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TRIACONTANOL: A VERSATILE PLANT GROWTH REGULATOR IN OVERCOMING ABIOTIC STRESSES – A REVIEW

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ABSTRACT

Plants are exposed to wide range of abiotic stresses such as salinity, drought, chilling, heavy metals, ultraviolet radiation and water logging and are detrimental to plant growth and development resulting in significant crop output losses around the world. Abiotic stress causes extensive alterations in cellular processes and affect many elements of plant physiology. Because plants are sessile, they have no choice but to respond to these. In this review, we have summarized our current understanding of Triacontanol (TRIA), a key growth-regulating signalling molecule in plants and its response to plants under different abiotic stress condition. The growth promoting role of TRIA in agricultural plants under abiotic stress has been focused on its synergistic interaction with phytohormones and induction of 9- β -L(+) adenosine, which has a similar structure to that of cytokinin. The current paper examines the role of exogenously applied TRIA in morpho-physiology and biochemistry of plants in terms of growth, photosynthesis, mineral and nutrient acquisition, yield and quality under stress as well as normal condition. The mode of action and its interaction with other phytohormones in regulating physio-biochemical processes and counteracting stress induced damages are also discussed in this article.

Keywords: Abiotic stress; Plant growth regulator; Triacontanol; Physio-biochemical processes.

Introduction

In plants, different environmental as well as abiotic stresses such as heavy metal, extreme cold, heat, drought, flooding and salinity stress are key restraints to the global agricultural system, limiting the economic yield, quality and quantity of variety of crop plants. Numerous efforts were made to date to get to the bottom of tolerance mechanisms to various environmental and abiotic stress condition (Roychoudhury and Chakraborty, 2013). Due to the complexity of plant abiotic stress tolerance mechanisms, which are driven by multigenic characteristics, substantial research is being conducted to generate plants with increased stress resistance. Stress resistance can, however, be designed through the induction of antioxidant pools, osmoprotectants accumulations, and the production of protective defence proteins (Roychoudhury *et al.*, 2009, Basu *et al.*, 2010). Plant growth regulator (PGRs) are important signalling molecules that control a variety of plant growth and development phases as well as abiotic stress tolerance, either directly or indirectly (Zaid and Mohammad, 2018). Triacontanol (TRIA) is one of relatively new plant growth regulator (Ries *et al.*, 1977) and is discovered in epicuticular waxes of plant (Kolattukudy and Walton, 1973). TRIA is a saturated primary alcoholic plant hormone (Naeem *et al.*, 2011) which was first discovered by Chibnall *et al.*, 1933. TRIA is also known as Miraculan in commercial markets, and its trade name is Mixatalol whereas the prepared forms of TRIA is known as Vipul and Miraculan (Mishra and Shrivastava, 1991). The

structural formula of TRIA is $\text{CH}_3(\text{CH}_2)_{28}\text{OH}$ and its molecular mass is 438.8 g mol^{-1} . Its exogenous application boosts plant biomass, crop yield, photochemical pigments, transpiration rate, photosynthetic rate, nutrient and water uptake, water use efficiency, nitrate reductase activity, free amino acids, sugars, soluble proteins, essential oil content, nitrogen fixation and active constituents (Aftab *et al.*, 2010; Aziz *et al.*, 2013; Naeem *et al.*, 2014). TRIA decreases the lethal effects of abiotic stress by regulating different stress mitigating genes (Sarwar *et al.*, 2021). TRIA has been shown to regulate a variety of physiochemical processes in both normal and stressed situation in diverse crop species such as in soybean (Krishnan and Kumari, 2008), sunflower (Aziz *et al.*, 2013) and wheat (Perveen *et al.*, 2014). TRIA, like any other PGRs, is considered to be a potential plant growth regulator (Naeem *et al.*, 2011). Under saline stress, foliar application of TRIA has been shown to influence a variety of physiological and biochemical processes (Perveen *et al.*, 2013). TRIA has also been demonstrated to have growth-stimulatory effects at different stages of development (Singh *et al.*, 2011). For example, in most economically important crop such as wheat, TRIA foliar spray at early vegetative and at anthesis has been shown to boost plant development and yield (Ries, 1991).

