University of São Paulo
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Tomato genotypes with contrasting cadmium (Cd) tolerance and their reciprocal grafts: Cd uptake, accumulation, and evaluation of biochemical, molecular, and physiological parameters

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Thesis presented to obtain the degree of Doctor in Science:
Area: Plant Physiology and Biochemistry

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RESUMO

Genótipos de tomateiro com tolerância contrastante ao cádmio (Cd) e suas enxertias recíprocas: absorção e acúmulo de Cd, e avaliação de parâmetros bioquímicos, moleculares e fisiológicos

O cádmio (Cd) é um metal pesado cuja concentração aumentou consideravelmente nas últimas décadas em vários países (devido a atividades antroprogênicas). Esse metal é potencialmente prejudicial à saúde humana e às plantas, sendo um dos contaminantes mais ameaçadores para o meio ambiente. No entanto, poucos são os estudos que abordam o desenvolvimento de estratégias de manejo para reduzir a contaminação por Cd em partes comestíveis de plantas, em consonância com o entendimento dos papéis desempenhados pela raiz e pela parte aérea no padrão de tolerância, além de enfocar em mecanismos endógenos relacionados. Embora o estudo de genótipos com tolerância ao Cd contrastante seja capaz de revelar contrastes importantes relacionados a mecanismos de tolerância, acúmulo e absorção do Cd, há precariedade de estudos focados em tomateiros enxertados reciprocamente em relação à tolerância ao Cd. Neste trabalho, nós realizamos um estudo sobre tomateiros enxertados utilizando genótipos com tolerância contrastante ao Cd. A enxertia recíproca entre um genótipo de tomateiro tolerante e outro sensível foi utilizada como uma ferramenta sem precedentes, a fim de fornecer uma primeira percepção sobre a contribuição órgão-tecido específica dos genótipos de tomateiro para os mecanismos de tolerância ao Cd, absorção e acúmulo em estágios iniciais de exposição ao metal pesado. Para tanto, nós estudamos a cinética de absorção de Cd. Avaliações de seis enzimas antioxidantes também foram realizadas, além do estudo do acúmulo de Cd, estresse oxidativo, fator de bioconcentração, síntese de fitoquelatina, expressão de genes codificantes para fitoquelatina sintases e transportadores de raiz, estado nutricional e avaliações de biomassa. Os resultados mostraram que, em comparação com as mudas enxertadas sobre a raiz sensível, as mudas enxertadas sobre a raiz tolerante apresentaram menor absorção e acúmulo de Cd e maior eficiência do sistema antioxidante enzimático em resposta à exposição ao Cd, bem como maior concentração de PCs em raízes. Por fim, avaliamos o teor de clorofila, proteoma e fosfoproteoma em folhas de tomateiros enxertados. Os resultados fornecem evidências pioneiras sobre a influência positiva do sistema radicular de uma cultivar tolerante ao proteoma de tomateiro exposto ao Cd, acoplado às respostas fosfoproteômicas induzidas pelo Cd em tomateiro enxertado, em um estágio inicial de exposição ao metal pesado.

Palavras-chave: Metais pesados, *Solanum lycopersicum*, Antioxidantes, Cinética de absorção de cádmio, Enxertias recíprocas, Expressão gênica, Fitoquelatinas, Fosfoproteômica, Proteômica, Tolerância a estresses abióticos, Segurança alimentar

ABSTRACT

Tomato genotypes with contrasting cadmium (Cd) tolerance and their reciprocal grafts: Cd uptake, accumulation, and evaluation of biochemical, molecular, and physiological parameters

