and ws = weight of juice sample.

2.4 | Quantification of Cd and nutrient concentration

Samples were dried in an oven at 60°C and subsequently grounded using mortar and pestle. Calcium (Ca), potassium (K), magnesium (Mg), phosphorus (P), sulfur (S), iron (Fe), manganese (Mn), copper (Cu), zinc (Zn), boron (B), and Cd concentrations were evaluated through ICP-OES (Inductively Coupled Plasma Optical Emission Spectrometry) analysis, which was preceded by nitro-perchloric digestion of the grounded samples. Three replications for each treatment were subjected to the analytical procedures carried out by the Soil Fertility Laboratory at Instituto Agronômico de Campinas (IAC, Brazil).

2.5 | Statistical procedures

The experiment was carried out in a completely randomized design with a factorial scheme 4 × 4 (treatments × organs) to analyze the Cd-induced effects on the mineral profile of roots, stems, leaf blades, and floral receptacle. The repeated measurement analysis was employed to assess the effect of treatments on plant height, stem diameter, and chlorophyll content throughout the time. The split-plot analysis was used to evaluate the effect of treatments (plots) on size and weight of fruits from different bunches (subplots). For production parameters and fruit physicochemical attributes, a one-way analysis of variance (ANOVA) was performed ($p \leq .05$). Before ANOVA, data were subjected to tests through the "Guided Data Analysis" tool of the statistical software SAS (SAS Institute 2011), in order to check whether they were in accordance to the assumptions for the ANOVA performance (i.e., normal distribution, variance homogeneity, and error independence). Moreover, data transformations were performed when indicated by this tool. The Tukey test was used to estimate the least significant range among means of treatments ($\alpha \leq .05$) for all variables, and a regression analysis ($p \leq .05$) was performed to evaluate the effect of treatments during the time.

3 | RESULTS

3.1 | Plant development

Two tomato cultivars with a contrasting tolerance degree to Cd toxicity, Yoshimatsu (tolerant) and Tropic Two Orders (sensitive), were grown in soil containing 0.04 (control) and 3.77 mg/kg Cd (contaminated). After 39 days of exposure to this metal, the tolerant cultivar exhibited a lower height than control plants, but this effect disappeared in advanced stages of development (Figure 1). The sensitive cultivar did not show significant differences in plant height (Figure 1).

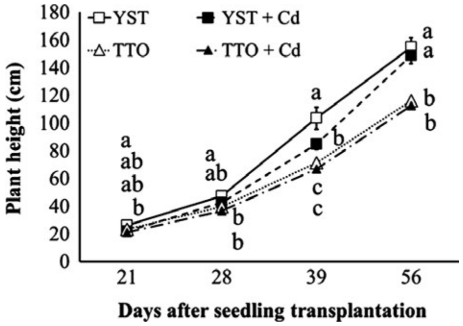

FIGURE 1 Plant height of tolerant and sensitive tomato cultivars, *Solanum lycopersicum* cvs. Yoshimatsu (YST) and Tropic Two Orders (TTO), respectively, which were grown in control and contaminated soils (0.04 and 3.77 mg/kg Cd, respectively). $n = 10$. Distinct letters denote different means by Tukey test ($\alpha \leq .05$) for comparisons among treatments within the same time of plant transplantation. Bars represent the standard errors of the means

The leaf area and dry weight were generally decreased in Cd-challenged plants, when compared to the control plants (Figure 2a,b). Only the sensitive cultivar presented significant reductions in the stem dry weight after exposure to Cd (Figure 2d). The specific leaf area (Figure 2c) and stem diameter (Figure S1) were not influenced by Cd, regardless of the tomato cultivar. The chlorophyll content increased through plant development in both Cd-treated and control plants (Table S3). The long-term Cd exposure did not affect the chlorophyll content in tolerant and sensitive cultivars, when compared to the plants grown in control soil (Table S3).

3.2 | Cd accumulation

Tomato cultivars exhibited Cd concentrations in the following descending order: leaf blades = roots > (peduncle + floral receptacle + sepals) > stem = peel and pulp of fruits from the first bunch (Figure 3a–c). When the influence of fruit bunch position was concerned, a general decreasing trend in Cd accumulation in tomato pulp (Figure 3b) and peel (Figure 3c) was observed concurrently to the advanced bunch position. Furthermore, the tolerant cultivar generally showed an increasing trend of Cd accumulation with respect to the sensitive cultivar, regardless of plant organ or tissue (Figure 3a–c). This difference was significant in roots (Figure 3a), as well as in fruits from the second (pulp and peel) and fourth bunches (pulp) (Figure 3b,c).

3.3 | Mineral profile

After exposure to Cd, both tolerant and sensitive tomato cultivars presented reductions in their root Mg concentration in comparison to plants that were grown in control soil (Figure 4a). Also in roots, S, Cu, Zn, Mn, and Fe concentrations showed a decreasing trend in Cd-challenged plants

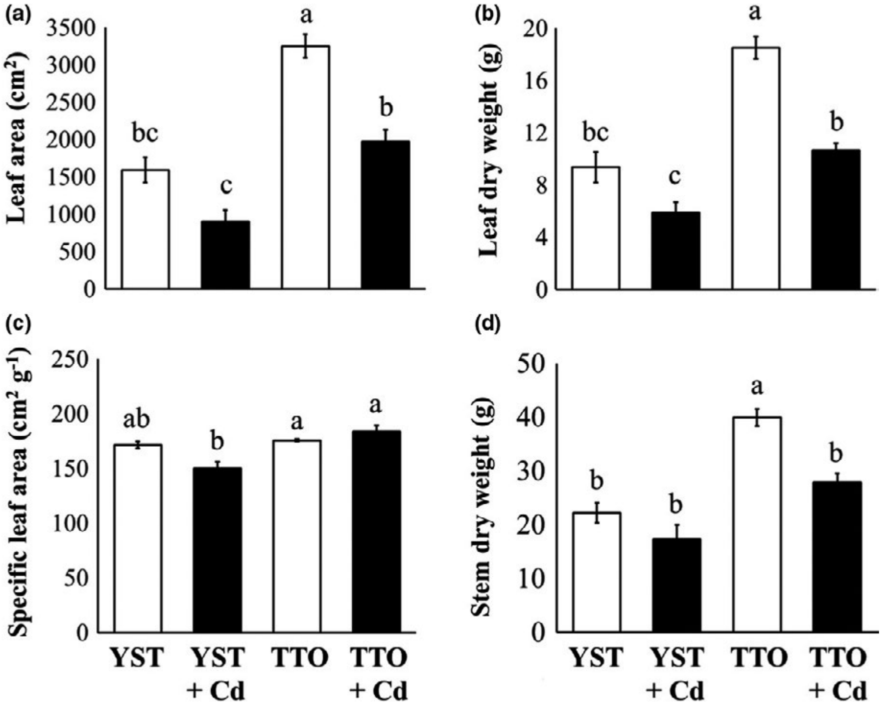

FIGURE 2 Leaf area (a) and dry weight (b), specific leaf area (c), and stem dry weight (d) of tolerant and sensitive tomato cultivars, *Solanum lycopersicum* cvs. Yoshimatsu (YST) and Tropic Two Orders (TTO), respectively, which were grown in control (white columns) and contaminated (black columns, +Cd) soils (0.04 and 3.77 mg/kg Cd, respectively). $n = 3$. Distinct letters denote different means by Tukey test ($\alpha \leq .05$). Bars represent the standard errors of the means

when compared to the control ones, regardless of the cultivar (Figures 4c and 5a–c). However, the root B concentration was increased in the sensitive tomato cultivar after Cd exposure (Figure 5d). For the others nutrients (N, P, K, and Ca), Cd caused no significant differences between Cd-challenged and control plants (Tables S4 and S5).

In general, nutrient concentrations in fruits decreased in the youngest bunches when compared to the old ones (Figures 6–10). However, depending on nutrient, fruit part, and genotype, the mineral profile of the fruits was also affected by Cd (Figures 6–10). In fruits from the second bunch, the pulp P concentration was reduced in both Cd-treated cultivars (Figure 6a). In contrast, Cd exposure increased the K concentration in the pulp of fruits from the second and third bunches in the tolerant cultivar (Figure 6c). However, the peel K and P concentrations were not affected by Cd exposure (Figure 6b,d).

Only the peel Ca concentration was strongly decreased in fruits from the first bunch in the tolerant cultivar after exposure to Cd (Figure 7b). When the S concentration in tomato pulp and peel was examined, a general decreasing trend occurred concurrently with the advanced bunch position, regardless of Cd exposure (Figure 7c,d). The Mg concentration in fruit pulp and peel was generally higher in the tolerant than the sensitive cultivar (Figure 8a,b). Moreover, fruits from the first and second bunches contained higher Mg concentrations than those from the third and fourth bunches (Figure 8a,b). The Fe concentration in tomato pulp and peel was lower in young than in old bunches (Figure 8c,d).

