Plant Physiology and Biochemistry 111 (2017) 318–328

Contents lists available at ScienceDirect

Plant Physiology and Biochemistry

journal homepage: www.elsevier.com/locate/plaphy

Research article

Zinc stress affects ionome and metabolome in tea plants

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ARTICLE INFO

Article history:
Received 11 August 2016
Received in revised form
10 December 2016
Accepted 11 December 2016
Available online 12 December 2016

Keywords:
Camellia sinensis (L.) O. Kuntze
Ion homeostasis
Metabolome
Zn stress

ABSTRACT

The research of physiological responses to Zn stress in plants has been extensively studied. However, the ionomics and metabolomics responses of plants to Zn stress remain largely unknown. In present study, the nutrient elements were identified involved in ion homeostasis and metabolomics changes related to Zn deficiency or excess in tea plants. Nutrient element analysis demonstrated that the concentrations of Zn affected the ion-uptake in roots and the nutrient element transportation to leaves, leading to the different distribution of P, S, Al, Ca, Fe and Cu in the tea leaves or roots. Metabolomics analysis revealed that Zn deficiency or excess differentially influenced the metabolic pathways in the tea leaves. More specifically, Zn deficiency affected the metabolism of carbohydrates, and Zn excess affected flavonoids metabolism. Additionally, the results showed that both Zn deficiency and Zn excess led to reduced nicotinamide levels, which speeded up NAD^+ degradation and thus reduced energy metabolism. Furthermore, element-metabolite correlation analysis illustrated that Zn contents in the tea leaves were positively correlated with organic acids, nitrogenous metabolites and some carbohydrate metabolites, and negatively correlated with the metabolites involved in secondary metabolism and some other carbohydrate metabolites. Meanwhile, metabolite-metabolite correlation analysis demonstrated that organic acids, sugars, amino acids and flavonoids played dominant roles in the regulation of the tea leaf metabolism under Zn stress. Therefore, the conclusion should be drawn that the tea plants responded to Zn stress by coordinating ion-uptake and regulation of metabolism of carbohydrates, nitrogenous metabolites, and flavonoids.

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1. Introduction

Tea [*Camellia sinensis* (L.)] is an evergreen shrub, mainly planted in acid soils (Lin et al., 2009). Soils with pH 6.5 and above are generally considered unsuitable for tea growth and the pH adjustment with acid materials such as aluminum sulphate or elemental sulphur are required before the tea plants are planted (Fung and Wong, 2001). However, the soil pH in the tea plantations of Northern China is often higher than 6.5, which not only inhibits the growth of tea plants, but also leads to Zn deficiency (Liang et al., 1995).

Zn plays multiple roles in basic biochemical processes, such as enzyme catalysis, protein synthesis, carbohydrate and auxin metabolism, energy dissipation, and tolerance of environmental stresses (Impa and Johnson-Beebout, 2012). During the past decade, the responses of plants, such as barley, rice, lettuce and beta vulgaris, *etc.*, to Zn application based on the correlativity of ion (Kim and McBride, 2009), the activity of enzymes (Subba et al., 2014; Barrameda-Medina et al., 2016), the synthesis of metabolites (Rose et al., 2012; Paradisone et al., 2015; Navarro-León et al., 2016) and the genetic expression (Assunção et al., 2010; Shi et al., 2013; Holler et al., 2014) had been reported. Venkatesan et al. studied the influence of zinc toxicity on nutrient uptake in the tea plants. They observed that Zn had an antagonism relationship with Fe in the tea leaves, promoted the translocation of Mg to the tea leaves, and suppressed the uptake of Mg in the tea roots (Venkatesan et al., 2006). Moreover, Mukhopadhyay et al. studied

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http://dx.doi.org/10.1016/j.plaphy.2016.12.014
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the effect of Zn deficiency and excess on structural, physiological, and biochemical changes of the young tea plants. They found that the accumulation of soluble sugars, reducing sugars and starch in the tea leaf and root tissues of Zn-optimum plants was higher than that in Zn-deficient or Zn-excess plants. At the same time, they noticed that ascorbate peroxidase (APX), catalase (CAT), and peroxidase (POD) activities were higher in the tea plants under Zn stresses (Mukhopadhyay et al., 2013).

So far, the comprehensive information about the uptake or accumulation of nutrient elements and metabolic profiling of Zn stress in the tea leaves has been still limited. The main objectives of this work are to examine metabolic and ionic changes in the tea plants responding to Zn stress and provide insights into the possible mechanisms of ionic homeostasis and metabolic responses to Zn stress in the tea plants.

