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REVIEW

CORONATINE: A POTENTIAL PHYTOTOXIN FOR INCREASING THE TOLERANCE OF PLANTS TO DROUGHT STRESS

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ABSTRACT

Drought and water deficiency are the leading factors that negatively threaten plant growth and development, resulting in significant yield losses in agricultural production. Severe drought events expected because of global warming reveal that serious steps should be taken to enhance the drought tolerance of agricultural crops. Coronatine (COR), a chlorosis-inducing and non-host-specific phytotoxin secreted by the pathogen *Pseudomonas syringae*, is structurally and functionally similar to jasmonates, but it is far more active as a plant growth regulator. Therefore, many studies have been conducted to understand the positive effect of COR application on drought stress tolerance in plants. This review assesses the potential of COR for improving plant drought tolerance by examining previous studies that investigated the effect of exogenously applied COR on antioxidant enzyme activities of plants exposed to osmotic stress simulated by polyethylene glycol PEG application or by not providing water. In addition, it was evaluated whether COR could have a dose-dependent effect on the antioxidant enzyme activities of plants under drought stress. According to the findings of the reviewed studies, COR treatment enhanced the plant drought tolerance by increasing the activity of antioxidant enzymes.

Keywords: Antioxidant enzymes, Coronatine, Drought Stress

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1. INTRODUCTION

1.1. Plants' Drought Stress Defence Mechanism

Plants are exposed to various environmental stresses throughout their lives that reduce their biosynthetic capacity and affect their productivity and growth. The main environmental stressor is drought, with the highest percentage of 26%, defined as a dry period long enough to cause a serious decrease in soil moisture content, as well as plant growth, development, and yield; therefore, these environmental factors should be recognized as the major issues of future climate change [1]. In recent years, with the emergence of the adverse effects of climate change, increasing food production demands and drought stress-related yield losses have attracted more attention [2].

Exposure to drought stress results in many biochemical and physiological alterations that disrupt normal growth and development. Drought stress generally causes growth suppression, stomatal closure, leaf senescence, disruption of the main components of photosynthesis, and inhibition of cell elongation and expansion. Furthermore, drought stress can enhance respiration while reducing the photosynthetic rate [3–4]. Osmotic stress caused by drought is a crucial damage factor that can cause dehydration of plant cells, degradation of photosynthetic pigments, and accumulation of active oxygen species (AOS) [5]. Plants can have methods to survive in their changing habitats by increasing their tolerance to drought stress, which mainly affects plants according to duration and severity [6–8]. One of the survival strategies is the antioxidant defence mechanism in plants. Plant antioxidant mechanisms, both enzymatic and non-enzymatic, are responsible for preventing or reducing the damage caused by AOS. In enzymatic systems, superoxide radicals (O_2) are detoxified to H_2O_2 and O_2 by superoxide dismutase (SOD), and

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then catalase (CAT) and ascorbate peroxidase (APX) can destroy H_2O_2. Glutathione reductase (GR) can also detoxify H_2O_2 through the ascorbate–glutathione cycle [8]. For plants without CAT, H_2O_2 could be detoxified by ascorbate peroxidase (APX) and glutathione reductase (GR) through the ascorbate–glutathione cycle within the chloroplasts [9]. However, drought stress causes a dysfunction of the scavenger enzyme system, leading to increased lipid peroxidation and, ultimately damage to the membrane [10]. Therefore, antioxidant enzymes efficiently convert H_2O_2 to H_2O_2 and O_2, which occur when plants are subjected to drought-induced water deficiency [11].