Mechanism of action of TRIA in plants

Naturally occurring growth substance Adenosine which is originally known as TRIM is elicited by TRIA (Ries *et al.*, 1990). TRIA elicits L(+) –adenosine which act as secondary

messenger (Naeem *et al.*, 2012). Adenosine monophosphate (AMP) is a portable source of L(+)- adenosine in plants, produced from adenosine diphosphate/adenosine triphosphate (Olsson and Pearson, 1990). In untreated plants, studies using adenosine deaminase revealed that L (+)- adenosine exists in an inactive racemic mixture with D(-)adenosine, with the remaining adenosine (99%) existing as D(-) isomer. After TRIA treatment, non-racemic L(+) –adenosine (11%) appeared to be released, affecting plant functions (Ries,1991). TRIA also caused L (+) – adenosine to develop in the roots of plants whose shoots were sprayed with nanomolar concentration for one minute (Ries and Wert, 1988). The adenosine from controlled plants and the adenosine from TRIA treated plants are identical to each other yet plant growth can be stimulated by only the pure adenosine from TRIA treated plants. TRIA ability to release L(+)- adenosine in the root tissue of rice seedlings within one minute of exposure to the shoots may have clarified the first step in the mode of action of TRIA (Ries *et al.*, 1990). It is hypothesize that the ratio of L(+)- to D(-) – adenosine is rapidly increased by TRIA at the tonoplast. According to research, TRIA (10⁻⁴ to 10⁻⁹ M) boosted ATPase activation of plasma membrane enriched vesicles from barley (*Hordeum vulgare* L.) in the presence of calmodium (Lesniak *et al.*, 1986). Exogenous L(+)- adenosine has been shown to cause a variety of physiological reactions in plants, including an increase in malate dehydrogenase activity (Savithiry *et al.*, 1992) and plant growth (Ries and Wert, 1992). Foliar application of picomole amount of L (+) – adenosine to apical leaves cause a transient alteration in Ca²⁺, Mg²⁺ and K⁺ content inside the stem apoplast solution phase within seconds (Ries *et al.*, 1992). Ries *et al.* (1993) reported that in tomato, cucumber and maize Ca²⁺, Mg²⁺ and K⁺ were all elevated in the presence of L(+)-adenosine. TRIA travels quickly through the leaf cuticle to the plasma membrane of

epidermal cell, where it causes the production of L (+)-adenosine, which is a type of TRIM. According to their method of action, exogenously administered TRIA and L (+)-adenosine are thought to travel quickly through the leaf cuticle to the plasma membrane of epidermal cells. The formation of L (+)- adenosine is then elicited by TRIA. According to research L (+) –adenosine elicits a swiftly conveyed signal throughout the entire plant. This causes a brief increase in the concentration of apoplastic ions inside stem cells. These findings are consistent and it confirms the usually quick reaction of plants to both TRIA and L (+)-adenosine (Ries, 1991). L (+) – adenosine cause the influx of Ca²⁺, Mg²⁺ and K⁺ ions withinside the cytosol via way of means of opening ion channels in the plasma membrane (Lesnaik *et al.*, 1986). As proposed by Reddy *et al.* (2011), the increase Ca²⁺ levels may cause it to bind to sensor protein such as calcium calmodium in a similar way. The Mg²⁺ and K⁺ ions have the potential to control a variety of metabolic process by a method of becoming an enzyme activator calmodium protein that has been activated and it may directly affect transcription factors such as (CAMTA3, GTL, MYB2, etc) and activate phosphatases and kinases resulting in gene expression which leads to enhanced development and faster growth of TRIA treated plants (Virdi *et al.*, 2015). TRIA calming effect can be related to its role in the regulation of growth hormones such as IAA, cytokinin and ABA as cell division in the apical root meristem is maintained by cytokinin and IAA and ABA aids in the biosynthesis of different antistress proteins, improves the antioxidant enzyme system and reduces ROS production, preserves membrane integrity and modulates the conductivity of the stomata which in turn improves photosynthetic activity, transpiration rate and water usage efficiency by increasing carbon dioxide availability to leaf mesophyll (Sarwar *et al.*, 2021).