The Mn concentration in tomato pulp was higher in fruits from the tolerant than the sensitive cultivar, moreover, fruits from the oldest bunches (i.e., first and second) accumulated more Mn than the youngest bunches (third and fourth, Figure 9a). In fruit peel of the sensitive cultivar, Mn concentrations were maintained in distinct bunches, whereas the tolerant cultivar produced fruits with decreased Mn concentrations in advanced bunch position (Figure 9b). Plant exposure to Cd provoked an increasing trend in the Cu concentrations in pulp and peel of fruits from the first bunch (Figure 9c,d). In contrast, Cd caused significant reductions in the Cu concentration in the pulp of fruits from the second bunch in the sensitive cultivar (Figure 9c).

In plants under Cd exposure, the Zn concentration was reduced in the tomato pulp of tolerant and sensitive accessions, especially in fruits from the first and second bunches, but these variations were not enough to cause significant differences between Cd-treated and control plants (Figure 10a,b). When B concentration in fruit pulp and peel is concerned, reductions were observed with advanced bunch position (Figure 10c,d). However, in certain bunches, Cd enhanced this reduction as observed in the pulp of fruits from the third bunch in the sensitive cultivar (Figure 10c), as well as in the

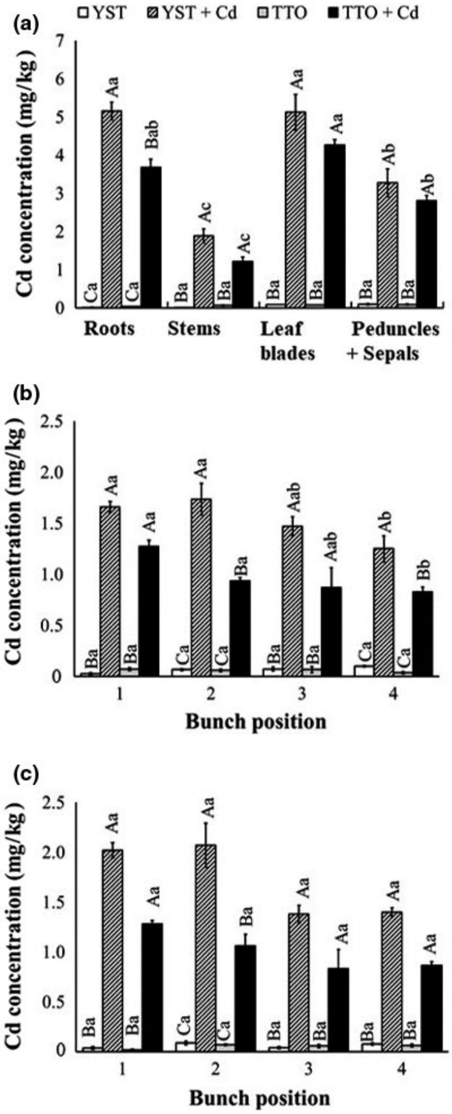

FIGURE 3 Cadmium (Cd) concentration in roots, stem, leaf blades, peduncle, and sepals (a), as well as in fruit pulp (b) and peel (c) of tolerant and sensitive tomato cultivars, *Solanum lycopersicum* cvs. Yoshimatsu (YST) and Tropic Two Orders (TTO), respectively, which were grown in control and contaminated soils (0.04 and 3.77 mg/kg Cd, respectively). $n = 3$. Distinct lowercase and uppercase letters denote different means by Tukey test ($\alpha \leq .05$) for comparisons of the same treatment in different organs/tissues, and for comparisons of all treatments inside each organ/tissue, respectively. Bars represent the standard errors of the means

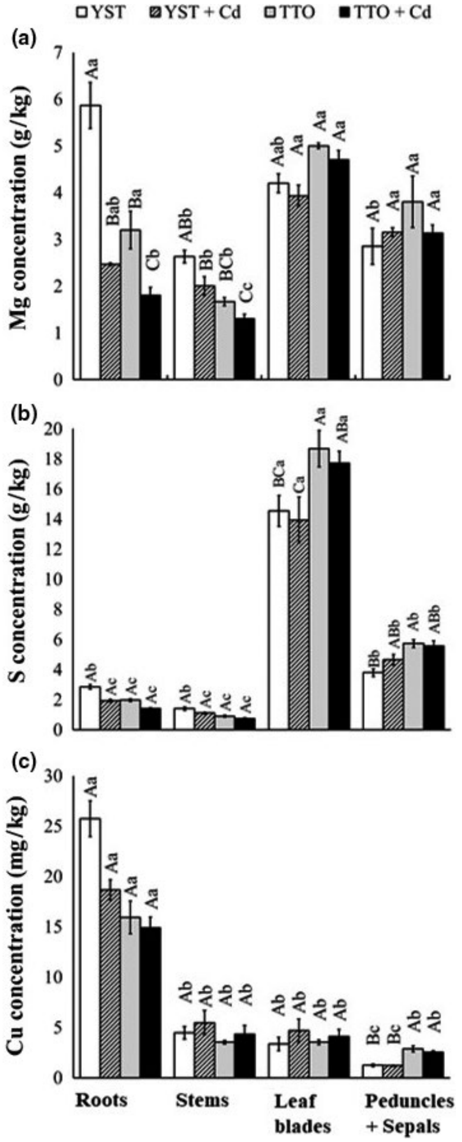

FIGURE 4 Magnesium—Mg (a), sulfur—S (b), and copper—Cu (c) concentration in different organs/tissues of tolerant and sensitive tomato cultivars, *Solanum lycopersicum* cvs. Yoshimatsu (YST) and Tropic Two Orders (TTO), respectively, which were grown in control and contaminated soils (0.04 and 3.77 mg/kg Cd, respectively). $n = 3$. Distinct lowercase and uppercase letters denote different means by Tukey test ($\alpha \leq .05$) for comparisons of the same treatment in different organs/tissues, and for comparisons of all treatments inside each organ/treatment, respectively. Bars represent the standard errors of the means

peel of tomato fruits that were produced in the first bunch of the tolerant cultivar (Figure 10d).

3.4 | Production parameters

The number of flowers was not affected by either plant exposure to Cd or bunch position, but the tolerant cultivar possessed generally more flowers than the sensitive one (Table S6). Although the fruit setting was decreased with the advanced bunch position, there were no significant changes between Cd-treated and control plants, regardless of the cultivar (Table S6). The number of fruits did show reductions in the youngest bunches when compared to the old ones, independent of genotype and Cd exposure (Figure 11a).

The fruit weight of the sensitive cultivar was naturally decreased in the youngest bunches, when compared to the old ones, and plant exposure to Cd was not enough to provide differences between control and Cd-treated plants (Figure 11b).

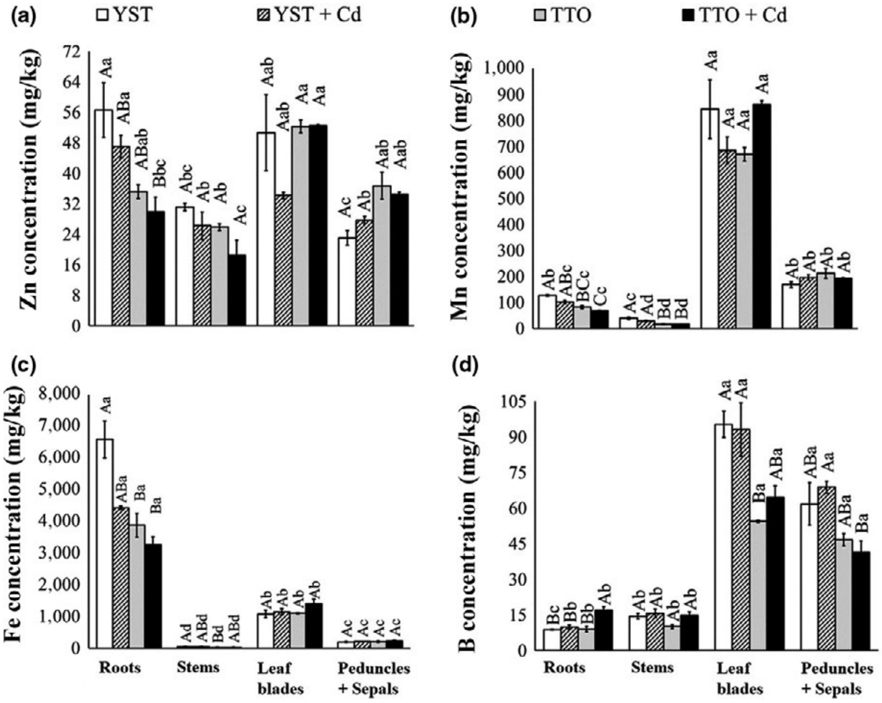

FIGURE 5 Zinc—Zn (a), manganese—Mn (b), iron—Fe (c), and boron—B (d) concentrations in different organs/tissues of tolerant and sensitive tomato cultivars, *Solanum lycopersicum* cvs. Yoshimatsu (YST) and Tropic Two Orders (TTO), respectively, which were grown in control and contaminated soils (0.04 and 3.77 mg/kg Cd, respectively). $n = 3$. Distinct lowercase and uppercase letters denote different means by Tukey test ($\alpha \leq .05$) for comparisons of the same treatment in different organs/tissues, and for comparisons of all treatments inside each organ/tissue, respectively. Bars represent the standard errors of the means

However, tolerant cultivars exhibited a trend of increasing fruit weight in plants under Cd exposure in comparison to control plants, being significantly higher in the youngest bunch (Figure 11b). Moreover, increases in fruit diameter and height were observed in the tolerant plants after cultivation in Cd-containing soil (Table 1). The sensitive tomato did not show differences in fruit dimensions due to Cd exposure (Table 1). Finally, plant yield of both sensitive and tolerant cultivars was not significantly affected by exposure to Cd (Figure 11c).