The internal molecules of plant hormones, produced in low concentrations, are the main controllers of plant development and growth, defined as the main molecules that coordinate a wide variety of signalling pathways in the responses to abiotic and biotic stress in plants [12]. Abscisic acid (ABA), auxin, brassinosteroid, cytokinin, ethylene, gibberellin, jasmonate, salicylic acid, and strigolactone are well-known plant hormones that function as growth regulators and facilitate environmental adaptations in plants [13–14]. Along with the detection of the stress signal, phytohormones are able to activate various adaptation processes in plants, as an example, stimulation of root growth, stomatal closure, and accumulation of osmolytes to deal with drought-induced stress [15]. In addition to controlling the growth and development of plants, JA and its active derivative products, recognized as jasmonates, are related to plant defence. They are also important in regulating plant stress responses to a variety of abiotic and biotic stresses, including drought. [16]. As a phytohormone, JA promotes tolerance to drought in plants in a variety of ways, including minimizing water loss by controlling stomatal closure and opening, also scavenging reactive oxygen species (ROS) by activating the enzymatic antioxidative system, and regulating root development [17-18]. Several studies have found that exogenous application of JA increased plant antioxidant activity under drought-stressed conditions. The study on wheat seedlings exposed to drought stress is an example of how exogenously applied JA enhanced dehydroascorbate reductase (DHAR), monodehydroascorbate reductase (MDHAR), APX and GR [19].

1.2. Phytotoxin Coronatine as a Plant Growth Regulator

Coronatine (COR) is a polyketide and a nonhost-specific phytotoxin that induces chlorosis in a wide range of species of plants. It is produced by numerous strains of the plant bacteria *Pseudomonas syringae*, including maculicola, tomato, glycinea, and atropurpurea [20–21]. COR is composed of two parts: coronamic acid (CMA), derived from isoleucine, and polyketide coronafacic acid (CFA). CMA and CFA are synthesized in different ways and bind via an amide bond to form the coronatine phytotoxin. Tamogami and Kodama (2000) reported that COR is an analog of jasmonic acid (JA) [22]. COR has structures and functions similar to those of jasmonates, so its activities are similar but not identical. Furthermore, it is known that the coronatine insensitive 1 receptor of plants is shared by both COR and jasmonates [22–24]. Previous research has shown that COR is approximately 1000 times more active than jasmonates, even at very low concentrations [25]. Although it is a phytotoxin, COR affects plant biology in multiple ways such as hypertrophy, inhibition of root elongation, cell wall thickening, tendril coiling, leaf senescence, chloroplast structure alteration, chlorosis, and accumulation of protease inhibitor for defence, and, as an elicitor, induces secondary metabolites in plants, such as volatiles, nicotine, and alkaloids [11, 20, 24, 25, 26, 27, 28, 29].

Several research findings have shown that COR has an important role as a plant growth regulator to improve tolerance or resistance to abiotic stress during the plant growth process through modulation of metabolism, inducing anthocyanin production, stomatal opening, the elicitation of plant defences, and hormone synthesis and transport [25–29]. Research shows that applying micro doses of COR to plants can alleviate the response of the plant to abiotic stresses, including salinity-induced stress in cotton [30], drought-induced stress in soybeans and cauliflower [31-32], heat-induced stress in wheat [33], and chilling stress in cucumber [34]. Previous research has demonstrated that COR improves resistance to plant stress by maintaining high photosynthetic performance and increasing antioxidant enzyme activities [31-35], as well as whether exogenously applied COR can alleviate or exacerbate the negative effects of drought stress in plants by influencing the response to plant stress. The purpose of this review was to assess previous studies that examined the effect of COR application on plant response under drought stress conditions, and to update the literature on the subject.

1.3. The Effect of COR on Plant Antioxidant Enzyme Systems Under Drought-Induced Stress

Wang et al. (2008) studied the antioxidant activities of maize seedlings under conditions of drought stress, depending on the application of COR [36]. They simulated drought stress by supplementing the nutrition solution with PEG-6000 (15%) after 24 hours of COR treatment. The application of COR revealed that the leaves had a high-water content. In addition to that, the activity of antioxidant enzymes increased significantly. As a result, 20 nmol L^{-1} of COR application was determined to reduce the negative consequences of drought stress in maize seedlings.

