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SO_2 Stress: Its effect on Plants, Plant Defence Responses and Strategies for Developing Enduring Resistance

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Abstract: In the present scenario of rising SO_2 in the atmosphere, the negative impact of this obnoxious gas on the plants is among major concerns in the field of agriculture and crop protection. From the scientific research conducted so far, it has been established that the main toxic effect of SO_2 on plant system is exerted by the resulting oxidative stress and generation of sulphite ions. Prominent adverse effect is observed on the overall plant growth and health, Photosynthetic efficiency and produce turn over. On the other hand, plant defence mechanism tries to counter the stress either by inhibiting the entry of the gas by or by detoxifying the excess sulphur and scavenging the resulted reactive oxygen species. Enzymes like superoxide dismutase, peroxidase, polyphenol oxidase, play a key role in the detoxifying process and a considerable amount of toxic sulphur is detoxified by forming S-containing sulphur compounds. This phenomenon is being utilized for the development of SO_2 resistant plant lines by over-expression of Cysteine synthase like genes. This review presents literature study of SO_2 induced effects on plants as well as plant resistance against it and approaches toward developing enduring resistance in plants.

Keywords: Sulphur dioxide stress, Sulphite toxicity, Abiotic stress, Oxidative stress response, Plant defence.

I. INTRODUCTION

In the optimum growing conditions plants maintain a meta-stable state in growth and reproduction. This structural organization and stable state is termed as 'Homeostasis'. The disruption of this homeostasis by the changes in the environmental factors exerts a negative impact on plant physiology and this can be defined as 'Stress' for the plants involved. The factors responsible for causing stress to plants can be classified into two broad categories i.e. Biotic and Abiotic stresses; where biotic stress is exerted on the plants by biological organisms (e.g. fungi, bacteria, insects and viruses) and abiotic stress which is the physical, chemical and environmental challenges met by the plants.

On the one hand, environmental factors like light, temperature, radiation can cause stress whereas on the other hand chemicals and physical factors like water deficit, overcrowding, and unusually high concentration of heavy metals, salt, obnoxious gaseous air pollutants also have a negative impact on plant homeostasis causing stress conditions. In plants, cellular and molecular processes triggered by these various stressor agents, are called stress responses. Stress response in plants is specific and goal oriented against each kind of adverse element that either leads to resistance or avoidance from the stressor agent or leading to susceptibility, senescence or death.

In the present context, air pollutant like SO_2, is an inevitable and prominent abiotic stress parameter which is a by-product of fuel consumption by electronic utilities, industrialization, fossil fuel utilisation and vehicular smoke. The continuous spike of SO_2 in the atmosphere has been recorded and analysed recently and it was observed to have increased about 50% in India in present decade. In 2014, India surpassed US to become second largest SO_2 emitting country [1]. So, detailed studies of the impact of this inevitable air pollutant on crop and other vegetation must be done to estimate the degree of threat it presents and to improvise effective plant protection protocols and methodologies to overcome it.

Chemically, SO_2 is a gaseous oxide of sulphur having an irritating, pungent smell and known to be toxic to biological organisms. It should be noted that Sulphur itself is an important micronutrient of plant for synthesising amino acids (Cysteine and Methionine), Vitamins (Biotine), Hormones (Ethylene, polyamines) and for photosynthetic oxygen production, electron transport and several others defence related enzymes and compounds [2]. Interestingly, in sulphur-deficit soil, plants can absorb sulphur from gaseous SO_2 for their utilization [3] but it should also be noted that acute (short term) and chronic (prolonged) exposure of high concentration of SO_2 have significant negative impact on the plant system [4], [5].

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To get a detailed account of a particular stress (in this case SO_2) upon a plant system, it is essential to follow two different approaches i.e. the damaging effect of that stressor element and the strategies of defence response of the plants to counter those effect.

The study of effects of SO_2 on plants was initiated after it became a constant factor in the environment. At the very beginning, secondary responses on morphological and physical impacts like stomatal closure and cell necrosis [6], [7], translocation inhibition [8], reduction in photosynthesis [9], disruption in the pH maintenance [10] were studied. But gradually the approach shifted towards correlating those stress effects with underlying primary effects like resulting sulphite accumulation [11], oxidative stress [12] etc.

