

## Ethylene and Gibberellic Acid Interplay in Regulation of Photosynthetic Capacity Inhibition by Cadmium

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Ever since the existence of man he knows the art of sowing seeds in soil and harvesting the produce. With subsequent gain of knowledge this practice developed into a range of activities and disciplines encompassed by modern agriculture. Over the years, contamination of soils and waters by heavy toxic metals has become a major concern for the environment, as well as, for human health. Among heavy metals, cadmium (Cd) toxicity is attributed, primarily to its ability to accumulate in living things, since plants and animals are not capable to metabolize large amounts of the metals. In agricultural soil it is added through sewage sludge, industrial waste, phosphatic fertilizers and urban activities [1]. Cadmium accumulation in plants alters mineral nutrients uptake, inhibits stomatal opening by interacting with the water balance of plant [2], impairs the activities of the Calvin cycle enzymes, inhibits photosynthetic rate [3] and lowers crop productivity [4].

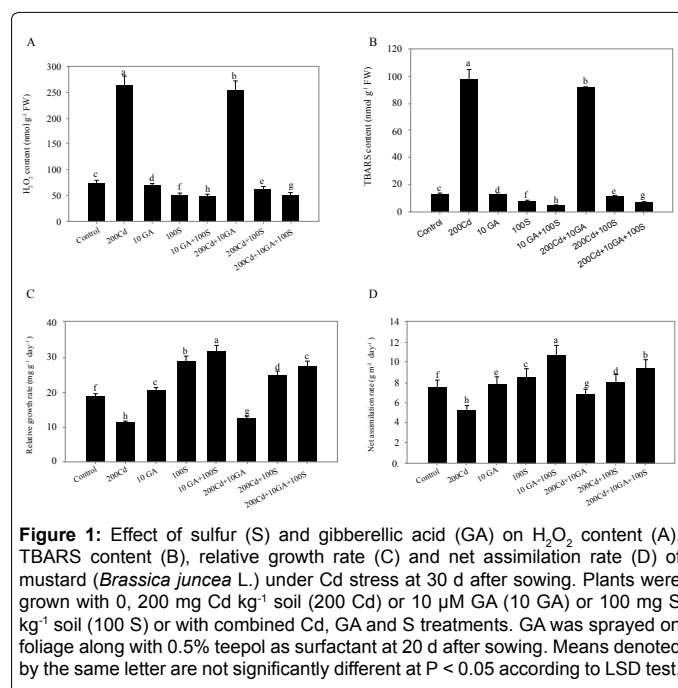
To avert the negative effects of Cd-induced oxidative stress several strategies have been adopted. Mineral nutrients as an integral part of our agricultural system have proven of paramount importance in reducing Cd toxicity. Studies conducted by our research group as well as others have shown that sulfur (S) regulates photosynthesis under optimal and stressful environments [5,6] and reduces Cd-induced oxidative stress through its involvement in plant antioxidant system [7,8]. We have shown that S-assimilation pathway, synthesis of cysteine and glutathione (GSH) and activity of ascorbate glutathione cycle enzymes are induced under Cd stress [8,9].

In addition, phytohormones have also been recognised as crucial signalling molecules involved in the control of plant responses under optimal and limited environmental conditions. It has been reported that application of 10  $\mu$ M gibberellic acid (GA) increased sulfur-use efficiency (SUE) of mustard (*Brassica juncea* L. Czern & Coss) plants treated with optimal-S (100 mg S kg<sup>-1</sup> soil) in comparison to the control plants. It was also found in this experiment that SUE was not increased at excess-S (200 mg S kg<sup>-1</sup> soil). The increase in SUE by GA was through the increase in growth, CO<sub>2</sub> exchange rate and use-efficiency of nitrogen (N) [10]. This study clearly indicates that GA could be a potential modulator of Cd stress alleviation through the increase in SUE of crops. Reports are also available for the mitigating effects of GA<sub>3</sub> on Cd-induced stress in plants [11-14]. Recently, we have shown that ethylene is involved in S-mediated alleviation of photosynthetic inhibition by Cd [6]. Sufficient-S (100 mg S kg<sup>-1</sup> soil) treatment reduced the Cd-induced oxidative stress in mustard considerably, while in contrast, excess-S (200 mg S kg<sup>-1</sup> soil) increased the oxidative stress in plants.