Cadmium (Cd) is a heavy metal whose concentration has increased considerably over the last few decades in several countries (due to anthropogenic activities). This metal is potentially harmful to human health and plants, and is one of the most threatening contaminants to the environment. However, there are few studies that deal with the development of management strategies to reduce the Cd contamination of edible parts of plants, in line with the understanding of the roles played by root and shoot in the tolerance pattern, as well as focusing on related endogenous mechanisms. Even though studying genotypes with contrasting Cd tolerance is able to reveal important contrasts related to Cd tolerance, accumulation and uptake, there is a lack of studies focused on reciprocally grafted tomato plants regarding Cd tolerance (that is, Cd-tolerant and Cd-sensitive genotypes grafted with each other as rootstock or scion). Here, we performed a study on grafted tomato plants using tomato genotypes with contrasting Cd tolerance. For the present work, reciprocal grafting between tolerant and sensitive tomato genotypes was used as a unprecedented tool, in order to provide a first insight into the organ-tissue-specific contribution of the tomato genotypes to Cd tolerance mechanisms, uptake and accumulation at early stages of exposure to Cd. We studied the Cd uptake kinetics of the tomato genotypes. Further, we studied enzymatic antioxidant responses in tomato plants. Evaluations of six antioxidant enzymes were performed in addition to the study of Cd accumulation, oxidative stress, bioconcentration factor, phytochelatin synthesis, expression of genes encoding phytochelatin synthases and root transporters, nutrient status and plant growth evaluations. The results showed that, compared with seedlings grafted onto the sensitive root, seedlings grafted onto the tolerant one showed lower Cd uptake, accumulation, and higher efficiency of the enzymatic antioxidant system in response to Cd exposure, in addition to higher concentrations of PCs in roots. Finally, we evaluated the chlorophyll content, proteome and phosphoproteome in leaves of grafted tomato plants. The results provide early evidence for the positive influence of the root system of a tolerant cultivar on the Cd-exposed tomato proteome coupled to Cd-induced phosphoproteomic responses in grafted tomato at an early stage of plant exposure.

Keywords: Heavy metals, *Solanum lycopersicum*, Antioxidants, Cadmium uptake kinetics, Reciprocal grafting, Gene expression, Phytochelatins, Phosphoproteomics, Proteomics, Abiotic stresse tolerance, Food security

1. INTRODUCTION

Cadmium (Cd) is a persistent environmental pollutant and heavy metal that is able to affect several metabolic processes in living organisms, including those related to physiological processes in plants (Marques et al. 2019, 2021). The increase in Cd concentrations in the environment over the last few decades is due to anthropogenic activities (e.g., production of mineral fertilizers, pesticides, intensive mining, waste disposal, and foundries). Cd is extremely toxic to biological systems, in part due to its high solubility in physiological conditions, and accumulation in living organisms (Kabata-Pendias, 2011).

Due to its high phytoaccumulation index, low soil adsorption coefficient, and high soil–plant mobility, Cd can be readily taken up by plants and accumulates in different edible plant parts, through which it enters the food chain (Sarwar et al. 2010; Shahid et al. 2017). Thus, besides affecting plant metabolism and physiology, Cd accumulation in crop plants poses a high risk to human health (Zhang et al. 2020). Furthermore, Cd exposure is able to impair functions of biological molecules and can induce fast and wide-ranging side effects on plant development, even at low concentrations in the growth media (Piotto et al. 2018). More studies using Cd-exposed crops are needed, as most of the studies that focused on Cd-induced plant responses have used non-crop species. Understanding the mechanisms of plant uptake, response, and tolerance to Cd stress in crop species is important to develop efficient strategies for mitigating the impacts of Cd contamination on crop yield and food safety, including through the generation of Cd-tolerant and Cd-excluding crop cultivars.

Tomato (*Solanum lycopersicum*) is one of the most cultivated and consumed fruits worldwide, besides serving as a model organism for fleshy-fruited plants: it is a very important crop from nutritional and economic points of view (Rodríguez-Celma et al. 2010). Among economically important commercial crops, tomato is considered a model organism due to several aspects, including its sequenced and small genome (Piotto et al. 2018). Moreover, a large number of tomato plants is grown in greenhouses, frequently using special substrates, fertilization techniques and reutilization of water. Thus, these plants are frequently subjected to an increased risk of heavy metal contamination by the use of Cd-contaminated water (Rodriguez-Celma et al. 2010; Borges et al. 2018), which explains the relevance of studies focused on the accumulation of Cd and patterns of plant response and tolerance to this heavy metal using tomato.

Grafting has been exploited extensively in fruit crops to reduce the negative influences of soil pathogens (Lee, 1994; Bletsos and Olympios, 2008). Since then, several other works have explored the use of grafting systems to separate the contribution of the root and shoot regarding the modulation of stress tolerance. In this context, a reciprocal grafting technique has been used from various plant species in response to different abiotic stresses, such as drought (Sánchez-Rodríguez et al. 2012; Han et al. 2013; Zhang et al. 2019) and Cd toxicity in the potential (Cd)-hyperaccumulator *Solanum photeinocarpum* (Huang et al. 2020a).

Intraspecific grafts mean rootstock and scion belong to the same botanical species, while interspecific grafts mean rootstock and scion belong to different species of the same genus (Goldschmidt, 2014). Previous studies used grafted tomato plants exposed to Cd toxicity by using microtom (Gratão et al. 2015; Alves et al. 2017) and intra or interspecific grats (Kumar et al. 2015a,b; Yuan et al. 2019; He et al. 2020; Liang et al. 2020; Xie et al. 2020).