2. Experiment

2.1. Materials and methods

Healthy and similarly grown 1-year-old seedlings of the tea plants (*Camellia sinensis* cv. Ruixue) were used in this study. The tea plants were planted in hydroponic boxes in the tea cultivation field of Tea Research Institute, Qingdao Agricultural University in Shandong province of China (36°19′ N, 120°23′ E, 54.88 m above sea level) for 4 months (from the beginning of September to the end of December). The environment was controlled as 250–280 μM m^{-2} s^{-1} photon flux density, 75–80% humidity and a 20/15 °C (16/8 h) day/night cycle. The tea plants were suspended in a hydroponic nutrient solution similar to that used by Xu et al., (2016), that is, 177 mg $Ca(NO_3)_2 \cdot 4H_2O$, 110 mg $(NH_4)_2SO_4$, 19 mg KH_2PO_4, 89.23 mg K_2SO_4, 256.25 mg $MgSO_4 \cdot 7H_2O$, 133.29 mg $Al_2(SO_4)_3 \cdot 18H_2O$, 2.33 mg Na_2-EDTA, 1.74 mg $FeSO_4 \cdot 7H_2O$, 3.73 mg $MnSO_4 \cdot H_2O$, 0.12 mg $Na_2MoO_4 \cdot 2H_2O$, 0.57 mg H_3BO_3, 0.097 mg $CuSO_4 \cdot 5H_2O$ were dissolved in a litre of distilled water. Subsequently, the concentrations of Zn were set as follows: deficiency (0 μM), moderation (1.5 μM, 7.5 μM and 15 μM), and excess (150 μM), with $ZnSO_4 \cdot 7H_2O$. The pH value was measured daily and adjusted to pH 4.2 ± 0.1 with H_2SO_4 (Xu et al., 2016). The treatments with different concentrations of Zn were named Zn0, Zn1.5, Zn7.5, Zn15 and Zn150 in this paper, respectively. The nutrient solutions were replaced every week to avoid over-concentration due to

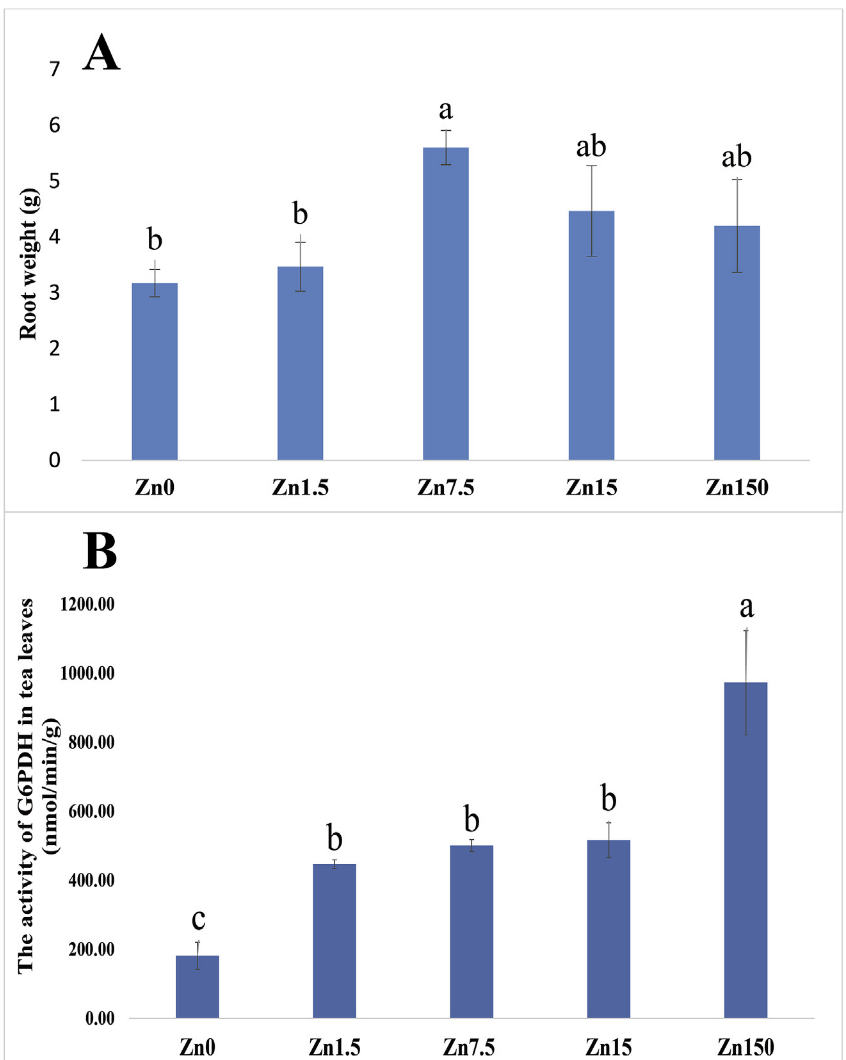

Fig. 1. A: Root weights of tea plant under different Zn treatments. B: The activity of G6PDH in the tea leaves under different Zn treatments. Error bars are standard deviations (n = 3). Different letters indicate significant differences ($P < 0.05$) among the treatments and control.

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