



Role of triazolic compounds in underlying mechanisms of plant stress tolerance:

A Review

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Abstract

Acclimation of plants to stress conditions depends upon activation of cascade of signaling networks involved in stress perception. Adjustment of antioxidant system to conserve a balance between the detoxification of reactive oxygen species and their production to preserve them at signaling level has been previously documented. Recently, the role of triazolic compounds like penconazole, paclobutrazole, triadimefon, and hexaconazole in the regulation of metabolic network under stress conditions emerge through crosstalk between chemical signaling pathways. Thus, stress signaling and metabolic balance are important areas with respect to increasing crop yield in adverse environmental conditions. This review outlines the recent advances on improvement in stress resistance by various triazolic compounds, aiming to identify new mechanisms of stress tolerance, and therefore, to contribute to sustainable crop yield under stress to bring some potential practical utilization in the future.

Keywords: crop improvement, signaling, stress, tolerance, triazolic compounds

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Introduction

A wide range of environmental stresses like salinity, drought, high light intensity, temperature extremes, and UV are possibly detrimental for plants, and plant productivity and growth are greatly influenced by them (Van Breusegem et al., 2001). Further, reduction of growth under such adverse environmental conditions has been previously observed in different studies (Shaheen et al., 2013; Shaki et al., 2019; Heydari et al., 2019). Indeed, adaptive mechanisms to stress are multifaceted and influenced by internal stress

resistance factors and external environmental causes. Plants apply some adaptive mechanisms to overcome on stress, but information about these mechanisms still is imperfect. In fact, expansion of techniques for enhancement of stress resistance in plants is important and has been a main attention of investigation in recent years.

Besides, a direct impact of stress on plants is accumulation of reactive oxygen species (ROS), which can damage DNA, proteins, and membrane lipids in cells (Patade et al., 2011). However, plants containing high levels of antioxidants (enzymatic and non-enzymatic) show considerable resistance to the oxidative damage caused by ROS (Parida

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and Das, 2005). Furthermore, the increase of compatible osmolytes include glycine betaine (GB), proline and carbohydrates in cytosol is another important strategy for the protection of plants in response to stress (Rasheed et al., 2010). Net photosynthesis is also affected by stress due to alterations in chlorophyll concentration, chloroplast structure, and damage of photosynthetic apparatus (Doganlar et al., 2010). Chlorophyll a and b, as well as carotenoids are among the main photosynthetic pigments, so that the changes in their levels were evaluated as the changes in photosynthetic rate. Further, carotenoids play a critical function in the mechanisms maintaining the photosynthetic apparatus contrary to destructive environmental elements by scavenging ROS formed under stress (Ramel et al., 2012).

There are numerous compounds, which act as cell signaling in response to stress (Palma et al., 2009). Triazolic compounds such as penconazole (PEN), paclobutrazole (PBZ), triadimefon (TDM), and hexaconazole (HEX) are the active ingredient of fungicides and plant growth regulators (Jaleel et al., 2006). They induce stress resistance by regulating a variety of physiological and morphological processes through signal transduction pathways. Thus, these compounds cause several responses in plants including inhibited gibberellin biosynthesis, stimulated root growth, reduced ROS damage, increased antioxidant potential, and induced phytohormones such as cytokinin and ABA (Manivannan et al., 2007; Merati et al., 2014). Therefore, the application of these compounds can alter the metabolic balance and result in stress-like symptoms to protect plants from abiotic stresses (Gaspar et al., 2002; Hassanpour et al., 2013).

Investigations recommend that exogenously applied triazoles in plants can help to identify some new mechanisms of stress tolerance, and therefore, will bring some potential practical utilization. The chief aim of this review was to enhance a new perception about the function of triazoles in growth adjustment of plants grown in stressful environment. This review focuses on recent advances made in research on

triazolic compounds induced resistance in plants under stress conditions.

Effects of triazoles on plant growth

Abiotic stresses noticeably influence the growth, development, and productivity of plants. Such adverse environmental conditions may decline the performance of the plant with decreased harvest from 50% to 70% (Kumar, 2020). Drought caused progressive reduction in the biomass of five licorice genotypes grown in the field (Hosseini et al., 2018). Babaei et al. (2021) showed that salinity reduced growth of *Crocus sativus* plants. High temperatures significantly declined the dry weight of *Brassica oleracea* seedlings (Rodríguez et al., 2015). Cadmium stress decreased growth traits in *Gossypium hirsutum* L. (Liu et al., 2014).