The comparison of plants with contrasting or differential degrees of tolerance/sensitivity to a given stress is a strategy to effectively determine the contribution of different mechanisms in plant tolerance to abiotic stresses, including Cd toxicity (Marques et al. 2019a). The results of some investigations have indicated that modulation of Cd tolerance and sensitivity in tomato plants are not totally explained in terms of Cd accumulation. In fact, in addition to Cd accumulation itself, tomato sensitivity to Cd exposure may be influenced by events such as magnitude of oxidative stress and mineral profile imbalances (Piotto et al. 2018). For example, in some studies on Cd impact on the metabolism of tomato genotypes with contrasting Cd tolerance, the activities of antioxidant enzymes in response to Cd stress under short-term exposure were evaluated (Borges et al. 2018; Carvalho et al. 2019).

The context presented above justifies scientific efforts to study biochemical, physiological, and molecular mechanisms of responses and tolerance coupled with the modulation of Cd accumulation and uptake in crops to cope with Cd toxicity. Cd uptake and accumulation by plants leads to oxidative burst signaling, which is usually considered an early biochemical response to Cd exposure (Marques et al. 2019a), together with other tolerance mechanisms that are activated even at early stages of Cd exposure. Thus, it is important to develop management strategies focusing on reducing the Cd uptake and Cd contamination of edible parts of tomato and crop plants in general, in line with the understanding about the role of root and shoot for the observed tolerance pattern, as well as on related endogenous tolerance mechanisms under short-term Cd exposure.

We consider that the use of tomato genotypes that show contrasting Cd tolerance can reveal important contrasts related to Cd tolerance, accumulation and uptake. Nevertheless, there is a lack of studies focused on intraspecific reciprocally grafted tomato plants regarding Cd tolerance (that is, Cd-tolerant and Cd-sensitive genotypes grafted with each other as rootstock or scion). The present study aimed to study Cd uptake and accumulation, as well as evaluating biochemical, molecular, and physiological parameters in tomato genotypes with contrasting cadmium (Cd) tolerance and their reciprocal grafts. *Solanum lycopersicum* cv. Calabash Rouge (CR) and *Solanum lycopersicum* cv. Pusa Ruby (PR) were previously characterized as Cd-tolerant and Cd-sensitive genotypes under short-term Cd exposure, respectively (Piotto et al. 2018). Here, also focusing on short Cd exposure, we performed a pioneering study on grafted tomato plants using these tomato genotypes with contrasting Cd tolerance. Thus, we provided a first insight into the organ-tissue-specific contribution of the tomato genotypes to Cd tolerance mechanisms, uptake and accumulation at early stages of exposure to Cd.

6. CONCLUSIONS AND FINAL CONSIDERATIONS

The data indicated that S/T presented a response pattern similar to T/T for most of the evaluated parameters. Thus, the presence of the tolerant root system is sufficient to couple the use of grafting to a lower Cd uptake over time, a better performance regarding chlorophyl content, reduced levels of MDA, and lower Cd uptake, translocation and accumulation compared to the self-grafted sensitive tomato genotype after short-term Cd exposure. At the early stage of plant exposure, the plants grafted onto the tolerant rootstock showed lower Cd-induced losses in biomass, for which an efficient enzymatic-antioxidant system, regulation of the Mg uptake and accumulation, and PC synthesis are involved. The use of reciprocal grafting was a valuable approach to provide a first insight into the determination of the organ-tissue-specific contribution of genotypes with contrasting Cd tolerance to modulation of Cd tolerance mechanisms, uptake and accumulation in tomato under short-term Cd exposure. In addition, grafting the sensitive shoot onto the tolerant rootstock triggered a pronounced response to Cd in terms of DAPs and higher number of Cd tolerance-related key DAPs. Thus, we provided early evidence on the positive influence of the root system of the tolerant cultivar on the Cd proteomic response and modulation of Cd tolerance in a Cd-sensitive tomato, associated with the first insight into cadmium-induced phosphoproteomic responses of grafted tomato genotypes. Taken together, these data open the door to future biotechnological use of grafting to enhance Cd tolerance in tomato. Furthermore, this study contributes to future works focused on a higher number of tomato genotypes with differential Cd tolerance, accumulation and translocation under short and long-term exposure to this heavy metal.

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