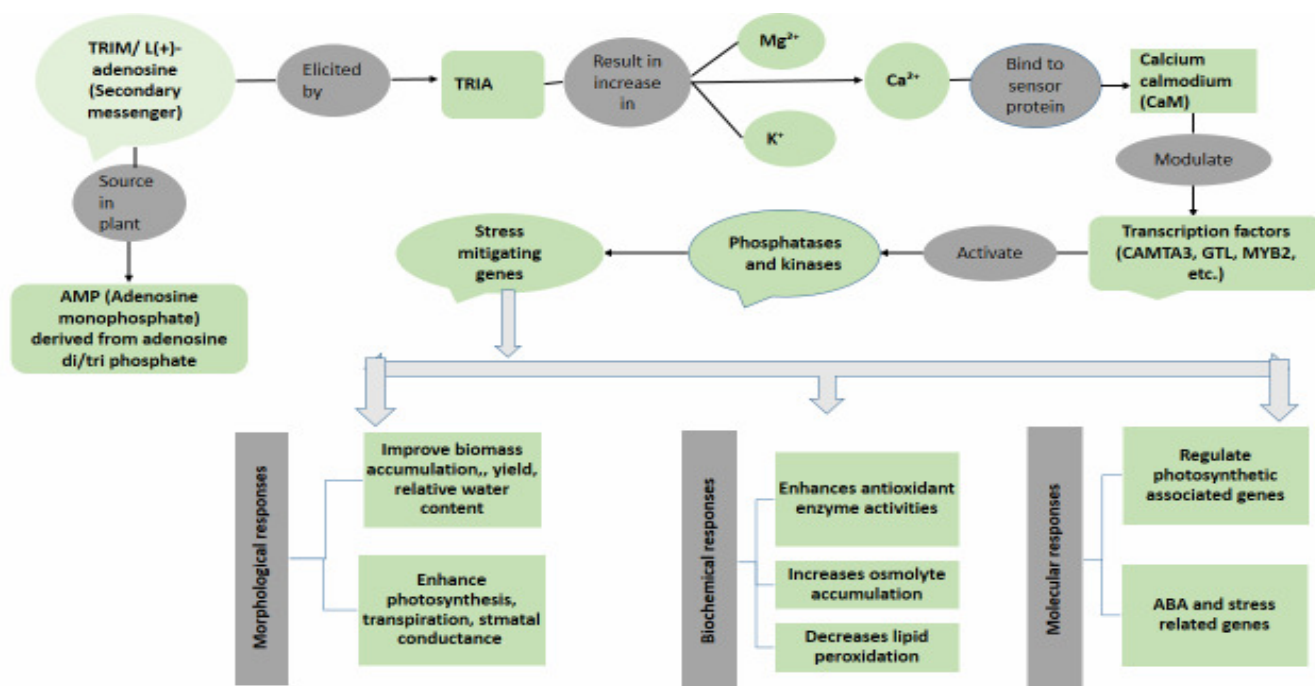


Fig. 1 : Mechanism of action of TRIA in plants.

Effect of TRIA on physio-biochemistry of plants under salt stress

The application of TRIA has a significant effect on physiological and biochemical characteristics of plants under

salt stress conditions. The findings of numerous researchers discussing the impact of TRIA in reducing the negative effects of salt stress on plant performance are summarised below (Table 1).

Table 1: Physio-biochemical response of several crop to treatment under abiotic stress.