3.5 | Fruit physicochemical attributes

After plant exposure to Cd, tomato firmness presented slight increases in fruits from the tolerant cultivar, Yoshimatsu, but it was not enough to provoke significant differences between Cd-treated and control plants (Figure S2a). Furthermore, plant cultivation in Cd-containing soil did not affect the total soluble solid content (TSS), which was similar in Yoshimatsu and Tropic Two Orders (Figure S2b). Juice titratable acidity (TA) (Figure S2c), pH (Figure S2d), and TSS/TA ratio (Table S7) depended on tomato cultivar, and none of these variables were influenced by the long-term exposure to Cd. The juice pH (Figure S2d) and TSS/TA ratio (Table S7) were lower in the tolerant than in the sensitive cultivar. By contrast, TA was higher in tomato cv. Yoshimatsu than tomato cv. Tropic Two Orders (Figure S2c), regardless of the presence of Cd in soil. When color parameters of the fruits are examined, no significant differences between Cd-treated and control plants occurred (Figure S3a,b, Table S7). However, the color tonality, h, was higher in the sensitive tomato cultivar when compared to the tolerant cultivar (Figure S3c).

Overall, the significant changes induced by Cd exposure on plant development, fruit attributes, and their nutritional status are presented in Table 2.

4 | DISCUSSION

Yoshimatsu (tolerant) and Tropic Two Orders (sensitive) are two tomato cultivars with contrasting tolerance to Cd toxicity that were identified in previous studies: after 7 days of plant exposure to 35 μmol/L $CdCl_2$ in hydroponics Tropic Two Orders exhibited remarkable decreases in leaf, stem, and root biomasses, presenting a decrease of 58% in the seedling dry weight, while Yoshimatsu showed no significant changes (preliminary data). Moreover, Tropic Two Orders exhibited leaf chlorosis and necrosis earlier than Yoshimatsu, in which such damages were less pronounced than in the sensitive

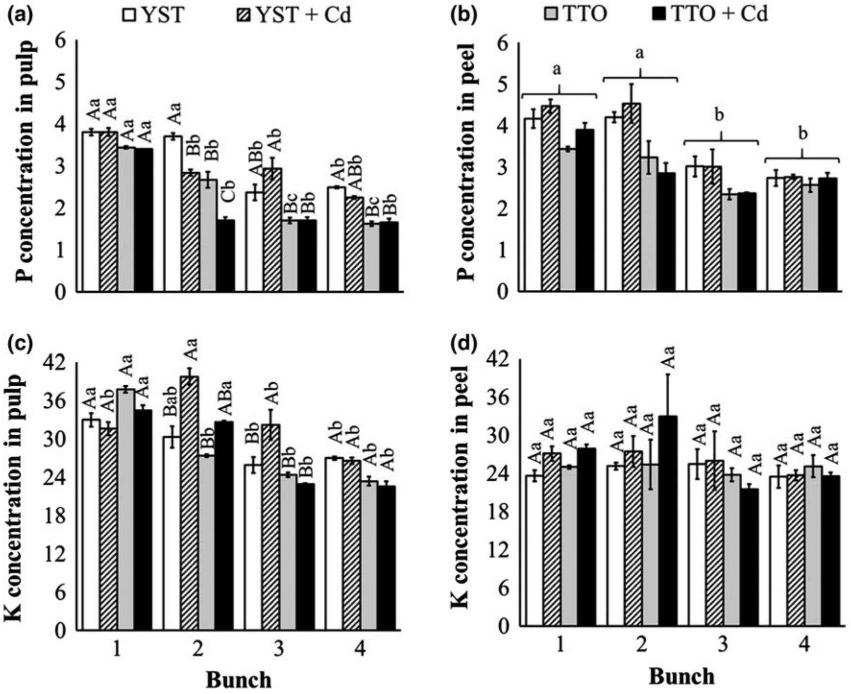

FIGURE 6 Phosphorus—P (a, b) and potassium—K (c, d) concentrations in pulp and peel of fruits from different bunches in tolerant and sensitive tomato cultivars, *Solanum lycopersicum* cvs. Yoshimatsu (YST) and Tropic Two Orders (TTO), respectively, which were grown in control and contaminated soils (0.04 and 3.77 mg/kg Cd, respectively). $n = 3$. Distinct lowercase and uppercase letters denote different means by Tukey test ($\alpha \leq .05$) for comparisons of the same treatment in different organs/tissues, and for comparisons of all treatments inside each organ/tissue, respectively. Plant exposure to Cd and bunch position exerted no significant changes on K concentration in tomato peel ($p > .05$). Bars represent the standard errors of the means

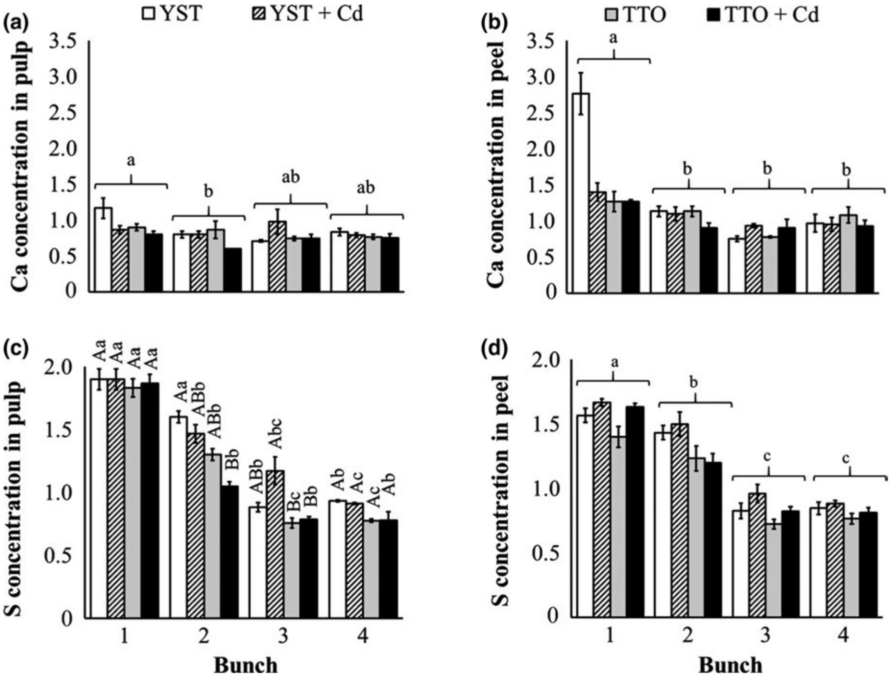

FIGURE 7 Calcium—Ca (a, b) and sulfur—S (c, d) concentrations in pulp and peel of fruits from different bunches in tolerant and sensitive tomato cultivars, *Solanum lycopersicum* cvs. Yoshimatsu (YST) and Tropic Two Orders (TTO), respectively, which were grown in control and contaminated soils (0.04 and 3.77 mg/kg Cd, respectively). $n = 3$. Distinct lowercase and uppercase letters denote different means by Tukey test ($\alpha \leq .05$) for comparisons of the same treatment in different organs/tissues, and for comparisons of all treatments inside each organ/tissue, respectively. Bars represent the standard errors of the means

tomato line. In this work, both cultivars were grown from seedling stage (29-day-old) to fruit production in soil containing 0.04 (control) and 3.77 mg/kg Cd (contaminated). The latter is a concentration similar to that allowed for arable lands, that is, 3.6 mg/kg Cd (CETESB 2014). This study aimed to answer the following questions: (1) What are the