Triazoles cause some morphological and biochemical alterations in plants such as a rise in root growth, a decline in damage caused by highly reactive ions, and an increase in antioxidant activity (Jaleel et al., 2007). Triazoles have been applied as safeguard for plants against abiotic stresses (Javid et al., 2011). PBZ has been known to regulate vegetative growth and enhance fruiting and flowering forms and increasing the harvest in many plants (Chandra and Roychoudhury, 2020). It inhibits the gibberellin synthesis that controls plants growth and development. PBZ reduces the plant height, enhances the stem diameter and leaf number, and alters root structure. PBZ is described to enhance the yield (Kondhare et al., 2014). The positive role of PBZ on plant growth could be related to its impact on enhancing internal CO₂ concentration and leaf thickness, enhancing water use efficiency, and increasing plant cell water retention (Kamran et al., 2020).

TCN enhanced the growth of most crops such as *Solanum lycopersicum* and *Zea mays* (Khan et al., 2008; Ahmad et al., 2013). TCN is a plant growth stimulator, as it has an active role in the upregulation of the main physiological activities required in various stages of plant growth (Ramos-Zambrano et al., 2020). Exogenous application of PEN prevented the negative effects of stress and

increased growth in Safflower Plants (Shaki et al., 2019). Studies have also reported the promoting effect of triazoles on cytokinin content, cell division, and consequently, growth improvement in other plants (Grossmann, 1990; Jaleel et al., 2008).

Impacts of triazoles on osmoprotection and osmoregulation

One of the main effects of environmental stress is the decrease of cell water content, causing in osmolytes enhancement, either by uptake of soil solutes or by synthesis of compatible solutes in cytoplasm to increase plant tolerance against the incurred osmotic stress (Zhifang and Loescher, 2003). Exogenous application of triazoles caused to increase resistance to osmotic stress by the accumulation of osmolytes (Heydari et al., 2019; Shaki et al., 2019). Further, Hassanpour et al. (2013) stated similar results that PEN treatment positively controlled the osmotic potential, K^+ and Ca^{2+} concentration, as well as proline content in *Mentha pulegium* plants under drought stress. Under drought condition, PBZ treatment enhanced proline content in barley (Rady and Gaballah, 2012). Triadimenol (TRI) treatment enhanced proline accumulation in *Solanum lycopersicum* L. under salt stress (Tuna, 2014). During the chilling stress, the proline content in both control and TDM-treated leaves increased remarkably, excluding the 4th day that TDM inhibited the accumulation of proline (Feng et al., 2003). Proline is produced from glutamate by 1-pyrroline-5-carboxylate synthetase (P5CS). Proline degradation is the reverse process of its biosynthesis and is catalyzed by proline dehydrogenase (PDH). Forghani et al., (2020) showed that high proline content of sweet sorghum was strongly associated with high activity of P5CS enzyme without any change in PDH in PBZ treatments under salinity.

Proline, as an osmolyte, plays an important function in preserving osmotic potential, aiding plants to preserve turgor under stress conditions (Sadiqov et al., 2002). This compound also protects protein configurations during dehydration (Aly and Latif, 2011). Sesame seedlings enhanced proline content under salinity, which was further augmented by PEN treatment,

thus decreasing the harmful impacts of stress (Heydari et al., 2019). Further, it is believed that triazoles may increase the ABA level (Jaleel et al., 2008), and therefore, enhanced ABA level by triazole treatment can be the cause for the proline accumulation in PEN-treated plants (Hassanpour et al., 2013).

Glycine betaine (GB) has vital role in supporting dehydration tolerance in plants (Ashraf and Foolad, 2007). PBZ increased GB content in *Stevia rebaudiana* under in vitro drought stress (Hajihashemi and Ehsanpour, 2013). We have also newly presented that salinity strangely boosted GB and proline content in safflower, in the presence of PEN, which suggests the participation of these solutes in osmotic regulation (Shaki et al., 2019). In a more common context, it could be said that the PEN-induced accumulation of compatible osmolytes such as proline and GB aids steadying proteins and membranes, therefore enhances the resistance against environmental stress (Shaki et al., 2019). Triazole treatment (Tebuconazole (TEB) and Propiconazole) to the drought-stressed plants decreased GB content in *Zea mays* L., but it was higher than that of control (Rajasekar et al., 2016). Pre-sowing seed treatment with triacontanol (TCN) enhanced glycine betaine in canola plants under both saline and non-saline conditions (Shahbaz et al., 2013).