S. No	Types of crop	Plant species	Abiotic stress	TRIA Concentration applied	Plant response	References
1	Vegetable crop	<i>Cucumis sativus</i> L.	Salinity	0.80 mg L ⁻¹	Enhanced growth, CO ₂ uptake, gas exchange, stomatal conductance, photosynthesis, transpiration rate, water use efficiency and nutrient uptake. It further increases the SOD, POD and CAT in all cucumber genotypes.	Sarwar <i>et al.</i> , 2021
		<i>Raphanus sativus</i>	Salinity	10µM	Stress with 0.25M NaCl reduced stem diameter, epidermal cell size, cortical cell thickness, vascular bundle width, cambial cell thickness, xylem and phloem widths, and trachea diameter. TRIA, on the other hand boosted all the above parameters mentioned above.	Cavusoglu <i>et al.</i> , 2008
2	Cereals	<i>Triticum aestivum</i>	Salinity	0, 10, 20 µM	TRIA increased growth, leaf water relation and dry biomass and reduced MDA, H ₂ O ₂ and proline content.	Perveen <i>et al.</i> , 2014
		<i>Triticum aestivum</i> L.	Aresnic	1µM	TRIA enhanced fresh and dry weight total of shoot, total chlorophyll, flavonoid and anthocyanin content, water use efficiency, stomatal conductance and internal CO ₂ .	Ali and Perveen, 2020
		<i>Zea mays</i> L.	Drought	0, 2, 5µM	Foliar application of TRIA enhanced chlorophyll content, CAT, proline, phenolics content and decreased oxidative stress attributes such as H ₂ O ₂ and MDA content.	Perveen <i>et al.</i> , 2016
3.	Medicinal plants	<i>Mentha arvensis</i>	Salinity	10 ⁻⁶ M	Growth, mineral nutrients, yield and quality traits were all improved with TRIA application.	Khannam and Mohammad, 2018
4.	Oil seeds	<i>Brassica napus</i> L.	Salinity	0, 0.5, 1 mg L ⁻¹	TRIA pre-sowing seed treatment enhanced canola shoot fresh weight, number of seeds, transpiration rate, photosynthetic rate, chlorophyll a/b ratio, electron transport rate, shoot and root K content. It also enhanced the free proline and glycine betaine content in canola.	Shahbaz <i>et al.</i> , 2013
		<i>Brassica napus</i> L.	Cadmium	10, 20µM	TRIA decreased Cd- induced stress by decreasing ROS, lipoxygenase activity, and lipid peroxidation. TRIA enhanced the amount of ascorbate, glutathione, and phytochelatin in the body, as well as the activity of antioxidant enzymes.	Maresca <i>et al.</i> , 2017
		<i>Helianthus annus</i> L.	Salinity	0,50,100µM	Under both saline and non-saline condition, foliar spray TRIA enhanced shoot and root fresh weights and length, transpiration rate, water use efficiency, stomatal conductance and assimilation rate while no prominent effect was visible on chlorophyll fluorescence attributes such as photochemical quenching and electron transport rate.	Aziz <i>et al.</i> , 2013
		<i>Glycine max</i> L.	Salinity	10µM	Chl a, b, and total chlorophyll concentration increased as well as there was enhancement in soluble sugar, proline content, relative water content and specific leaf area.	Krishnan and Kumari, 2008

(i) Yield and quality

TRIA not only improves the development and physio-biochemical characteristics but also enhances the quality, content and yield of several crops (Naeem *et al.*, 2009, 2010, 2011). Application of TRIA also proved to enhance yield attributes under salt stress. When subjected to salt stress, all genotypes of cucumber (green long, market more, summer green and 20252) shown reduction in total number of fruit and weight. Foliar spray of the TRIA ameliorates the lethal effect of salt stress and improved the fruit number and weight in all four genotype (Sarwar *et al.*, 2021). Shahbaz *et al.*, 2013 observed the similar findings on *Brassica napus* L. only shoot fresh weight and number of seeds per plant increased after pre-sowing treatment with TRIA at a concentration of 1 mg L⁻¹. Bhandari (2021) reported that, in Kohlrabi (*Brassica oleracea* var. gongyloides L.) the highest harvest index was computed with TRIA @2 ml L⁻¹ (0.39), which was statistically comparable to 1 ml L⁻¹ (0.35) and 1.5 ml L⁻¹ (0.33). The findings of 46 field test, which was experimented in different parts of the world showed no remarkable increase in yield of agricultural crop except for one which was conducted in Japan. Soil application of TRIA at 0.057- 4g ha⁻¹ boosted yield quality by 17-21% (Naeem *et al.*, 2012). TRIA foliar spray at various growth stages significantly enhanced the grain yield per plant, number of grains per plant and total grain yield per plant and 100-seed weight in both cultivator of wheat i.e. S-24 and MH-97 under both salt-stress and non-stress condition. In both salt-stress and non-stress plants, TRIA administration at the vegetative + boot stages was more successful in improving yield quality as compared to TRIA application at other phases of development (Perveen *et al.*, 2014). Combination of TRIA and potassium improved the weight per fruit and number of fruits per plant in tomato. Thus, the use of TRIA (1 M) in combination with a basal treatment of potassium (90 kg k/ha) appears to be economically sound for boosting the growth, yield and quality (Khan *et al.*, 2009). TRIA applied to the leaves of sunflower cultivars significantly increased the shoot and root fresh weight in both saline and non-saline conditions (Aziz *et al.*, 2013).