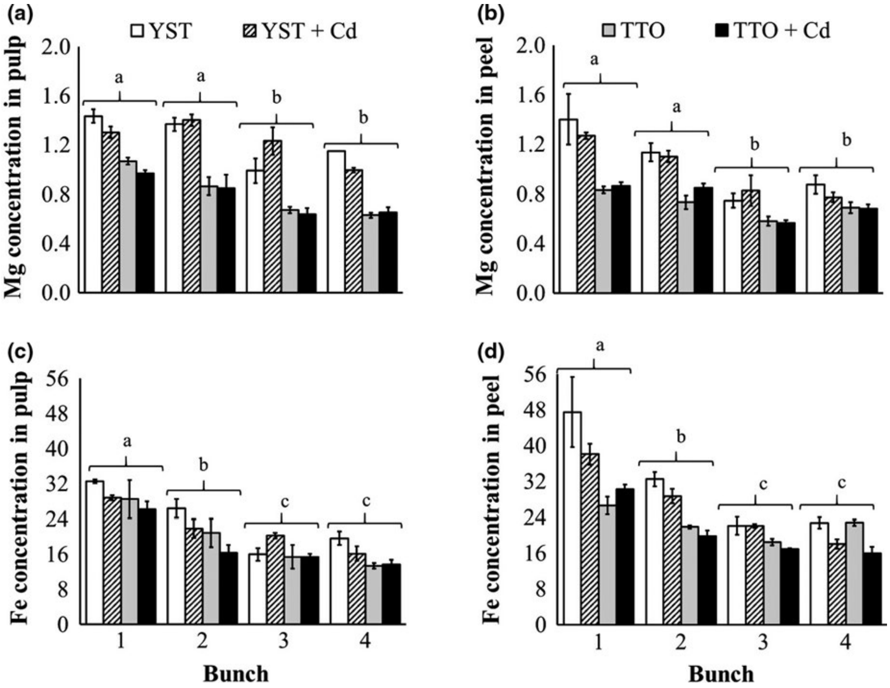

FIGURE 8 Magnesium—Mg (a, b) and iron—Fe (c, d) concentrations in pulp and peel of fruits from different bunches in tolerant and sensitive tomato cultivars, *Solanum lycopersicum* cvs. Yoshimatsu (YST) and Tropic Two Orders (TTO), respectively, which were grown in control and contaminated soils (0.04 and 3.77 mg/kg Cd, respectively). $n = 3$. Distinct letters denote different means by Tukey test ($\alpha \leq .05$) for comparisons of the same treatment in different organs/tissues, and for comparisons of all treatments inside each organ/tissue, respectively. Bars represent the standard errors of the means

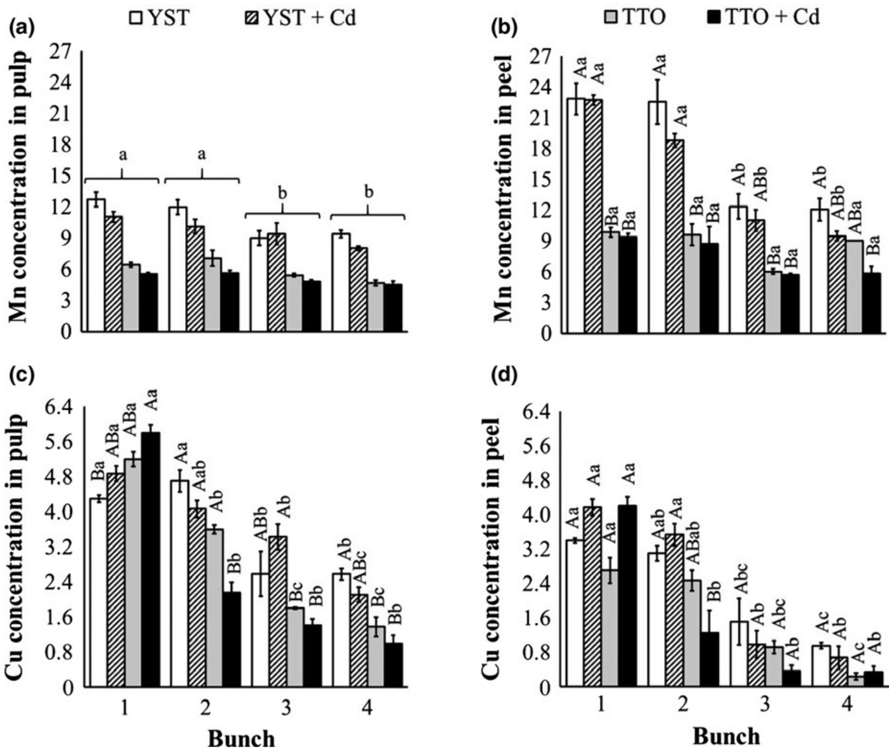

FIGURE 9 Manganese—Mn (a, b) and copper—Cu (c, d) concentrations in pulp and peel of fruits from different bunches in tolerant and sensitive tomato cultivars, *Solanum lycopersicum* cvs. Yoshimatsu (YST) and Tropic Two Orders (TTO), respectively, which were grown in control and contaminated soils (0.04 and 3.77 mg/kg Cd, respectively). $n = 3$. Distinct lowercase and uppercase letters denote different means by Tukey test ($\alpha \leq .05$) for comparisons of the same treatment in different organs/tissues, and for comparisons of all treatments inside each organ/tissue, respectively. Bars represent the standard errors of the means

effects of long-term Cd exposure on tomato plant development and fruit features? (2) How much Cd is translocated to the tomato fruits in plants that were grown in Cd-containing soil? (3) Can tolerance mechanisms be associated with advantageous fruit attributes in commercial tomato cultivars under Cd exposure?

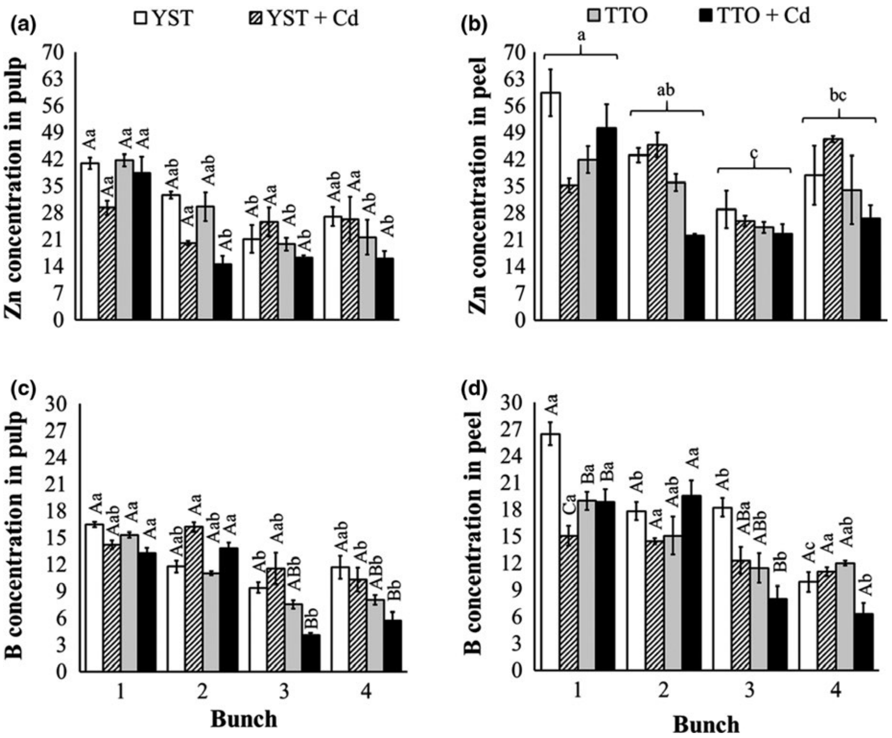

FIGURE 10 Zinc—Zn (a, b) and boron—B (c, d) concentrations in pulp and peel of fruits from different bunches in tolerant and sensitive tomato cultivars, *Solanum lycopersicum* cvs. Yoshimatsu (YST) and Tropic Two Orders (TTO), respectively, which were grown in control and contaminated soils (0.04 and 3.77 mg/kg Cd, respectively). *n* = 3. Distinct lowercase and uppercase letters denote different means by Tukey test (α ≤ .05) for comparisons of the same treatment in different organs/tissues, and for comparisons of all treatments inside each organ/tissue, respectively. Bars represent the standard errors of the means

4.1 | Low Mg status is associated with plant acclimatization to long-term Cd exposure

The continuous plant development in Cd-containing soil validates previous reports that tomato is able to acclimate to long-term Cd exposure, reaching sexual maturity (Gratão et al., 2012; Hédiji et al., 2015; Hussain et al., 2017), producing fruits (Figure 11a), and maintaining yield (Figure 11c) despite some impacts on plant growth (Figures 1 and 2, Figure S1, Tables S3 and S6). Although the mechanism behind this plant ability is poorly understood, data from the current study suggest a relation with reduced Mg concentration in roots, the only macronutrient that was altered between Cd-stressed and control plants' vegetative organs (Figure 4a). This hypothesis is supported by previous studies in which the low Mg status was coupled to enhanced antioxidant potential in rice (Chou, Chao, Huang, Hong, & Kao, 2011), beneficial outcomes in *Arabidopsis* leaves (Hermans, Chen, Coppens, Inzé, & Verbruggen, 2011), and better barley development after Cd exposure (Kudo, Kudo, Uemura, & Kawai, 2015). Preliminary data associated Mg-driven tolerance mechanisms with the maintenance of suitable root development in tomato under short-term Cd exposure (6 days), but the plant capacity to reduce Mg status was only observed in tolerant tomato accessions.