Furthermore, carbohydrates accumulate in plants under stress, playing a leading role in osmoprotection, osmotic adjustment, carbon storage, and radical scavenging (Karimi et al., 2014; Parida and Das, 2005). It is well documented that high content of carbohydrate under stress conditions prevent oxidative injury in cells (Hassanpour et al., 2013). It has also been described that they could preserve structure of proteins in stress conditions. The hydroxyl groups of these combinations may replacement for water to protect hydrophilic relations in protein structures and so, inhibit denaturation of protein (Hassanpour et al., 2013). The greater amount of carbohydrates under triazole application might be the result of stimulation of chlorophyll biosynthesis, as the main photosynthetic pigments, and probably photosynthesis rate in plants (Hassanpour et al., 2013; Heydari et al.,

2019; Shaki et al., 2019). There are several indications about the impacts of various triazolic compounds on plants. PBZ treatment enhanced carbohydrate content in wheat under stress conditions (Hajhashemi et al., 2007). Propiconazole (PCZ) application improved the salt tolerance in *Catharanthus roseus* plants by antioxidant enzymes activities and enhancing plant growth (Jaleel et al., 2008). Application of TCN was able to counter salt stress in soybean plants by increasing relative water content and soluble sugars (Krishnan and Kumari, 2008). PEN application enhanced soluble sugar content in canola plants under drought stress (Rezayian et al., 2019). TCN priming helped rice plants to improve the water status under drought stress through osmotic adjustment, as attained by the accumulation of some osmolytes, including proline, free amino acids, and total soluble sugars (Alharbi et al., 2021). These results propose the assumption that triazoles are participated in the osmotic regulation by keeping the balance between osmolytes metabolism and stress tolerance in plants (Shaki et al., 2019).

Effects of triazoles on antioxidant system

During oxidative stress, some operations are involved in the production of ROS in plant cells. These processes create more hurtful oxygen radicals, which can terminate regular metabolism by oxidative injury of protein, nucleic acids and lipids when they are manufactured excessive (McCord, 2000). Plants apply a complex and effective system for ROS elimination, which includes particular ROS-suppressing enzymes such as catalase (CAT), superoxide dismutase (SOD), peroxidase (POX), and ascorbate peroxidase (APX), as well as non-enzymatic compounds like phenolic compounds, carotenoids, flavonoids, anthocyanins, tocopherol, ascorbate (AsA), and glutathione (GSH) (Salah et al., 2011; Bano et al., 2014). It is now widely accepted that the activities of these antioxidants keep a balance between the amount of production and deletion of ROS under stress conditions (Türkan et al., 2005). A relationship between antioxidant ability and stress tolerance has been previously described in various plants (Demiral and Türkan, 2005; Sekmen et al., 2007; Rezayian et al., 2018).

Recently, Heydari et al. (2019) witnessed that PEN treatment might be caused the decrease of ROS in the leaves of sesame plants (Heydari et al., 2019). Their findings indicate that the activities of antioxidants are directly or indirectly regulated by PEN, thereby providing protection against abiotic stress. Further, Rezayian et al. (2018) reported the induction of antioxidant enzyme activities by PEN in drought-stressed canola cultivars (Rezayian et al., 2018). They showed that PEN alleviated the negative effects of stress in drought tolerant cultivar. Hassanpour et al. (2012) have also recommended a like mechanism to be responsible for PEN-induced stress tolerance in *Mentha pulegium* L. Such similar findings were also reported in TDM-treated plants (Bhattacharjee, 2008) and PBZ-treated plants (Berova et al., 2002). Srivastav et al. (2010) proposed the positive role of PBZ in up-regulation of CAT, SOD, and POD activities in *Mangifera indica* under salinity. PBZ treatment induced CAT and APX activity in pea plants under severe salinity condition (Sofy et al., 2020). Similarly, application of other triazolic compounds such as HEX and TDM enhanced antioxidant enzymes activity in *Manihot esculenta* (Gomathinayagam et al., 2009) and wheat (Aly and Latif, 2011). Mohammadi et al. (2017) found a proportional relationship between expression level of *CAT*, *SOD*, *POX*, and *APX* genes and enzyme activity of Perennial ryegrass samples. *CAT*, *SOD*, *POX*, and *APX* genes expression patterns at the mRNA level were positively linked to alterations in *CAT*, *SOD*, *POX*, and *APX* activities under drought treatment and application of PBZ.

Furthermore, lower level of MDA content observed in triazole-treated plants could be related to the increased activities of antioxidative enzymes (Berova et al., 2002; Jaleel et al., 2007; Hojati et al., 2011). Exogenous TEB reduced salt-induced oxidative damage in cucumber plants by preventing the overproduction of ROS and lipid peroxidation (Mohsin et al., 2019). Triazoles could even express more isoforms of antioxidant enzymes in plants under such stressful conditions (Hassanpour et al., 2012).