(ii) Growth and flowering

TRIA applied either through the root medium or to the leaves, has been shown to improve the growth and productivity of vegetables and cereals crop in a variety of experiments (Ries *et al.*, 1978; Ries and Wert, 1977). Perveen (2014) reported that when TRIA was applied foliarly particularly at the vegetative + boot stages dry biomass (shoot and root dry weight), total leaf area per plant was increased significantly. TRIA treatment with 1.0 and 2.5 mg/L during the vegetative shoot stage lead to advance flowering and improve the physiological activity, number of flowering and quality of potted *Bougainvillea* plants cultivated under natural condition. It further improved the vegetative growth at 5.0 mg/L (Khandaker *et al.*, 2013). Foliar spray of TRIA along with potassium K₉₀ + TRIA 1μM enhanced number of leaf per plant, height per plant, area per leaf and fresh and dry weight per plant (Khan *et al.*, 2009). Within 8 hours, 10 μg/l TRIA in the nutrient solution greatly enhanced the leaf area of rice seedlings and the dry weight of the entire plant within 3 days of planting (Ries and Wert, 1977).

(iii) Photosynthesis

Sal stress has a significant impact on the chlorophyll content of cucumber genotypes. After being treated with foliar TRIA, all four cucumber genotypes showed a significant increase in chlorophyll. Green long produced the highest chlorophyll content whereas salt-sensitive summer green produced the lowest. Due to NaCl based salinity and foliar spray of TRIA, data for photosynthetic characteristics such as stomatal conductance, photosynthetic activity and transpiration rate differed significantly. Under both salt-stress and non-stress circumstances, foliar spray of TRIA improved the stomatal conductance, transpiration and photosynthetic rate (Sarwar *et al.*, 2021). Ali and Perveen, 2020 noticed that in arsenic-induced wheat, foliar treatment of triacantanol (1 μM) considerably increased the flavonoid and anthocyanin content, Stomatal conductance (gs) and internal CO₂. Pre-sowing treatment with TRIA lead to slight increase in photochemical quenching, electron transport rate as well as water use efficiency (Shahbaz *et al.*, 2013). Under drought stress, chl a, chl b and total chlorophyll content did not alter however, on the other hand, foliar application of TRIA enhanced the chla and total chlorophyll content under both drought stress and non-stressed condition (Perveen *et al.*, 2016). TRIA foliar spray of 100μM resulted in a significant improvement in photosynthetic rate in both sunflower cultivar. Also sunflower Cv. SMH-917 showed a significant enhancement in transpiration rate at 50μM foliar spray (Aziz *et al.*, 2013).

(iv) Osmolytes

In wheat cultivar, the soluble proteins increased considerably. In terms of soluble proteins, cultivar S-24 outperformed cultivar MH-97, but the differences was more pronounced in non- saline condition. Under salt stress, when TRIA was administered at the vegetative growth stage total phenolic levels increased significantly (Perveen *et al.*, 2014). Foliar spray of TRIA improved the accumulation of glycine betaine, proline and phenolics (Sarwar *et al.*, 2021). Under non-saline conditions, pre-sowing treatment with TRIA increased leaf proline while glycine betaine was increased in both saline and non-saline condition (Shahbaz *et al.*, 2013). In another study, Perveen (2016) reported that foliar application of TRIA increased proline content under both drought stress and non-stressed condition. Also, TRIA foliar application decreased and increased GB content under drought stress and non-stress condition respectively.