The defence response that is directed against these stresses can be categorised on the basis of their function i.e. either formation of a strategy to avoid and screen out SO_2 gas; or to reduce the detrimental effect of the air pollutant that enters into the plant system. The structural barriers like lignifications formed in response to SO_2 [13] fall under the first approach i.e. to block the entry of the stressor element whereas the accumulation of antioxidants like flavonoids, phenols [14], ascorbic acid [15] and increased activity of scavenger enzymes [12] contribute to the second line of defence that confers resistance to the plant against adverse effects resulted by SO_2 exposure.

After the defence strategies came into knowledge, improvisation to develop SO_2 tolerant varieties became a goal in this field of research. Most of the efforts on this ground has been made on the principle that plants should be able to utilize the excess SO_2 as a source of sulphur and to convert it into essential compounds like sulphur containing amino acids i.e. Cysteine or methionine. Several transgenic approaches were carried out keeping this principle in the centre [16]

In the following section an account of three aspects of the present field of research have been presented i.e. impact of SO_2 on plant; plant defence response against those effects and approaches towards developing SO_2 resistant plant varieties.

II. IMPACT OF SO_2 ON PLANTS

A. Effect on overall morphology and growth of plants:

Prolonged exposure to SO_2 fumigation is reported to have a negative impact upon plant growth where length of root and shoot were seen to be stunted after chronic SO_2 application [17]. On a comparative account, up to 50% reduction of annual height and 70% reduction of diameter increase rate have been reported at the site where SO_2 amount in air was higher than permissible limit [18]. Besides this, yellowing of leaf tissues and upward curling of leaf lamina under low doses of SO_2 have been observed. With the increase in SO_2 concentration, lamina curling was observed to be associated with drying and developing brittleness. Higher concentration of SO_2 also impacted rootlets which becomes yellowish brown. Along with these, dry weights of seedlings, weakness of the petioles were also observed to get reduced by SO_2 exposure [19]. In Prosopis juliflora, petiole length is reported to become reduced in response to Sulphur dioxide fumigation and at the same time, dry weight of leaf had been increased [20]. Report of appearance of circular dry blotches in SO_2 exposed Cajanus cajan and Amaranthus paniculatus plant had been published earlier [21]. Alteration of morphological features like reduction of distribution of epidermal cells and decrease in stomatal frequency were observed in Sida cordifolia and Catharanthus roseus in response to SO_2 containing automobile gases. But the size of the stomata and epidermal cell increased significantly in the pollution exposed plant [22], [23]. On the contrary, in Cajanus cajan, Amaranthus paniculatus, stomatal frequency of both lower and upper surface of leaves, had been observed to be increased with exposure to elevated concentrations of SO_2. The increase in stomatal frequency was explained by the fact that sulphur dioxide inhibits the growth and expansion of leaf surface thus increasing the frequency of stomata [24].

B. Effect on photosynthesis, photosystem machinery and photosynthetic pigments:

SO_2 reportedly has an antagonistic effect on plant photosynthesis which in turn has neegtive correlation with the height and girth of plant axis. Apparent quantum yields were decreased by 1.5 fold and the photosystem II being most sensitive to SO_2, its photochemical efficiency dropped severely after exposure to SO_2 [18]. Maximum photochemical efficiency of PS-II (Fv/Fm) of a healthy leaf is between 0.74 and 0.85 [25], [26] and this photochemical efficiency of PS-II is generally negatively correlated with degree of SO_2 exposure [27]. Reversible inhibition of Photosynthesis by SO_2 fumigation is effected by inhibition of essential Calvin cycle enzymes like Fructose bisphosphatase and Ribulose bisphosphate carboxylase [28]. Along with it, reduction of total chlorophyll content was also reported [18], [23]. The possible reason might be the inhibitory effect of SO_2 on chlorophyll metabolism determined in previous study [29]. In Prosopsis sp., similar result has been obtained upon exposure to SO_2 [20]. Lesser detrimental impact in the level of carotenoid accumulation has been observed due to its possible protective nature in photo-oxidation. The increase of pheophytin in SO_2 stressed plants actually signifies the degradation of chlorophyll because Pheophytin is the by-product of chlorophyll degradation [23].

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C. Stomatal closure and conductance:
A drop in the cellular pH i.e. increasing acidification in cell was observed to be caused by sulphur dioxide fumigation. It is one of the major factors in SO_2 induced stomatal closure mostly due to the decrease in cellular pH resulting from SO_2 dissolution into cellular water content thus producing sulphuric acid ($SO_2 + H_2O \rightarrow [SO_2.H_2O] \rightarrow HSO^{3-} + H^{+} \rightarrow SO_3^{2-} + 2H^{+}$) [30]. This event interferes with the H+ channel and membrane polarity causing inhibition of K+ pump leading to stomatal closure [31] which is another reason affecting the photosynthetic yield. Another inhibitory factor responsible for stomatal closure is abscisic acid (AbA) hormone whose production is increased in the leaf in response to SO_2 stress. The higher accumulation of AbA leads to stomatal closure in the stress exposed plant [7]. Stomatal conductance also gets reduced in the case of high SO_2 exposur$_e$ thus causing inhibition in gaseous exchange and physiological processes of photosynthesis and respiration [18], [32].