However, this study reveals that both tolerant and sensitive cultivars possess this ability (Figure 4a), indicating that mechanisms coupled to an appropriate management of the Mg status in Cd-challenged tomato plants may be activated earlier or faster in tolerant than in sensitive cultivars. Another interesting point is that the tolerant cultivar showed several symptoms of Cd-induced phytotoxicity, including decreased plant height in certain developmental stages (Figure 1), large reductions in the fruit set when compared to sensitive cultivar (Table S6), and clear visual changes in the leaf shape (data not shown), which support trends of modifications in the specific leaf area (Figure 2c). However, at the same time, the tolerant cultivar produced bigger and heavier fruits in Cd-treated than in control plants (Figure 1, Table 1), indicating that this cultivar is able to change photoassimilate distribution to favor fruit growth during Cd-induced stress, hence supporting yield (Figure 11). It is not known whether such changes are a direct effect from the increased Cd accumulation (Figure 3a–c) or a cultivar-specific ability to change plant features to cope with Cd-induced stress.

Anyways, the immediate plasticity or capacity for a rapid adaptive response of the tolerant cultivar could be traits important for its survival and even its offspring under nonoptimal environmental conditions. According to Mueller (2017), such fast responses were previously used by farmers to select the best accessions of other plant species (e.g., *Polygonum erectum* L.—a seed crop used during the premaize agricultural systems) and, in a similar way, these features can be further explored by breeders to choose tomato accessions with superior adaptability in soils contaminated with Cd. From the ecological point of view, improvement of fruit features might enhance tomato dispersion through increases in the fruit attractiveness (bigger fruits) or even to help tomato progeny fitness by supporting additional storage compounds (heavier

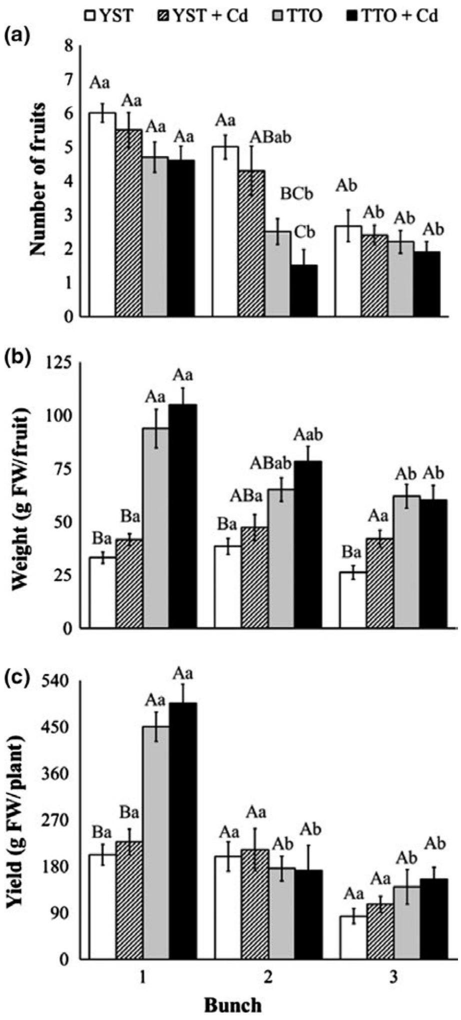

FIGURE 11 Number of fruits (a), fruit weight (b), and yield (c) from the first to the third bunch in tolerant and sensitive tomato cultivars, *Solanum lycopersicum* cvs. Yoshimatsu (YST) and Tropic Two Orders (TTO), respectively, which were grown in control and contaminated (+Cd) soils (0.04 and 3.77 mg/kg Cd, respectively). $n = 10$. Distinct lowercase and uppercase letters denote different means by Tukey test ($\alpha \leq .05$) for comparisons the same treatment in different bunches and all treatments inside each bunch, respectively. Bars represent the standard errors of the means

fruits). Accordingly, improvement in germination was observed in seeds from plants of tomato cv. Yoshimatsu under Cd exposure, while performance of seeds from the sensitive cultivar presented no differences in Cd-stressed plants when compared to control ones (Carvalho et al., 2018).

4.2 | Cadmium-induced modifications in the nutrient uptake and distribution affect fruit mineral status, which also depends on tomato genotype, fruit part, and bunch position

In contrast to the Cd accumulation in plants (Figure 1a), the concentration of several nutrients was decreased in tomato roots (Figures 4 and 5), indicating that Cd prevents their uptake. This antagonist effect, which was also reported in other tomato cultivars (Dong, Wu, & Zhang, 2006; Hédiji et al., 2015; López-Millán, Sagardoy, Solanas, Abadía, & Abadía, 2010), is probably due to Cd-induced alterations in the activity of plasma membrane transporters (Migocka & Klobus, 2007), as well as due to sharing of transporters between Cd and some nutrients (Korshunova, Eide, Clark, Guerinot, & Pakrasi, 1999; Thomine, Wang, Ward, Crawford, & Schroeder, 2000). The last assumption is especially consistent for Mn and Fe transporters that are enrolled in Cd absorption and translocation in several species (Sasaki, Yamaji, Yokosho, & Ma, 2012; Thomine et al., 2000; Wu et al., 2016), indicating that Cd uptake occurs at the expense of Mn and Fe absorption (Figure 5b,c), so decreasing their accumulation in fruits, especially in the peel of those from the fourth bunch (Figures 8d and 9b).

Therefore, in addition to the problems regarding Cd accumulation, modifications in the fruit mineral composition should be evaluated in order to avoid potential nutritional deficiencies in humans due to the low intake of the plant-origin nutrients as a consequence of Cd exposure (Teklić, Lončarić, Kovačević, & Singh, 2013). It has been demonstrated that Cd disturbs the suitable translocation of nutrients to tomato fruits (Hédiji et al., 2015; Kumar et al., 2015), however, differences between tomato pulp and peel have not been considered before.

Moreover, this work showed that the magnitude of such disturbances also depends on fruit bunch position (Figures 6–10). For instance, in the sensitive cultivar, large reductions in B concentration in tomato peel and pulp were especially observed in fruits from youngest bunches (Figure 10c,d). In the tolerant cultivar, however, decreases in B concentration were only detected in tomato peel, particularly in fruits from the first (oldest) and, at in a lesser extent, third bunches (Figure 10c,d). The data indicated that, despite increased B uptake in the sensitive cultivar (Figure 5), Cd exposure may induce B retaining in vegetative organs, so partially decreasing B translocation to the fruits. For the tolerant cultivar, accumulation of this micronutrient in the peduncle and/or sepals, in addition to no increases in B absorption, significantly impaired B translocation to fruit peel.

Despite detection of some modifications in fruit parameters, most of them were less pronounced when compared to other studies in which tomato plants were subjected to long-term Cd exposure, and such results can be associated with the use of different cultivation systems (hydroponics or its variations vs. soil). The direct implication is the overestimation of Cd accumulation because the uptake of essential and nonessential elements is generally enhanced in hydroponics when compared to soil (Alvarenga, 2013), so increasing Cd-induced side-effects on plant development and yield. Accordingly, a decreasing Cd concentration was

TABLE 1 Diameter and height of fruits from the first to the third bunches of tolerant and sensitive tomato cultivars, *Solanum lycopersicum* cvs. Yoshimatsu (YST) and Tropic Two Orders (TTO), respectively, which were grown in control and contaminated (+Cd) soils (0.04 and 3.77 mg/kg Cd, respectively)

	Treatments				
Bunch	YST	YST + Cd	TTO	TTO + Cd	Average
Diameter (mm)					
1	40.46 (1.27)	42.07 (1.19)	58.05 (2.04)	60.80 (1.63)	50.35 (1.53)a
2	40.67 (1.41)	45.70 (1.91)	52.17 (1.59)	57.97 (2.36)	49.13 (1.82)ab
3	37.24 (1.29)	44.36 (1.45)	51.81 (1.80)	54.35 (2.17)	46.94 (1.68)b
Average	39.46 (1.33)c	44.04 (1.52)b	54.01 (1.81)a	57.71 (2.06)a	
Height (mm)					
1	34.36 (0.96)	36.85 (0.97)	48.40 (1.83)	50.23 (1.15)	42.46 (1.23)a
2	35.31 (1.24)	38.39 (1.65)	42.49 (1.35)	46.15 (1.88)	40.59 (1.53)ab
3	30.76 (1.32)	37.72 (1.58)	42.74 (1.11)	43.88 (1.85)	38.78 (1.47)b
Average	33.48 (1.18)c	37.65 (1.40)b	44.54 (1.43)a	46.75 (1.63)a	

Distinct letters denote different means by Tukey test ($\alpha \leq .05$) for comparisons among treatments or bunch position. Values inside parentheses are the standard errors of the means. $n = 3$.