(v) Mineral and nutrient acquisition

In all genotypes of cucumber, foliar application of TRIA improved the ionic content in all genotypes when compared to the non-sprayed plant. TRIA causes the synthesis of secondary messenger (TRIM), which activates the influx of ions like Mg²⁺, K⁺ and Ca²⁺ by opening their channels in plasma membrane (Sarwar *et al.*, 2021). In wheat cultivar, exogenous TRIA treatment enhanced shoot K⁺ levels at various growth stages but it had no effect on root K⁺ content under both saline and non-saline condition. Under both saline and non-saline condition, foliar applied TRIA significantly enhanced the shoot and root Ca²⁺ levels in both cultivar at various growth stages however under non-saline condition 10 μM TRIA was more beneficial for both cultivar (Perveen *et al.*, 2014). Further, at 150 Mm NaCl, TRIA at 0.5 mg L⁻¹ enhanced the root and shoot K (Shahbaz *et al.*, 2013).

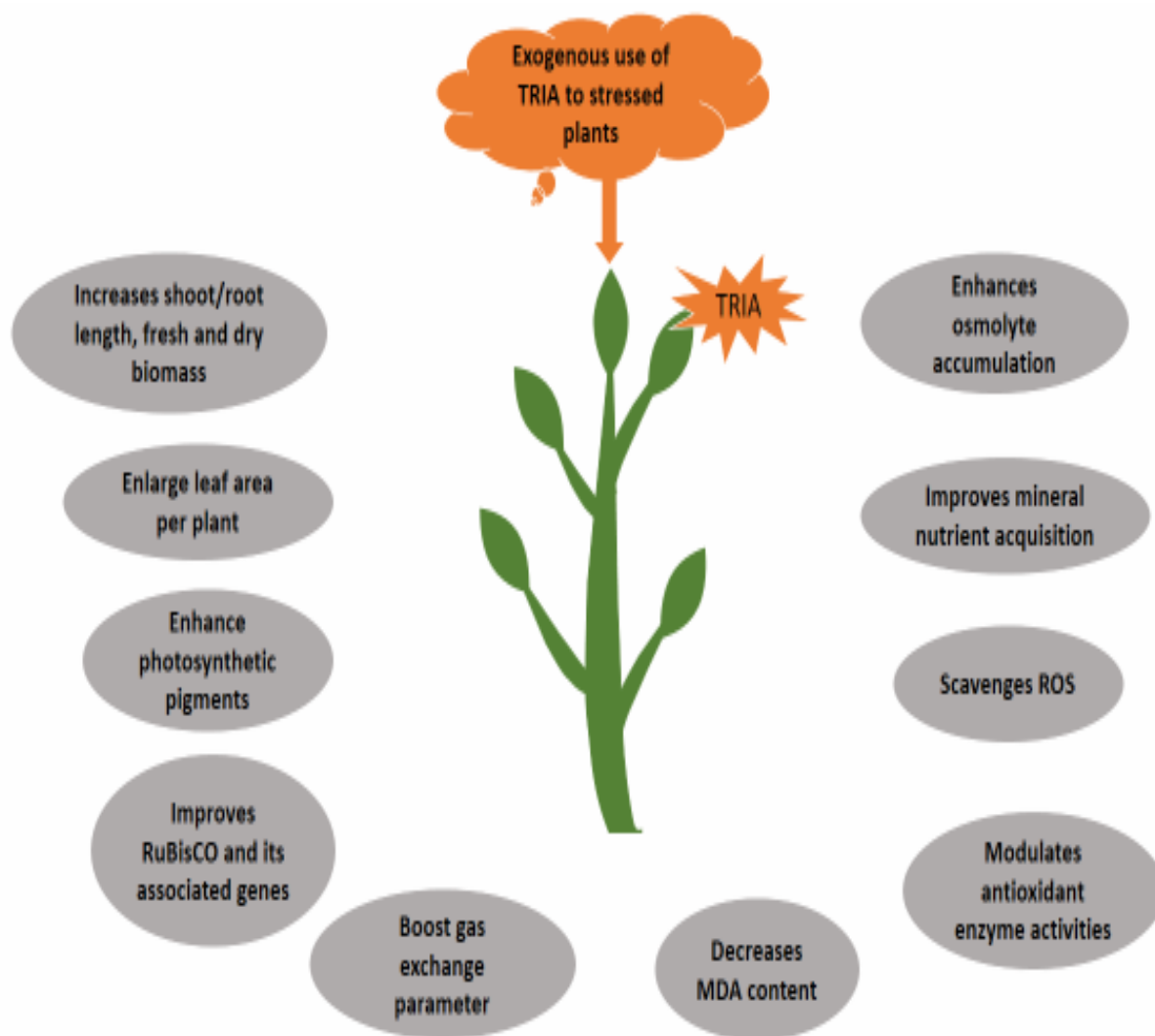


Fig. 2 : Role of TRIA in stressed plants

Triacontanol- regulated genes

There is not much research conducted in terms of regulation of gene expression by TRIA which would aid to better understanding about the molecular response of plants to TRIA. The isolation and identification of TRIA-regulated genes revealed TRIA molecular involvement in plants. Chen (2002) conducted a research on TRIA-regulated genes and reported that, a substantial majority of TRIA-responsive genes were photosynthesis-related genes and remaining were stress-associated genes. TRIA increased the expression of photosynthetic related genes while decreasing the expression of stress related genes. The degree of regulation varied among photosynthetic genes. During study, twelve genes were found to be up-regulated in Northern blots while two were found to be down-regulated. Ten recognised genes encoding eight photosynthetic and photo respiratory protein, a