We have also recently reported that PEN caused an increase in H₂O₂ levels in salt-stressed safflower plants (Shaki et al., 2019). Similar findings were presented in other plant species

treated with different triazolic compounds like paclobutrazol-treated *Catharanthus roseus* (Jaleel et al., 2007), PCZ-treated *Vigna unguiculata* (Manivannan et al., 2007), and PEN-treated *M. pulegium* (Hassanpour et al., 2012) under stress conditions. It seems that triazoles are able to induce stress-like symptoms for stimulation of antioxidative system. This might be the reason for the general increase in H₂O₂ level in plants.

Furthermore, PEN application caused more induction of flavonoid in rice seedlings (Chutipaijit et al., 2009). It is also well-documented that triazolic composites could increase the content of phenolics in plants (Hassanpour et al., 2013). So, flavonoid augmentation in the PEN-treated plants may possibly be due to the induction in biosynthesis of phenolic combinations. It should also be noted that an increase in the activity of phenylalanine ammonia-lyase (PAL), a key enzyme at the entry point of phenylpropanoid pathway, may be related to the resistance to stress through biosynthesis of active metabolites, such as phenols (Gao et al., 2008). Triazoles may function in a defense system by increasing phenolic compounds following the increase in PAL activity and even its gene expression. Overall, triazole-induced PAL activity might be a result of phenolic compounds production in plants which promotes defense system and stress tolerance (Shaki et al., 2019). Moreover, the enhancement of ascorbic acid content was reported in PBZ-treated *Dioscorea rotundata* plants (Jaleel et al., 2007). It was also documented that increased ascorbic acids in the TDM-treated plants was well-correlated with the increased APX contents, as the main antioxidant enzyme in the chloroplast (Jaleel et al., 2006). The rise in AsA and GSH contents in PBZ-treated plants could reveal the stimulatory effects on the enzymes of the AsA-GSH cycle, especially APX activity (Sofy et al., 2020). Enhanced α -tocopherol content was perceived in *Vigna unguiculata* plants treated with PCZ under drought condition (Manivannan et al., 2007). The increased endogenous AsA and GSH due to HEX application to the soil may have protected the canola plants from NaCl-induced oxidative damage by adjusting the cellular redox state (Akbari et al., 2011).

In sum, a positive and close correlation might be assumed between the activities of antioxidant systems and triazolic compounds under stress conditions in plants.

Effects of triazoles on proteins

There are numerous studies which confirm the decline of protein under stress conditions (Parida and Das, 2005; Hu et al., 2010; Hassanpour et al., 2013; Rezayian et al., 2018). The decline in protein amount may be due to the reduction in protein synthesis, protein denaturation, and deactivation of enzymes involved in protein synthesis (Hassanpour et al., 2013). The total protein content decreased in *M. pulegium* under drought conditions and PEN-treated plants maintained higher soluble protein. On the other hands, treatment of *M. pulegium* with PEN resulted in higher total chlorophyll contents. According to these results, it has been described that chlorophyll reduction is connected to protein degradation (Hassanpour et al., 2013). It is also well documented that more protein amount in triazole-treated plants could be the result of triazole effect on cytokinin content (Fletcher et al., 2010). Thus, the reports show that triazoles may decline the adverse impacts of stress by prevention of protein degradation.

Application of TCN increased protein content in rice plants (Chen et al., 2002). Additionally, NaCl stress reduced the total soluble protein content in canola plants, and the HEX treatment augmented the total soluble protein content (Akbari et al., 2011). TEB application caused non-significant change in protein content in *Solanum lycopersicum* L. under salinity (Tuna et al., 2014). In water stress conditions, PBZ treatment enhanced total soluble protein in okra (*Abelmoschus esculentus* L.). The improved yield of okra by PBZ treatment might be because of its impact on synthesis of protein (Iqbal et al., 2020).

Hassanpour et al. (2013) have also reported that PEN application to drought-stressed *M. pulegium* plants created several novel protein bands with the different molecular weights. It seems that PEN application on stressed plants can induce several proteins, which may be participated in adaptation to stress conditions. The presence of new proteins

under stress conditions by PEN proposes that PEN application could aid to improve stress tolerance genotypes and participate to stress adaptation in plants (Hassanpour et al., 2013).

We have also recently witnessed a linear decline in the amount of total soluble protein in salt-stressed safflower plants while exogenously applied PEN had a positive impact on its content in all stressed and unstressed plants (Shaki et al., 2018). In addition, the findings suggest that the up-regulation of proteins in PSII by PEN treatment could aid to enhanced photochemical efficiency, as identified by a upper photosynthesis, in PEN-treated *M. pulegium* plants (Hassanpour et al., 2013).