TABLE 2 Significant changes observed in plant development, fruit attributes, and their nutritional status after growing of tolerant and sensitive tomato cultivars, *Solanum lycopersicum* cvs. Yoshimatsu (YST) and Tropic Two Orders (TTO), respectively, in soil contaminated with cadmium (3.77 mg/kg Cd)

	Tomato cultivars	
Variables	YST	TTO
Plant height	↓	
Leaf area		↓
Leaf dry weight		↓
Stem dry weight		↓
Fruit fresh weight	↑	
[Mg] roots	↓	↓
[B] roots		↑
[P] tomato pulp (2nd bunch)	↓	↓
[K] tomato pulp (2nd and 3rd bunches)	↑	
[Cu] tomato pulp (2nd bunch)		↓
[B] tomato pulp (1st bunch)	↓	

Analysis of variance, *F* test ($p \leq .05$), followed by Tukey test ($\alpha \leq .05$) were used for comparisons of treatments' means. $n = 3$–10, depending on the variable.

observed in roots, leaves, and fruits of plants from this work, when compared to plants that were grown in hydroponics with 20 µmol/L $CdCl_2$ for 90 days (Hédiji et al., 2010), or in vessels filled with sand that received drip irrigation with 25 µmol/L $CdCl_2$ (Kumar et al., 2015). Such phenomena are probably related to physicochemical soil properties that can retain Cd ions by reducing their mobility and/or availability to the plants (Kabata-Pendias, 2011). Decreases in Cd uptake can also be provided by soil microorganisms, which increases solubilization of nutrients that may compete with Cd in sites for its absorption and translocation (Dourado et al., 2013; Madhaiyan et al., 2007; Sebastian & Prasad, 2016a). In addition, some organisms from soil microbiological community can change plant response to Cd exposure by altering hormonal balance of plants, and by modifying generation of reactive oxygen species, which are important signaling molecules (Cuypers et al., 2016; Dourado et al., 2013; Madhaiyan et al., 2007).

4.3 | Floral receptacle and its related structures act as a barrier to Cd translocation to fruits

The current data concerning Cd accumulation in vegetative organs (Figure 3a) are not in line with previous works, which showed that roots always possess a higher Cd concentration than leaves (Alves et al., 2017; Hédiji et al., 2015; Kumar et al., 2015; López-Millán et al., 2010; Monteiro et al., 2011). Four main hypotheses that do not exclude each other support this result: (1) The high transpiration rate of leaflets from the selected leaves (youngest and fully expanded leaves) provided the increased Cd accumulation, probably because they were one of the main organs for gas exchange at the end of the tomato biological cycle; (2) Changes in Cd distribution and remobilization during the end of reproductive stage provoked Cd accumulation in the leaflets; (3) The use of leaflets, rather than the complete tomato leaves, may overestimate Cd concentrations due to the exclusion of rachis that, as an extension of stems, may have a low Cd accumulation; and (4)

A "dilution effect" on the root Cd concentrations might have occurred due to both an increased root development in adult plants and a reduced Cd uptake in soil-cultivated plants, when compared to the hydroponic-cultivated ones.

In reproductive organs, data indicated that both cultivars presented a mechanism to limit Cd translocation to the fruits by depositing this metal in the floral receptacle and its related structures, that is, peduncle and sepals (Figure 3a–c). This mechanism may explain why fruits, during distinct development stages, contained a lower Cd concentration than flowers, as observed previously by Hédiji et al. (2010, 2015). From the ecological point of view, this mechanism may protect tomato progenies from the potential side-effects of increased Cd accumulation in fruits and even seeds. However, this mechanism may cause fruit set reductions (Table S6), and trigger fruit abortion (Hédiji et al., 2010, 2015). Moreover, it was not totally efficient in limiting Cd translocation to fruits, as this metal was accumulated in tomato peel and pulp. Interestingly, Cd accumulation was further enhanced in the tolerant cultivar (Yoshimatsu), indicating the presence of differential protective apparatus against Cd toxicity. Accordingly, Yoshimatsu's seeds, which exhibited the highest Cd concentration, also presented the best germination rate in comparison to Tropical Two Orders' seeds (Carvalho et al., 2018).

Although Yoshimatsu exhibited several relevant traits for plant cultivation in Cd-contaminated soils (i.e., improvements in fruit size and weight), its enhanced capacity for Cd accumulation is a potential problem to human health, in which Cd can trigger infertility (Alaee et al., 2014), kidney and bone diseases, and cancer (Järup & Åkesson, 2009; Nair et al., 2013). By contrast, Tropic Two Orders, which was also able to maintain yield after Cd exposure, produced fruits with a lower Cd concentration in their peel and pulp. In addition, the selection of fruits from the youngest bunches (Figure 1b,c), in which a "dilution effect" may occur due to increases in tomato biomass (Figure 11b), can further decrease the amount of Cd that enter in the food chain. Even so, Cd concentration in fruits exceeded the amount allowed for human consumption in vegetables (Figure 3b,c) (Commission of the European Communities, 2014). Therefore, agricultural and health organizations should run field experiments in order to evaluate Cd concentration in crops that are grown in contaminated soils with certain Cd concentrations that are allowed for arable lands. In such experiments, physicochemical and microbiological soil composition, farmland cultivation system, as well as plant species with contrasting root morphology must be considered as all these factors may affect Cd availability, mobility, absorption, and/or accumulation in plants (Castaldi & Melis, 2004; Hirzel, Retamal-Salgado, Walter, & Matus, 2017; Kabata-Pendias, 2011; Kibria et al., 2006; Madalcho, 2016; Manciulea & Ramsey, 2006; Nogueirol et al., 2016; Norton et al., 2017).

In conclusion, the impacts of long-term Cd exposure on plant development and fruit features depend on the tomato cultivar, which may present modifications in the plant height, leaf area, stem dry weight, and nutritional status. Even so, sensitive and tolerant cultivars are able to acclimatize to long-term Cd exposure, probably through mechanisms associated with reductions in the Mg status. Cadmium is accumulated in vegetative and reproductive organs of both cultivars, but the tolerant plant showed usually a higher Cd concentration than the sensitive cultivar. Tomato pulp and peel presented Cd concentrations that ranged from 0.83 to 2.07 mg/kg, also revealing that plants grown in soil accumulate less Cd in fruits than those cultivated in hydroponic systems, when compared to the previous studies. Although Cd reaches the fruits from the first to the fourth bunches, the floral receptacle and its related structures may act as a barrier to Cd entrance in fruits. The magnitude of the Cd-induced changes in the mineral profile varies according to plant cultivar, organ, tomato tissue, and bunch position of fruit. Moreover, Cd exposure is able to improve fruit size and weight in the tolerant tomato cultivar.

ACKNOWLEDGMENTS

This work was supported by Fundação de Amparo à Pesquisa do Estado de São Paulo—FAPESP [grant numbers 2009/54676-0 and 2013/15217-5] and Conselho Nacional de Desenvolvimento Científico e Tecnológico—CNPq [476096/2013-8]. We are grateful to Dr. Cláudio Roberto Segatelli and Aparecido da Silva for the crop management assistances.

CONFLICT OF INTEREST

None declared.

ORCID

Marcia E. A. Carvalho http://orcid.org/0000-0002-7221-5380
Fernando A. Piotto http://orcid.org/0000-0001-9728-6938
Salete A. Gaziola http://orcid.org/0000-0003-2382-6684
Angelo P. Jacomino http://orcid.org/0000-0003-0863-6698
Marijke Jozefczak http://orcid.org/0000-0003-0800-3532
Ann Cuypers http://orcid.org/0000-0002-0171-0245
Ricardo A. Azevedo http://orcid.org/0000-0001-7316-125X

REFERENCES

Alaee, S., Talaiekhozani, A., Rezaei, S., Alaee, K., & Yousefian, E. (2014). Cadmium and male infertility. *Journal of Infertility and Reproductive Biology*, *2*, 62–69.

Alvarenga, M. A. R. (2013). *Tomate: Produção em campo, em casa-de-vegetação e em hidroponia*. Lavras, Brazil: Editora Universitária de Lavras.