ribosomal protein S9, a Dof zinc finger protein and a rice cDNA with unknown function as well as a novel gene were among the twelve up-regulated genes. The gene encoding an ABA-and stress related protein, as well as wounding-related protein were shown to be down-regulated. In this study, one of the down-regulated clones was found to be a gene for the ABA-induced protein OsAr1. Exogenous ABA, salt stress, and mannitol stress have all been shown to increase OsAr1 transcript in the shoot (Vaidynathan *et al.*, 1999). A gene for

wounding-inducible protein WIP1 was down-regulating gene (Rohrmeier and Lehle, 1993).

Cross talk of Triacontanol with other plant growth regulator

Plant growth regulator are a class of chemical compound found in nature that regulate physiological process even at low concentrations. Growth, differentiation and development are the key process that are influenced. Other processes such as stomatal movement may also be influenced as well. Auxin is the first identified plant hormone and other avenues of research led to the discovery of the following hormones: Gibberellins (GA) were discovered as a result of plant pathogenesis; attempt to cultivate tissues resulted in the production of Cytokinins (CK); Abscisic acid (ABA) was created by controlling abscission and dormancy while ethylene was created by the impacts of illuminating gas and smoke. Other compounds such as brassinosteroids, tuberonic acid, jasmonates, salicylic acid and peptides have recently been added to the list of plant hormones (Davies, 2010). Auxin, gibberellins, brassinosteroids and cytokinins are all considered fundamental for formation of mutant phenotypes in which biosynthesis of hormone or perception is affected. Cytokinins direct cell multiplication while gibberellins advance cell prolongation and auxin are engaged with both processes. Besides brassinosteroids are