D. Production of Reactive oxygen species:
The main toxic effect of Sulphur dioxide is mediated by the production of Sulphite (SO_3^{2-}) and Bisulphite (HSO_3^{-}) radicals after dissolution of sulphur dioxide into cellular water [33]. The detoxification process (discussed later in this article) initiated by the plant system, converts toxic Sulphite to less harmful Sulphate radicals but as a by-product of the reaction, Reactive Oxygen Species (ROS) like peroxide (H_2O_2), superoxide radicals ($O_2^{.-}$) and hydroxyl radical ($OH^{.}$) is generated. Production of excess ROS is one of the key indications of SO_2 stress upon plant systems [34]. The damage of PS-II as discussed earlier as a notable SO_2 inflicted damage- is also a prominent source of ROS production- as studied in Fragaria sp. [12].

The hyper-accumulation of ROS is detrimental and causes adversity in normal plant function in seve al ways. The oxidative stress exerts negative impact on nucleic acid and proteins. But the most destructive effect is exerted on cellular and membrane lipid which gets rapidly peroxidised [35], [36], [37] by ROS. The increasing amount of peroxidised lipid has a cytotoxic effect that causes tissue death additionally cell necrosis happens due to ROS impact by hypersensitive reaction [38]. Thus the tissue necrosis in SO_2 stress can be explained by the production of ROS and its consequences. In Arabidopsis, hyper-accumulation of ROS was detected after 72 hours of SO_2 fumigation in increased concentration where peroxide accumulation was increased by about 90% in the stressed plant than that of the control untreated plants thus elucidation the inter-relation between SO_2 and ROS [34]. It should be noted that, on one hand, ROS inflicts damage in plant system but on the other hand, it acts as a secondary messengers and plays a role in initiating stress response and defence pathways [35], [39], [40].

E. Other physiological effects:
Reduction of relative water content (RWC) in Flannel weed and Periwinkle has been reported to be the effect of SO_2 present in vehicular exhausts. Higher RWC helps in maintaining water balance and provides resistance during osmotic stress and drought stress and it explains the fact that the plants less resistant to SO_2 fumigation tends to lose more water content than more resistant varieties [23]. Nitrogen content of leaf also gets reduced as a result of negative impact of SO_2 as seen in Alnus sieboldiana [18]. Reduction of CO_2 fixation and more respiration which lead to breakdown of stored carbohydrate products have been reported as an effect of SO_2 exposure in Prosopsis sp. [20].

III.PLANT DEFENCE RESPONSE TO REDUCE THE RESULTING STRESS

To counter the SO_2 induced stress, plants respond by altering morphological and biochemical profile either to block the entry of the harmful gas in internal tissue system or to reduce or nullify the resulting stress caused by it.

A. Structural barriers to block entry of SO_2:
Alteration of other micro-morphological parameters like striations on stomatal guard cell, thickening of guard cell wall, occlusion of stomata, increase in the frequency and length of the trichome had also been reported [23]. It has become established that the increase in trichome frequency has a linear relation with the increasing concentration of SO_2. In pigeon pea, increasing SO_2 concentration leads to gradual increase in trichome density. It was observed in the same study that trichome generation was more on upper surface of leaf than that of lower. The increased trichome has a protective role against the SO_2 stress as it provides a mechanical sink of excess sulphur pollutant and as well as provides tiny pockets of fresh air by trapping those on leaf surface thus creating a micro-environment with less polluted air [24]. The increases of trichome actually obstruct the stomatal aperture thus blocking the entry of SO_2 whereas an observation reduction in stoma aperture is another outline defence mechanism by limiting the entry site of the toxic gas to enter in intertal tissue system as reported in Muntingia calabura and Ixora coccinia [41].