Alves, L. A., Monteiro, C. C., Carvalho, R. F., Ribeiro, P. C., Tezotto, T., Azevedo, R. A., & Gratão, P. L. (2017). Cadmium stress related to root-to-shoot communication depends on ethylene and auxin in tomato plants. *Environmental and Experimental Botany*, *134*, 102–115. https://doi.org/10.1016/j.envexpbot.2016.11.008

Araújo, N. O., Aroucha, E. M. M., Nascimento, L. V., Ferreira, R. M. A., & Lopes, W. A. R. (2016). Spatial variation of physicochemical characteristics in *Formosa papaya* fruits. *Idesia (Arica)*, *34*, 5–9. https://doi.org/10.4067/S0718-34292016005000023

Bayçu, G., Gevrek-Kürüm, N., Moustaka, J., Csatári, I., Rognes, S. E., & Moustakas, M. (2017). Cadmium-zinc accumulation and photosystem II responses of *Noccaea caerulescens* to Cd and Zn exposure. *Environmental Science and Pollution Research International*, *24*, 2840–2850. https://doi.org/10.1007/s11356-016-8048-4

Bayçu, G., Rognes, S. E., Özden, H., Gören-Saglam, N., Csatári, I., & Szabó, S. (2017). Abiotic stress effects on the antioxidative response profile of *Albizia julibrissin* Durazz. (Fabaceae). *Brazilian Journal of Botany*, *40*, 21–32. https://doi.org/10.1007/s40415-016-0318-3

Bergougnoux, V. (2014). The history of tomato: From domestication to biopharming. *Biotechnology Advances*, *32*, 170–189. https://doi.org/10.1016/j.biotechadv.2013.11.003

Branco-Neves, S., Soares, C., Sousa, A., Martins, V., Azenha, M., Gerós, H., & Fidalgo, F. (2017). An efficient antioxidant system and heavy metal exclusion from leaves make *Solanum cheesmaniae* more tolerant to Cu than its cultivated counterpart. *Food and Energy Security*, *6*, 123–133. https://doi.org/10.1002/fes3.114

Carvalho, C. R. L., Mantovani, D. M. B., Carvalho, P. R. N., & Moraes, R. M. M. (1999). *Análises químicas de alimentos*. Campinas, Brazil: ITAL.

Carvalho, M. E. A., Piotto, F. A., Nogueira, M. L., Gomes-Junior, F. G., Chamma, H. M. C. P., Pizzaia, D., & Azevedo, R. A. (2018). Cadmium exposure triggers genotype-dependent changes in seed vigor and germination of tomato offspring. *Protoplasma*. in press. https://doi.org/10.1007/s00709-018-1210-8

Castaldi, P., & Melis, P. (2004). Growth and yield characteristics and heavy metal content on tomatoes grown in different growing media. *Communications in Soil Science and Plant Analysis*, *35*, 85–98. https://doi.org/10.1081/CSS-120027636

CETESB. (2014). *Valores orientados para solos e águas subterrâneas no estado de São Paulo*. São Paulo, Decisão de diretoria no. 045/2014/E/C/I, de 20 de fevereiro de 2014.

Chou, T.-S., Chao, Y.-Y., Huang, W.-D., Hong, C.-Y., & Kao, C.-H. (2011). Effect of magnesium deficiency on antioxidant status and cadmium toxicity in rice seedlings. *Journal of Plant Physiology*, *168*, 1021–1030. https://doi.org/10.1016/j.jplph.2010.12.004

Commission regulation – EU. (2014). No 488/2014 of 12 May 2014 amending regulation (EC) no 1881/2006 as regards maximum levels of cadmium in foodstuffs. *Official Journal of the European Union*.

Cuypers, A., Hendrix, S., Reis, R. A., Smet, S., Deckers, J., Gielen, H., … Keunen, E. (2016). Hydrogen peroxide, signaling in disguise during metal phytotoxicity. *Frontiers in Plant Science*, *7*, 470. https://doi.org/10.3389/fpls.2016.00470

Dong, J., Wu, F., & Zhang, G. (2006). Influence of cadmium on antioxidant capacity and four microelement concentrations in tomato seedlings (*Lycopersicon esculentum*). *Chemosphere*, *64*, 1659–1666. https://doi.org/10.1016/j.chemosphere.2006.01.030

Dourado, M. N., Martins, P. F., Quecine, M. C., Piotto, F. A., Souza, L. A., Franco, M. R., … Azevedo, R. A. (2013). *Burkholderia* sp. SCMS54 reduces cadmium toxicity and promotes growth in tomato. *Annals of Applied Biology*, *163*, 494–507. https://doi.org/10.1111/aab.12066

FAOSTAT. (2016). Retrieved from http://faostat3.fao.org/browse/rankings/commodities_by_regions/E

Fidalgo, F., Azenha, M., Silva, A. F., Sousa, A., Santiago, A., Ferraz, P., & Teixeira, J. (2013). Copper-induced stress in *Solanum nigrum* L. and antioxidant defense system responses. *Food and Energy Security*, *2*, 70–80. https://doi.org/10.1002/fes3.20

Fidalgo, F., Freitas, R., Ferreira, R., Pessoa, A. M., & Teixeira, J. (2011). *Solanum nigrum* L. antioxidant defence system isozymes are regulated transcriptionally and posttranslationally in Cd-induced stress. *Environmental and Experimental Botany*, *72*, 312–319. https://doi.org/10.1016/j.envexpbot.2011.04.007

Gallego, S. M., Pena, L. B., Barcia, R. A., Azpilicueta, C. E., Iannone, M. F., Rosales, E. P., … Benavides, M. P. (2012). Unravelling cadmium toxicity and tolerance in plants: Insight into regulatory mechanisms. *Environmental and Experimental Botany*, *83*, 33–46. https://doi.org/10.1016/j.envexpbot.2012.04.006

Gratão, P. L., Monteiro, C. C., Carvalho, R. F., Tezotto, T., Piotto, F. A., Peres, L. E. P., & Azevedo, R. A. (2012). Biochemical dissection of *diageotropica* and *Never ripe* tomato mutants to Cd-stressful conditions. *Plant Physiology and Biochemistry*, *56*, 79–86. https://doi.org/10.1016/j.plaphy.2012.04.009

Gratão, P. L., Monteiro, C. C., Tezotto, T., Carvalho, R. F., Alves, L. R., Peters, L. P., & Azevedo, R. A. (2015). Cadmium stress antioxidant responses and root-to-shoot communication in grafted tomato plants. *BioMetals*, *28*, 803–816. https://doi.org/10.1007/s10534-015-9867-3

Gratão, P. L., Polle, A., Lea, P. J., & Azevedo, R. A. (2005). Making the life of heavy metal-stressed plants a little easier. *Functional Plant Biology*, *32*, 481–494. https://doi.org/10.1071/FP05016

Hédiji, H., Djebali, W., Belkadhi, A., Cabasson, C., Moing, A., Rolin, D., … Chaïbi, W. (2015). Impact of long-term cadmium exposure on mineral content of *Solanum lycopersicum* plants: Consequences on fruit production. *South African Journal of Botany*, *97*, 176–181. https://doi.org/10.1016/j.sajb.2015.01.010

Hédiji, H., Djebali, W., Cabasson, C., Maucourt, M., Baldet, P., Bertrand, A., … Gallusci, P. (2010). Effects of long-term cadmium exposure on growth and metabolomic profile of tomato plants. *Ecotoxicology and Environmental Safety*, *73*, 1965–1974. https://doi.org/10.1016/j.ecoenv.2010.08.014

Hermans, C., Chen, J., Coppens, F., Inzé, D., & Verbruggen, N. (2011). Low magnesium status in plants enhances tolerance to cadmium exposure. *New Phytologist*, *192*, 428–436. https://doi.org/10.1111/j.1469-8137.2011.03814.x

Hirzel, J., Retamal-Salgado, J., Walter, I., & Matus, I. (2017). Cadmium accumulation and distribution in plants of three durum wheat cultivars under different agricultural environments in Chile. *Journal of Soil and Water Conservation*, *72*, 77–87. https://doi.org/10.2489/jswc.72.1.77

Hussain, I., Ashraf, M. A., Rasheed, R., Iqbal, M., Ibrahim, M., Zahid, T., … Saeed, F. (2017). Cadmium-induced perturbations in growth, oxidative defense system, catalase gene expression and fruit quality in tomato. *International Journal of Agriculture and Biology*, *19*, 61–68. https://doi.org/10.17957/IJAB/15.0242

Hussain, M. M., Saeed, A., Khan, A. A., Javid, S., & Fatima, B. (2015). Differential responses of one hundred tomato cultivars grown under cadmium stress. *Genetics and Molecular Research*, *14*, 13162–13171. https://doi.org/10.4238/2015.October. 26.12

Iannone, M. F., Groppa, M. D., & Benavides, M. P. (2015). Cadmium induces different biochemical responses in wild type and catalase-deficient-tobacco plants. *Environmental and Experimental Botany*, *109*, 201–211. https://doi.org/10.1016/j.envexpbot.2014.07.008

Järup, L., & Åkesson, A. (2009). Current status of cadmium as an environmental health problem. *Toxicology and Applied Pharmacology*, *238*, 201–208. https://doi.org/10.1016/j.taap.2009.04.020

Jozefczak, M., Remans, T., Vangronsveld, J., & Cuypers, A. (2012). Glutathione is a key player in metal-induced oxidative stress defenses. *International Journal of Molecular Sciences*, *13*, 3145–3175. https://doi.org/10.3390/ijms13033145

Kabata-Pendias, A. (2011). *Trace elements in soils and plants* (4th ed.). Boca Raton, FL: CRC Press.