fundamental for cell extension, however may potentially be involved in cell division (Hardtke *et al.*, 2007). New hormones and plant growth regulators being discovered and their mode of action and metabolic interrelationship are being studied through research. Among these is Triacontanol (TRIA), a growth regulator that was identified in natural waxes a few decades ago has been lately employed for commercial applications. Even at very low foliar concentrations, it can have a stimulating effect (Khandaker *et al.*, 2013). Because TRIA is a secondary molecule in plant growth, it is not considered a plant hormone. Other growth regulators however, do not have the same effect on plant growth and yield as TRIA according to several research (Naeem *et al.*, 2012). According to studies TRIA, along with other plant hormones, has been shown to regulate a variety of metabolic processes in agricultural plants under both normal and stressed condition. TRIA crosstalk with other plant hormones is poorly documented in the literature. It has shown synergistic as well as antagonistic outcomes with different plant hormone. When TRIA and chloromequat chloride (CCC) were administered to *Artemisia annua* L. seedlings, they had antagonistic influence on endogenous hormone level (Shukla *et al.*, 1992). TRIA showed an additive effect on growth and essential oil production in *Thymus mastichina* L. when combined with benzyladenine (BA) or benzyl amino purine (BAP) and indole-3-butyric acid (Fraternale *et al.*, 2003). In *Solanum lycopersicum*, TRIA alone or in conjunction with potassium improved plant height leaf area and fresh and dry weight. The use of foliar TRIA, basal potassium and potassium-TRIA combined treatments all enhanced the leaf nitrogen, phosphorous and potassium content and also considerably improved the weight per fruit, fruit output per plant and number of fruits per plant (Khan *et al.*, 2009). According to findings of study on *Pisum sativum*, the TRIA on its own has no influence on the growth and yield but have shown notable effects only when paired with other plant growth regulators as auxin, gibberellins and cytokinins. The application of TRIA, gibberellins, cytokinin and auxin resulted in the highest green pod yields which is followed by the application of TRIA, cytokinin and auxin (Segura and Joaquin, 2021). In *Artemisia annua* L., a combined foliar application of TRIA + GA₃ (TRIA 1.5 mg l⁻¹ + GA₃ 75 mg l⁻¹) enhanced the biomass, artemisinin content and overall crop production (Aftab *et al.*, 2010). When the result was compared to the control, the exogenous use of salicylic acid and Triacontanol has a significant impact on different growth features, fruiting and yield of strawberry, however for all the examined parameters the interaction of these two growth regulators were non-significant (Baba *et al.*, 2017). The foliar application of 10⁻⁶ concentration of GA₃ + TRIA significantly improves the development, yield, morphine content and biochemical properties in *Papaversomniferum* L. (Khan *et al.*, 2006). Gatica *et al.* (2008) discovered that indole acetic acid (IAA) and BAP have a similar effect on somatic embryogenesis. Further, according to Karam *et al.* (2017), NO and TRIA have a mutually synergistic impact in mitigating arsenic-induced damage in coriander. According to studies, TRIA and JA worked in an antagonistic manner at the biophysical level (in model membrane or at the organism level) (Swamy *et al.*, 2009). Similarly TRIA and JA have a negative influence on in vitro rhizogenesis of tomato tissues. TRIA also boosted growth and development by causing the production of additional growth promoting compounds such as IAA, GA,

UDP-N-acetyl glucoamine, serotonin, gallate, melatonin and trigonelline (Soundararajan *et al.*, 2018).

Conclusion

Abiotic stress is a serious agricultural issue that affects plant physiology and biochemistry by causing osmotic stress, ionic imbalance, oxidative stress, membrane disorganisation and the production of ROS. As a result, exogenous administration of PGRs is one of the key strategies now being used to improve the resistance of plants. TRIA is a powerful PGR that can successfully modify a variety of plant physio-biochemical processes, including growth, photosynthesis and productivity in a variety of crop. The substantial accumulation of shoot and root K⁺ and Ca²⁺ content and low accumulation of Na⁺ and Cl⁻ content could explain the TRIA-induced increase in plant biomass. According to above-mentioned literature, TRIA opens up new techniques for plant resilience to numerous environmental stimuli because it has the ability to reduce stress-induced toxicity by modifying stress-induced changes in morpho-physiological, metabolic and developmental processes in various economically important crops. However, study on its production, method of action and receptors involved in signalling while regulating numerous development and metabolic processes in terms of regulation of gene expression in agricultural plant is required.

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