Ai et al. (2008) investigated the role of COR in helping to improve drought resistance of two different rice varieties. The first cultivar, Handao 297, has tolerance to drought stress, and the second cultivar, Yuefu, has a sensitivity to drought stress. Different amounts of COR were applied to each variety to achieve the same effect on the tolerance to drought of both rice cultivars. In preliminary experiments, three-leaf seedlings were treated for 24 hours with COR at concentrations of 0.01 µM and 0.1 µM, which were found to be effective against the application of PEG 6000 (20%). Drought tolerance is increased similarly in two rice cultivars by applying COR, but optimal concentrations differ: a low concentration of 0.01 µM for the drought-tolerant variety and a high concentration of 0.1 µM for the drought-sensitive variety is required to mitigate the negative effects of drought-induced stress by activating antioxidant enzymes and trying to prevent membrane peroxidation and denaturation of biological molecules. Ai et al. (2008) defined the accumulation of proline, H_2O_2, and malondialdehyde (MDA) as drought-induced stress markers. Based on this, Wu et al. (2012) discussed how the application of COR and methyl jasmonate (*MeJA*) exogenously affects defence-related metabolism under drought-induced stress conditions in cauliflower. In this research, when the seedlings expanded to the fourth leaf stage, 0.1 µM COR, and 10 µM MeJA were applied with foliar spray for 24 hours. Then, water deficit stress was applied to the seedlings by not giving them water for 8 days.

Treatment with COR and MeJA increased the activity of CAT, SOD, APX, peroxidase (POD) and GR. According to the findings of this study, both COR and MeJA play a positive role in increasing the activity of non-enzymatic and enzymatic antioxidants, as well as in reducing the production of lipid peroxide in cauliflower seedlings. Both can reduce the negative effects of drought stress and improve resistance to water stress in cauliflower seedlings by promoting defence-related metabolism.

Like the previous study by Ai et al. (2008), Li et al. (2010) also worked on two different winter wheat cultivars, ChangWu134 as drought tolerant and Shan253 as drought sensitive, but unlike the other study, they applied the same concentration of COR (0.1 µM) to both cultivars at the three-leaf stage. COR application increased CAT activity in both cultivars during drought conditions. Furthermore, APX, POD and SOD activities increased in the ChangWu134 variety. Contrary to the findings of the previous study, APX, POD, and SOD activities in the drought sensitive Shan253 cultivar were not affected by COR treatment except for GR activity. According to the results, COR effects on the root / shoot ratio and dry weights, relative water content, ABA, and CAT activity were observed under drought stress. In this case, they were unable to define a significant difference in the improvement of stress tolerance by applying 0.1 µM COR between the two cultivars. Finally, they have revealed that the enhancement of stress tolerance with COR should be independent of genotype.

We also studied to determine whether pretreatment with COR improves the tolerance of chickpea roots (*Cicer arietinum* L. ICC 4958 cultivar) under conditions of osmotic and heat stress, or both stresses combined. This was the first report on stress combinations studied. Depending on preliminary experiments, we decided to apply 0.01 µM COR for 24 h and then 6% PEG (PEG-6000) to inducing osmotic stress or heat stress (35°C–44°C; the temperature is gradually increased by 1°C every 15 minutes and held for 1 hour) for 3 days. COR enhanced the activities of H_2O_2-scavenging enzymes, including POD under osmotic stress, CAT under heat stress, and CAT and POD under both stresses when applied together. We reported that 0.01 M COR pre - treatment significantly reduced the negative effects of all stress conditions on the roots of cultivar ICC 4958 by decreasing H_2O_2 production and increasing antioxidant enzyme activity [37]. Another study by Hao et al. (2013) discussed the function of exogenously applied COR in coping with the adverse effects of drought stress in soybean, which is drought sensitive. 0.1 µM COR was applied to soybean seedlings in three stages of the leaf by foliar spray. After 24 hours, the seedlings were kept without water for 7 days for drought-stress applications.