Kibria, M. G., Osman, K. T., & Ahmed, M. J. (2006). Cadmium and lead uptake by rice (*Oryza sativa* L.) grown in three different textured soils. *Soil and Environment*, *25*, 70–77.

Korshunova, Y. O., Eide, D., Clark, W. G., Guerinot, M. L., & Pakrasi, H. B. (1999). The IRT1 protein from *Arabidopsis thaliana* is a metal transporter with a broad substrate range. *Plant Molecular Biology*, *40*, 37–44. https://doi.org/10.1023/A:1026438615520

Kudo, H., Kudo, K., Uemura, M., & Kawai, S. (2015). Magnesium inhibits cadmium translocation from roots to shoots, rather than the uptake from roots, in barley. *Botany-Botanique*, *93*, 345–351. https://doi.org/10.1139/cjb-2015-0002

Kumar, P., Edelstein, M., Cardarelli, M., Ferri, E., & Colla, G. (2015). Grafting affects growth, yield, nutrient uptake, and partitioning under cadmium stress in tomato. *HortScience*, *50*, 1654–1661

López-Millán, A.-F., Sagardoy, R., Solanas, M., Abadía, A., & Abadía, J. (2010). Cadmium toxicity in tomato (*Lycopersicon esculentum*) plants grown in hydroponics. *Environmental and Experimental Botany*, *65*, 376–385. https://doi.org/10.1016/j.envexpbot.2008.11.010

Madalcho, A. B. (2016). The effect of aboveground biomass removal on soil macronutrient over time in Munesa Shashemane, Ethiopia. *Food and Energy Security*, *5*, 56–63. https://doi.org/10.1002/fes3.77

Madhaiyan, M., Poonguzhali, S., & Sa, T. (2007). Metal tolerating methylotrophic bacteria reduces nickel and cadmium toxicity and promotes plant growth of tomato (*Lycopersicon esculentum* L.). *Chemosphere*, *69*, 220–228. https://doi.org/10.1016/j.chemosphere.2007.04.017

Manciulea, A., & Ramsey, M. H. (2006). Effect of scale of Cd heterogeneity and timing of exposure on the Cd uptake and shoot biomass, of plants with a contrasting root morphology. *Science of the Total Environment*, *367*, 958–967. https://doi.org/10.1016/j.scitotenv.2006.01.015

Melo, L. C. A., Alleoni, L. R. F., Carvalho, G., & Azevedo, R. A. (2011). Cadmium and barium toxicity effects on growth and antioxidant capacity of soybean (*Glycine max* L.) plants, grown in two soil types with different physicochemical properties. *Journal of Plant Nutrition and Soil Science*, *174*, 847–859. https://doi.org/10.1002/jpln.201000250

Méndez, A. A. E., Pena, L. B., Benavides, M. P., & Gallego, S. M. (2016). Priming with NO controls redox state and prevents cadmium-induced general up-regulation of methionine sulfoxide reductase gene family in *Arabidopsis*. *Biochimie*, *131*, 128–136. https://doi.org/10.1016/j.biochi.2016.09.021

Migocka, M., & Klobus, G. (2007). The properties of the Mn, Ni and Pb transport operating at plasma membranes of cucumber roots. *Physiologia Plantarum*, *129*, 578–587. https://doi.org/10.1111/j.1399-3054.2006.00842.x

Minolta. (2017). Retrieved from http://sensing.konicaminolta.com.br/2015/08/compreendendo-o-espaco-de-cor-cie-lch/

Monteiro, C. C., Carvalho, R. F., Gratao, P. L., Carvalho, G., Tezoto, T., Medici, L. O., … Azevedo, R. A. (2011). Biochemical responses of the ethylene-insensitive *Never ripe* tomato mutant subjected to cadmium and sodium stresses. *Environmental and Experimental Botany*, *71*, 306–320. https://doi.org/10.1016/j.envexpbot.2010.12.020

Mueller, N. G. (2017). Documenting domestication in a lost crop (*Polygonum erectum* L.): Evolutionary bet-hedgers under cultivation. *Vegetation History and Archaeobotany*, *26*, 313–327. https://doi.org/10.1007/s00334-016-0592-9

Nair, A., Degheselle, O., Smeets, K., Van Kerkhove, E., & Cuypers, A. (2013). Cadmium-induced pathologies: Where is the oxidative balance lost (or not)? *International Journal of Molecular Sciences*, *14*, 6116–6143. https://doi.org/10.3390/ijms14036116

Nogueirol, R. C., Monteiro, F. A., Gratão, P. L., Silva, B. K. A., & Azevedo, R. A. (2016). Cadmium application in tomato: Nutritional imbalance and oxidative stress. *Water, Air, and Soil pollution*, *227*, 210. https://doi.org/10.1007/s11270-016-2895-y

Norton, G. J., Travis, A. J., Danku, J. M. C., Salt, D. E., Hossain, M., Islam, M. R., & Price, A. H. (2017). Biomass and elemental concentrations of 22 rice cultivars grown under alternate wetting and drying conditions at three field sites in Bangladesh. *Food and Energy Security*, *6*, 98–112. https://doi.org/10.1002/fes3.110

Pompeu, G. B., Vilhena, M. B., Gratão, P. L., Carvalho, R. F., Rossi, M. L., Martinelli, A. P., & Azevedo, R. A. (2017). Abscisic acid-deficient sit tomato mutant responses to cadmium-induced stress. *Protoplasma*, *254*, 771–783. https://doi.org/10.1007/s00709-016-0989-4

SAS Institute. (2011). *SAS/STAT user's guide: Version 9.3*. Cary, NC: SAS Institute.

Sasaki, A., Yamaji, N., Yokosho, K., & Ma, J. F. (2012). Nramp5 is a major transporter responsible for manganese and cadmium uptake in rice. *Plant Cell*, *24*, 2155–2167. https://doi.org/10.1105/tpc.112.096925

Sebastian, A., & Prasad, M. N. V. (2016a). Modulatory role of mineral nutrients on cadmium accumulation and stress tolerance in *Oryza sativa* L. seedlings. *Environmental Science and Pollution Research*, *23*, 1224–1233. https://doi.org/10.1007/s11356-015-5346-1

Sebastian, A., & Prasad, M. N. V. (2016b). Iron plaque decreases cadmium accumulation in *Oryza sativa* L. and serves as a source of iron. *Plant Biology*, *18*, 1008–1015. https://doi.org/10.1111/plb.12484

Štolfa, I., Pfeiffer, T. Ž., Špoljarić, D., Teklić, T., & Lončarić, Z. (2015). Heavy metal-induced oxidative stress in plants: Response of the antioxidative system. In D. Gupta, J. Palma & F. Corpas (Eds.), *Reactive oxygen species and oxidative damage in plants under stress* (pp. 127–163). Cham, Switzerland: Springer Inter Pub.

Teklić, T., Lončarić, Z., Kovačević, V., & Singh, B. R. (2013). Metallic trace elements in cereal grain – A review: How much metal do we eat? *Food and Energy Security*, *2*, 81–95. https://doi.org/10.1002/fes3.24

Thomine, S., Wang, R., Ward, J. M., Crawford, N. M., & Schroeder, J. I. (2000). Cadmium and iron transport by members of a plant metal transporter family in *Arabidopsis* with homology to Nramp genes. *Proceedings of the National Academy of Sciences of the United States of America*, *97*, 4991–4996. https://doi.org/10.1073/pnas.97.9.4991

Wu, D., Yamaji, N., Yamane, M., Kashino-Fujii, M., Sato, K., & Ma, J. F. (2016). The HvNramp5 transporter mediates uptake of cadmium and manganese, but not iron. *Plant Physiology*, *172*, 1899–1910. https://doi.org/10.1104/pp.16.01189

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Carvalho MEA, Piotto FA, Gaziola SA, et al. New insights about cadmium impacts on tomato: Plant acclimation, nutritional changes, fruit quality and yield. *Food Energy Secur*. 2018;e00131. https://doi.org/10.1002/fes3.131