International Journal of Environmental Science and Technology (2019) 16:8401–8410
https://doi.org/10.1007/s13762-019-02234-5

ORIGINAL PAPER

Dimethylthiourea antagonizes oxidative responses by up-regulating expressions of pyrroline-5-carboxylate synthetase and antioxidant genes under arsenic stress

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Received: 26 July 2018 / Revised: 23 November 2018 / Accepted: 21 January 2019 / Published online: 28 January 2019

Abstract
Dimethylthiourea is an important plant growth regulator that mediates various physiological and metabolic processes of the plants. In the present study, role of dimethylthiourea in conferring arsenic stress tolerance to *Cajanus cajan* L. was investigated. Exposure to arsenic resulted in oxidative damage as evidenced by decreased germination percentage, radicle length, biomass accumulation, membrane stability index, protein, glyoxalase I and II, and antioxidants, together with enhanced cell death, reactive oxygen species, lipid peroxidation and activity of lipoxygenase in *C. cajan* L. However, exogenous application of dimethylthiourea along with arsenic decreased the reactive oxygen species and lipoxygenase activity, while increased the membrane stability index and antioxidants activities. Moreover, dimethylthiourea also up-regulated the glyoxalase (I and II) activity and the gene expression of antioxidants under arsenic stress. Also, dimethylthiourea application reduced the arsenic content than that measured in arsenic alone treated samples. Interestingly, treatment of dimethylthiourea uplifted the contents of ascorbic acid and glutathione, together with proline via up-regulating the activity and gene expression of pyrroline-5-carboxylate synthetase, one of the chief enzymes of its biosynthetic pathway. Enlisted findings suggested that dimethylthiourea can improve plant resistance to arsenic toxicity by regulating the gene expression of antioxidants and proline biosynthesizing enzymes, thereby reducing reactive oxygen species, lipid peroxidation and arsenic accumulation.

Keywords *Cajanus cajan* L. · Cell death · Gene expression · Glyoxalase system · Lipoxygenase · Proline · Reactive oxygen species

Introduction

Contamination of arsenic (As) in soil and groundwater has become an environmental concern as it possesses serious threats to living systems (Abbas et al. 2018). Plants growing in contaminated soil or irrigated with polluted water accumulates excess amount of As that results in oxidative stress. Accumulation of As leads to various morphological, physiological and biochemical disorders including reduced seed germination and biomass, stunted growth, reductions in the number of leaves and leaf area thereby pace of photosynthesis, stomatal conductance, rate of transpiration, ATP synthesis, mineral contents, flow of energy and yield responses (Talukdar 2014; Kumari et al. 2018).

Although As is a non-redox metalloid, its exposure provokes generation of reactive oxygen species (ROS) including superoxide ($O_2^{\cdot-}$), hydroxyl radical, hydrogen peroxide (H_2O_2), etc. (Anjum et al. 2016). Under stress condition, another cytotoxic compound, i.e., methylglyoxal (MG) is produced (Hasanuzzaman and Fujita 2013). These ROS and MG are highly reactive and well known to oxidize membrane lipids and proteins. Also, the lipids are peroxidized enzymatically by lipoxygenase (LOX) (Yadu et al. 2017a). This unrestrained deterioration of macromolecules via ROS and their catabolic enzymes leads to cellular damage and cell death eventually (Xalxo and Keshavkant 2017).

To get rid of this deleterious ROS, plant cells are armed with defensive machinery comprising enzymatic {superoxide dismutase (SOD), catalase (CAT), etc.}

Editorial responsbility: M. Abbaspour.

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