Further, it was found that 10  $\mu$ M GA, sufficient-S or combination of both reduced the oxidative stress induced by Cd. The oxidative stress observed as content of H<sub>2</sub>O<sub>2</sub> and thiobarbituric acid reactive substances (TBARS) determined by adopting the methods of Okuda et al. [15] and Dhindsa et al. [16], respectively (Figure 1), and ethylene (Figure 2) induced under Cd stress were maximally reduced by the combined treatment of GA and sufficient-S. It was noteworthy that combined treatment of GA and sufficient-S produced optimal ethylene to bring the maximal photosynthetic response under Cd stress. This treatment (GA+S) maximally alleviated Cd stress effect and increased

net assimilation rate (NAR) and relative growth rate (RGR) by 25.3% and 47.1%, respectively compared with the control (Figure 1). However, it was not clear if the alleviation effects were brought about by GA or ethylene. As a relationship exists between GA and S-assimilation [10] and ethylene and S-assimilation [17], there appears to develop an intimate relationship between GA and ethylene in Cd stress alleviation. The interplay among phytohormones and their signalling network are considered important for abiotic stress tolerance. To find a GA and ethylene network in Cd tolerance and alleviation we conducted an experiment, the findings of which are briefly reported below: (Figure 1).

We used modulators of GA and ethylene to substantiate the information on the interplay between these two hormones in S-mediated alleviation of photosynthetic inhibition by Cd. The inhibition of GA biosynthesis by cycocel (CCC) did not affect the response of plants induced by combined treatment of GA and S and resulted in the increased photosynthetic capacity (NAR) of plants. On the contrary,



**Figure 1:** Effect of sulfur (S) and gibberellic acid (GA) on H<sub>2</sub>O<sub>2</sub> content (A), TBARS content (B), relative growth rate (C) and net assimilation rate (D) of mustard (*Brassica juncea* L.) under Cd stress at 30 d after sowing. Plants were grown with 0, 200 mg Cd kg<sup>-1</sup> soil (200 Cd) or 10  $\mu$ M GA (10 GA) or 100 mg S kg<sup>-1</sup> soil (100 S) or with combined Cd, GA and S treatments. GA was sprayed on foliage along with 0.5% teepol as surfactant at 20 d after sowing. Means denoted by the same letter are not significantly different at P < 0.05 according to LSD test.

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inhibition of ethylene biosynthesis by aminoethoxyvinylglycine (AVG) inhibited ethylene and photosynthetic capacity of plants grown with combined dose of GA and S (Figure 3). Application of AVG caused equal reduction in photosynthetic capacity of Cd treated plants grown with sufficient-S alone or GA+S (Figure 3). The study supported the postulation that ethylene was more responsible than GA in the alleviation of photosynthetic capacity inhibition by 200 mg Cd kg<sup>-1</sup> soil (high Cd) (Figure 2).

It may be said that there exists hormone signalling network for triggering plant response under optimal and stressful environment. The interplay between ethylene and GA regulates photosynthetic capacity inhibition by Cd in plants receiving 100 mg S kg<sup>-1</sup> soil.

In our earlier report [6] it was shown that sufficient-S (100 mg S kg<sup>-1</sup> soil) increases GSH synthesis by the increasing the activity of ATP sulfurylase and cysteine content resulting in more efficient detoxification of oxidative stress than excess-S (200 mg S kg<sup>-1</sup> soil). It was also shown that treatment of sufficient-S led to optimal ethylene formation from cysteine through S-adenosyl methionine (Ado-Met) in addition to the synthesis of GSH. Plants treated with Cd exhibited

high ethylene evolution although sensitivity of plants to the ethylene was less. This resulted in photosynthetic inhibition, but the restoration of photosynthesis was possible with exogenously-sourced ethylene at 200 µl l<sup>-1</sup> concentration. This reflected that ethylene played role in S-mediated alleviation of photosynthetic inhibition by Cd (Figure 3).