B. Detoxification of SO_2 and recovery of Photosynthesis:
The detrimental impact of sulphur dioxide on photosynthetic yield is largely due to inhibition on enzymes and cellular toxicity caused by it. Less susceptible plants tend to detoxify the cellular toxicity thus restoring the photosynthetic

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yield. This detoxification process mediated by chlorophyll is observed to be more efficient in light condition than in dark condition. The main toxic agent formed by SO_2 is bisulphite and sulphite radicals become reduced thus minimizing its toxic effect. Another strategy to minimize the SO_2 toxicity is to incorporate sulphur into amino acids like Cysteine and Methionine [42]. Besides these, a study on Arabidopsis revealed that increase in the amount of water soluble non-protein sulphydryl content and glucosinolates also act as biological sink for excess Sulphur [43].

C. Alteration in the efficiency of physiological processes:
As the leaf nitrogen content gets reduced in sulphur dioxide stress, plants tend to be more efficient in Photosynthetic Nitrogen Use Efficiency (PUNE). The requirement of utilizing own resources in an efficient manner, it is not limited to PUNE but also in Water Use Efficiency (WUE) which was also observed to be increased in stress condition caused by Sulphur dioxide fumigation [18].

D. Increased accumulation and activity of ROS scavenger molecules:
As the key role in inflicting damage in SO_2 stressed plant- is attributed to ROS accumulation, increased production of scavenger molecule is one of the most prominent defence response in SO_2 stress. Activity of Catalase and POD were observed to be increased greatly in flannel weed and periwinkle. Catalse has a role to quench ROS whereas POD has a very specific role to remove Sulphite resulting by the desolation of SO_2 in cellular water [23]. Among CAT and POD, although CAT has a high capacity to scavenge Reactive Oxygen Species but it does not have much affinity to H_2O_2 which is the principle ROS produced in SO_2 stress. In contrast, POD- having a greater affinity to H_2O_2- is the key enzyme acting as principle scavenger enzyme acting in SO_2 stress [39]. Another advantagious to plants in up-regulating the POD activity is that this enzyme plays a crucial role in different defence-related cellular processes that contribute in withstanding the oxidative stress induced by sulphur- dioxide [44]. Another antioxidant enzyme whose activity is important in tolerance to SO_2 stress- is GSH. The maintenance of Redox buffering is mediated by this enzyme [45] and beside this, it also acts as co-substrate of GSX. This GSX helps in H_2O_2, scavenging but most notably it reduces the peroxidised lipid thus reducing the cytotoxic effect of it [46]. So on one hand, GSH-GSX scavenges the ROS to reduce the oxidative stress and on the other hand, they help to nullify the damages already caused by the ROS. Ascorbic acid is mainly found in two forms i.e. reduced form and oxidised form (Dehydroxyascorbate or DHA). Among these two, in unstressed plant, the reduced form is abundant which rapidly converted to DHA in stressed condition [47]. In SO_2 stress, resulting oxidative stress by $^{\cdot}O_2^-$ and H_2O_2 in turn oxidises the Ascorbic acid and converts to DHA catalyzed by the enzyme Ascorbate peroxidase (Apx) [48]. DHA which is unstable by nature, is converted to oxalic acid and threonic acids [49] and thus scavenging the superoxide and peroxide radicals, Ascorbic acid down-regulates the chain initiation of Sulphite oxidation thereby blocking a source of more ROS production. In several experiments on Vigna radiata, Solanum esculentum, Zea mays, increased concentration of Ascorbic acid has been reported in response to prolonged SO_2 fumigation for 45 Days [15]. In calculating the Air Pollution Tolerance Index (APTI) in SO_2 exposed road side plants [50], [51], [52]. Ascorbic acid is a crucial parameter because of its radical scavenging property. Higher the ascorbic acid concentration, more resistance power is conferred upon the plant and it is seen that the plants at polluted site shows more APTI values than that of non- polluted sites [41].

E. Genetic regulation of ROS-scavenging enzymes:
In Arabidopsis, differential expression of 2780 genes has been observed in response to sulphur dioxide fumigation. Up-regulation of genes of Cytochrome P450, Heat shock proteins and Pathogen-related proteins (PR proteins) had been observed in Arabidopsis shoot. Beside these genes, other antioxidant encoding genes for Peroxidases (POD), Glutathione peroxidises (GPX) and SOD (Cu/Zn-SOD) also get up-regulated [34].