Effects of triazoles on photosynthesis

The reduction in photosynthetic rates under stress conditions is mainly due to the reduction in water potential. Photosynthesis is also inhibited when high concentrations of toxic ions like Na⁺ and Cl⁻ are accumulated in the chloroplasts (Zhang et al., 2005). Further, the reduction in chlorophylls content under stress due to increasing of chlorophyllase enzyme has been reported in numerous studies, and chlorophyll level has been applied such as a sensitive pointer of the cellular metabolic status (Chaves et al., 2009; Chutipaijit et al., 2011; Gengmao et al., 2015; Rahdari et al. 2012). Saha et al. (2010) detected a linear decline in the contents of chlorophylls, xanthophylls, and carotenoids as well as the severity of chlorophyll fluorescence in *Vigna radiata* under stress conditions (Saha et al., 2010). In addition, photosystem II (PSII) is a moderately sensitive constituent of the photosynthetic machine to stress (Allakhverdiev et al., 2000). A significant decline in the performance of PSII, electron transport chain, stomatal conductance, photosynthetic efficiency, function of oxygen evolving complex, and assimilation rate of CO₂ under stress conditions has been previously noticed (López-Climent et al. 2008; Pompelli et al. 2010; Kalaji et al. 2011).

Commonly, triazolic compounds are known to increase the photosynthesis rate due to heightened chlorophyll content through an induction in chlorophyll biosynthesis or inhibition

of chlorophyll degradation (Hassanpour et al., 2013). A study on cereals has proved that carotenoid and chlorophylls contents are influenced by triazolic combinations such as PBZ and its analogues, diclobutrazol and TDM (Khalil, 1995). We have also recently found that chlorophylls and carotenoid contents enhanced under salinity and exogenously applied PEN increased its content more in safflower plants (Shaki et al., 2018). Furthermore, PEN application in drought-stressed plants boosted the chlorophyll content in *M. pulegium* leaves (Hassanpour et al., 2013). Similar results were consistent with the findings in *Triticum aestivum* and *Solenostemon rotundifolius* under other triazolic compounds (Kishorekumar et al., 2007; Aly and Latif, 2011). Further, studies suggest that the increase of photosynthesis by TDM could be ascribed to the increase in ribulose 1, 5-bisphosphate carboxylase (Rubisco) activity by triazolic compounds (Yan and Pan, 1992).

It has also been hypothesized that the increase in chlorophyll level could possibly attribute with enhanced cytokinin level under PEN, which in turn augments chloroplast differentiation and chlorophyll biosynthesis, inhibiting chlorophyll degradation (Fletcher et al., 2000).

PBZ application has been documented to increase chlorophyll in maize plants under normal or stress conditions (Kamran et al., 2020). PBZ enhanced photosynthetic rate and Rubisco activity in peanut (Yan and Pan, 1992). Applications of PBZ in chickpea were found to maintain higher rates of photosynthesis, Fv/Fm ratio, and water use efficiency under drought conditions (Soumya, 2014). The enhancement of intercellular CO₂ level and modification in stomatal conductance was considered as reasons for higher photosynthesis in PBZ treated *Amorphophallus campanulatus* (Gopi and Jaleel, 2009; Manivannan et al., 2007). TCN may boost the photosynthetic process through increasing the number and size of chloroplasts and chlorophyll synthesis (Borowski et al., 2000; Muthuchelian et al., 2003). The content of chlorophyll a and b was enhanced in stressed cucumber seedling by TEB treatment (Mohsin et al., 2019). TCN application augmented ¹⁴CO₂ fixation and synthesis of chlorophyll a and b and

also carotenoid in *Erythrina variegata* seedlings under stress conditions (Naeem et al., 2011).

Conclusion and future prospects

Research has revealed that triazolic compounds help plants, to some extent, to cope with adverse environmental conditions. It is supported by the regulation of oxidative system and soluble proteins, reduction in lipid peroxidation, enhancement of photochemical efficiency, and osmotic adjustments in plant cells. Therefore, these compounds could be used for improvement of plant growth and productivity in such severe conditions. Furthermore, results of these studies indicated that triazoles minimize the negative effects of stress with evidence of less membrane

damage, which is critical for amelioration of stress in plants. Identification and characterization of underlying mechanisms involved in triazoles signaling under unsuitable environmental conditions could be an actual way for more plant yield and may cause enhancement in food safety in near future. In addition, more investigation is required to reveal triazole-induced mechanism of multi-stress protection, chiefly from the issue of interaction, interrelation, and crosstalk with phytohormones and stress responsive genes.

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