When COR-applied plants were compared with control plants under drought stress, it was determined that the activities of CAT, POD, SOD, and APX were much higher in the leaves of COR-treated plants. Furthermore, in these plants, the amount of proline increased and the accumulation of malondialdehyde and hydrogen peroxide decreased with the application of COR. This means that exogenously pre-treating soybeans with COR can reduce the negative consequences of drought stress. In a similar study by Xu et al. (2020), the effect of exogenously applied COR on the antioxidant enzyme levels of tobacco (sensitive to drought stress) under PEG-induced drought conditions was investigated. Tobacco was pretreated with 0.001 µM COR in Hoagland nutrient solution for 24 hours, then the seedlings were subjected to PEG-6000 (20%). All drought-exposed plants have been shown to show higher antioxidant enzyme activities, while those treated with COR showed 25.36%, 27.33%, 47.61% and 20.91% higher SOD, CAT, APX, and GR activities in response to PEG-induced drought stress, respectively. According to the findings, COR-induced stress tolerance decreased the adverse effects of drought on tobacco by enhancing antioxidant enzyme activities.

Another study to discuss tolerance developed by the application of COR to drought-stressed plants includes winter wheat seeds (*Triticum aestivum* L.) from JiMai22 (drought-tolerant) and LiangXing99 (drought-sensitive). When the seedlings grew two leaves, unlike previous studies, they were first treated with PEG-6000 (20%) within a Hoagland nutrient solution to simulate drought stress, and then COR was applied by spraying in the amount of 1 µM COR. Although COR was performed after the PEG application, no considerable differences in the results were observed. The water stress alleviating capacity of JiMai22 (moisture-insensitive) was greater than that of LiangXing99 (moisture-sensitive) due to the higher activity of defence-related antioxidant enzymes and reduced accumulation of MDA [38].

Another research by Yu et al. (2021) aimed to determine how COR affects the homeostasis of reactive oxygen species (ROS), water balance, and antioxidant regulation in detached maize plants to mitigate the effects of drought stress. After being treated for 12 hours each with 0.001 M COR and distilled water, the maize plants were subsequently exposed to 10% (w/v) polyethylene glycol (PEG 6000) for 5 hours. Compared to the control, the SOD and POD activity increased by 19.1 and 14.6% under well-watered conditions, respectively, while the CAT activity was slightly different, although the difference was not statistically significant. Furthermore, PEG treatment markedly increased SOD, POD, and CAT activities in all plants, and SOD, POD, and CAT activities were also higher in plants treated with COR under drought stress compared to control plants. These findings suggested that COR could enhance maize drought tolerance by controlling ROS homeostasis to maintain water loss rate and antioxidant enzyme activity [39].

The study by Wang et al. (2023) examined the changes in physiological and transcriptome abundance that COR regulates in C. leucochlora seedling leaves from plants that have been subjected to drought. According to their research, COR increased drought resistance by preserving osmotic adjustment, decreasing membrane lipid peroxidation, preserving photosynthetic capability, and improving the antioxidant defence system under water deficiency stress. Activity of antioxidant enzymes compared to the well-watered control; drought stress significantly increased the activity of antioxidant enzymes.

However, compared to untreated plants under drought stress, 0.1 nmol L^{-1} COR treatment significantly increased SOD, POD, CAT, and APX activities. Compared to drought stress, D+COR treatment increased SOD activity by 17.23%. A similar rising trend in activity was seen in POD, CAT, and APX. Compared to the drought stress treatment, D+COR improved the three characteristics by 14.92%, 13.36%, and 21.95%, respectively. When plants were under drought stress, COR had a significant impact on antioxidant enzyme activities, increasing tolerance to drought in C. leucochlora seedlings by scavenging ROS and minimizing oxidative damage [40]. The dose-dependent effect of COR on the antioxidant enzyme activities of various species of plants under drought stress is summarized in Table 1.

Table 1. The dose-dependent effect of COR on antioxidant enzyme activities of varied species of plants under drought stress conditions.