F. Synthesis of Lignin, Proline and other constituents:
It has been discussed earlier that enzyme POD has a major protective role in the oxidative stress induced by sulphur dioxide. Besides this, POD is involved in cellular defence by cross-linking the phenolics and synthesis of Lignin. The increased amount of Lignin plays a vital role to strengthen the leaf and stem tissues thereby protecting the internal tissue system from SO_2 invasion [53]. Lignifications in response to SO_2, has been reported in Leucaena leucocephala and Pinus needle leaves [54], [13]. The up-regulation if POD genes and other related genes are involved in Phenylpropanoid pathway which in turn produces several defence molecules and modifies the activity of several secondary metabolites which act to confer protection against the detrimental effects of exposure to SO_2 [55]. Proline is a stress induced amino acid that has a multifunctional role in osmotic balance maintenance, sub-cellular structure stabilization. Besides all these, Proline also helps in scavenging free radicals. There is a particular property of Proline that makes it more important in SO_2 induced stress i.e. to reduce cellular acidification [56] which is commonly a result of dissolving of sulphur dioxide into the cellular water content. Higher accumulation of Proline in SO_2 stressed Prosopsis sp. was reported in an earlier study elucidating its role in this particular stress [20]. Similar results in terms of increased proline accumulation were also recorded in Cynodon dactylon tolerant variety than that of susceptible varieties [57].

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IV. APPROACHES TOWARDS DEVELOPING SO_2 TOLERANT PLANT VARIETIES

When a clear idea has been obtained about how a plant responds to counter the negative impact of SO_2 stress, manipulation to enhance those responses can be a useful approach towards raising SO_2 tolerant plant varieties.
To develop SO_2 resistant transgenic lines, focus was initially set such as to enable the plant to utilise the excess SO_2. Cysteine, an important sulphur containing amino acid, is synthesised by Cystine synthase (CSase) gene. Nicotiana tabacum, showed increased tolerance against Sulphur dioxide stress after transformation using CSase gene [16]**.** Gene delivery at both Chloroplast and Cytosol conferred tolerance against excess SO_2. It was observed that in the SO_2 exposed transgenic plants, Cysteine and GSH content were increased and Sulphite content were seen to be in comparatively lower amount. Thus it was concluded that CSase gene over-expression leads to increased activity of Cysteine synthase that mediates incorporation of excess Sulphur into Cysteine and GSH to reduce the Sulphite mediated toxicity [16]. As discussed earlier, Sulphite radical is one of the major toxic radicals generated by Sulphur-dioxide. Thus, neutralising this radical will provide tolerance against the toxic gas. Sulphite oxidase (SO) is one such enzyme that utilises Sulphite and converts it to less toxic Sulphate. In Arabidopsis, a transgenic approach was followed by over-expressing SO by upregulation of AtSO gene. And the transgenic lines of Arabidopsis showed greater resistance against SO_2 as it showed delayed senescence than wild lines whereas, silencing of SO gene by RNAi technique, increased the susceptibility in the Sulphur dioxide mediated stress. It was also determined that SQD1, MST1 and MST2 are late responsive genes that become activated in Arabidopsis after 24 hrs of SO_2 fumigation [58]. Although in a later transgenic study with HyPR1 gene, it was revealed that besides SO gene, Msr-A and Fds genes were attributed with more positive significance in SO_2 tolerance. The role of HyPR1 gene was relatd to the interaction with Sulphite utilising enzymes and their genetic regulation [59].

V. CONCLUSION

On the whole it can be said that although SO_2 is a source of Sulphur to the plant that are sulphur- deficient, prolonged exposure of this gas, leads to chronic injury while short time exposure of high concentration causes acute injury in plants. Mainly the sulphite radical, being toxic and reactive, is responsible for the primary damage symptoms like leaf yellowing, chlorosis, necrotic spots and leaf drying. In the later stages, sulphite reduction and photosystem damage leads to production of the ROS which disrupts the cellular integrity and gradually leading to extensive tissue necrosis. Cellular acidification, stomatal closure is among other secondary negative impact of SO_2 exposure.On the other hand, plant employs its defensive measures to counter the detrimental effects exerted by sulphur- dioxide. Often these defensive measures are aimed towards two different goals. One is to block the entry of the pollutant gas either by creating structural barriers like excess trichome development, lignification on cell walls and by reducing stomatal pore size or sometimes reducing its frequency. Another strategy is to nullify or reduce the negative impact by different biochemical components like Ascorbic acid, SOD, Peroxidases, GSH, GPX, Proline, POD and PR. These biochemical constituents have been observed to have an anti-oxidative property which is useful to counter the SO_2 induced stress exerted on plant.

Thus, during SO_2 stress, a two-way interaction occurs where the stress and plant defence response interplays with each other and this decides the outcome of sulphur dioxide exposure. Of the different strategies to establish enduring resistance against this stress, utilization of genes that are implicated in SO_2 tolerance to generate transgenic lines is the most promising.

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