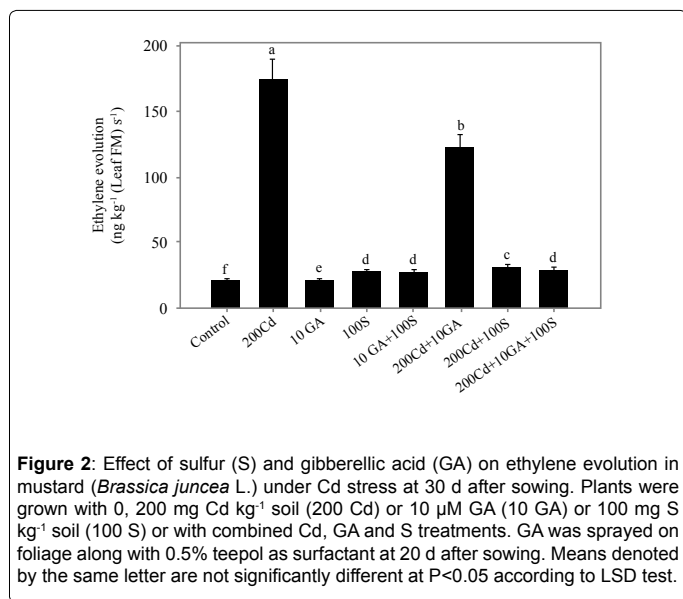
The interaction of ethylene and GA has been reported in the literature. The study has shown that GA and ethylene metabolism genes are expressed in the majority of plant organs, and both GA and ethylene precursor ACC are synthesized ubiquitously [18]. De Grauwe et al. [19] reported that a functional GA response pathway is required for the increased ethylene biosynthesis eto2-1 (ethylene overproducing mutant) since gai eto2-1 (gibberellins insensitive; ethylene overproducing double mutant) does not overproduce ethylene, showing dependence of ethylene on GA. Recently, it has been demonstrated that active ethylene signalling results in decreased GA content, thus stabilizing DELLA proteins [20]. Proteins from DELLA family are rapidly destabilized after GA treatment through degradation by 26S proteasome [21]. In addition ethylene affects DELLA stability primarily via changes in GA concentration. These studies show that the two hormones, ethylene and GA interact with each other and their interaction could be synergistic or antagonistic.

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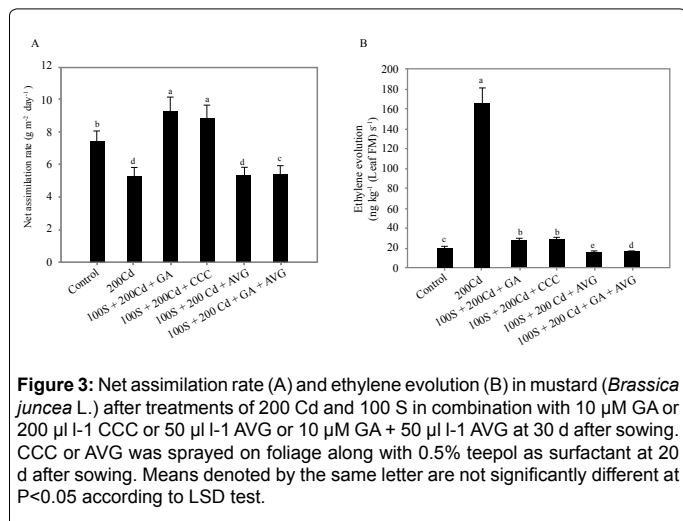
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**Figure 2:** Effect of sulfur (S) and gibberellic acid (GA) on ethylene evolution in mustard (*Brassica juncea* L.) under Cd stress at 30 d after sowing. Plants were grown with 0, 200 mg Cd kg<sup>-1</sup> soil (200 Cd) or 10 µM GA (10 GA) or 100 mg S kg<sup>-1</sup> soil (100 S) or with combined Cd, GA and S treatments. GA was sprayed on foliage along with 0.5% teepol as surfactant at 20 d after sowing. Means denoted by the same letter are not significantly different at P<0.05 according to LSD test.



**Figure 3:** Net assimilation rate (A) and ethylene evolution (B) in mustard (*Brassica juncea* L.) after treatments of 200 Cd and 100 S in combination with 10 µM GA or 200 µl l<sup>-1</sup> CCC or 50 µl l<sup>-1</sup> AVG or 10 µM GA + 50 µl l<sup>-1</sup> AVG at 30 d after sowing. CCC or AVG was sprayed on foliage along with 0.5% teepol as surfactant at 20 d after sowing. Means denoted by the same letter are not significantly different at P<0.05 according to LSD test.

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