PLANT	COR	TREATMENT	PEG6000 (%)/DAY WITHOUT WATER	RESULTS OBTAINED	REFERENCES
Maize	20 nmol L^{-1}	24 hours nutrient solution	15%	Enhanced the PEG induced drought tolerance by increasing the antioxidant activity.	Wang et al. (2008)
Two Rice Cultivars Handao 297 (tolerant)/ Yuefu (sensitive)	0.01 µM / 0.1 µM	24 hours nutrient solution	20%	Applied concentrations are the optimal for each cultivar to activate antioxidant enzymes.	Ai et al. (2008)
Cauliflower (Brassica oleracea L.)	0.1 µM	Foliar spray	8 days	Both MeJA and COR enhanced the activity of antioxidant enzymes such as SOD, POD, CAT, APX, and GR.	Wu et al. (2011)
Winter Wheat Seedlings ChangWu134 (tolerant) Shan253 (sensitive)	0.1 µM	24 hours nutrient solution	20%	COR increased CAT activity for both cultivars, also increased the activities of SOD, POD and APX in the ChangWu134 variety.	Xiangwen et al. (2010)
Chickpea (Cicer arietinum L. cv ICC 4958)	0.01 µM	24 hours nutrient solution	6 %	COR enhanced the activities of H_2O_2 scavenger enzymes such as catalase (CAT) under heat stress, ascorbate peroxidase (POD) under PEG stress, and CAT and POD under combined stresses.	Arıkan et al. (2013)
Soybean	0.1 µM	Foliar spray	7 days	Exogenously applied COR can alleviate drought stress; therefore, SOD, POD, CAT and APX activities were higher in plants applied COR compared to controls.	Hao et al. (2013)
Tobacco (Nicotiana tabacum L.) (sensitive)	0.001µM	24 hours nutrient solution	20%	COR- treated ones showed 25.36%, 27.33%, 47.61% and 20.91% more higher SOD, CAT, APX, and GR activities in response to PEG-induced drought stress, respectively.	Xu et al. (2020)
Winter wheat (Triticum aestivum L) JiMai22 (insensitive) LiangXing99 (sensitive)	1 µM	Foliar spray	20%	COR applicated after PEG-induced drought conditions but no significant difference was observed. Water stress alleviating ability of JiMai22 (insensitive) was greater than that of LiangXing99 (sensitive) by activating higher defence related antioxidant enzymes activity.	Wang et al. (2020)
Maize	0.001 M	5 hours	10%	Activities of SOD, POD, CAT in leaves of maize seedlings under 10% PEG treatment were enhanced by COR pretreatment.	Yu et al. (2021)
C. leucochlora seedling	0.1 nmol L^{-1}	Foliar spray	15 days	Compared to untreated plants under drought stress, COR treatment significantly increased SOD, POD, CAT and APX activity in C. leucochlora seedlings.	Wang et al. (2023)

2. CONCLUSION

Drought stress is a serious constraint that limits plant development and growth. Although COR has been identified as a new plant growth regulator, its effect on defence-related mechanisms in plants, especially tolerance, to drought has not yet been clarified. The objective of this review was to summarize studies on the effects of COR on the ability of various plant species to respond to drought stress. All studies show that the application of COR influences the drought resistance capacity of plants, although the amount and method of application vary. However, different concentrations of COR should be applied under the same drought conditions to achieve the same effect on improving drought tolerance in drought-sensitive and tolerant species. Studies investigating the application of COR with different amounts and methods under drought stress show that COR is effective in developing tolerance against drought, but this effect may be directly proportional to its amount. When the studies are examined, it can be determined that a higher concentration of COR is applied in the spraying method compared to the addition of the nutrient solution. However, it cannot be said that a high dose of COR always stimulates the antioxidant enzyme mechanism of the plant and increases the plant's tolerance to stress. For example, the lowest amount of COR (0.001 μM) was studied in tobacco under 20% induced drought stress PEG-6000, and it was determined that even this amount could increase the activity of antioxidant enzymes. Therefore, further studies should be conducted to determine the optimal concentration that should be applied to obtain the maximum benefit from COR.

CONFLICT OF INTEREST

The author stated that there are no conflicts of interest regarding the publication of this article.

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