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Review paper

Physio-biochemical and molecular perspectives of TRIA-mediated growth responses in plants

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Triacontanol (TRIA) is a pivotal endogenous plant growth regulator with effective metabolic activator found in plant epicuticular waxes and in beewaxes as the palmitate ester. It is a non-toxic, pollution-free, low-cost, high-efficiency, broad-spectrum plant growth regulator. It was found after a series of experiment that TRIA plays a significant role in promoting the growth and yields of corn, rice, wheat, tomato, carrot, cucumber, lettuce, soybean, potato, peanuts, chilli pepper, cotton and ornamental plants like rose etc. TRIA causes rapid responses in enhancing growth of the crop and the growth in rice, tomato and maize about 20% is enhanced by this treatment. The response is very rapid, an increased growth within 10 minutes. It is very much insoluble in water and is applied as foliage on the leaf at a very low concentration i.e.0.01mg/litre. However, further investigations are necessary to elucidate the possible role of TRIA on plant growth regulation, physio-biochemical as well as molecular activities and secondary metabolite biosynthesis in plants subjected to various biotic and abiotic stresses. The present review covers the pivotal role of TRIA in plant growth regulation, their mode of action and significance in improving the plant productivity and quality of both agricultural as well horticultural crops.

Key words: *Tricontanol (TRIA), growth regulation, yield, biochemical and molecular responses*

INTRODUCTION

TRIA, a metabolite act as a secondary messenger, improves plant growth, as well as the yield and quality characteristics of various crops (Ries, 1985), and it increases the rate of several biochemical and physiological processes (Ries and Houtz, 1983; Ries, 1991; Naeem et al., 2009, 2010). For example, triacontanol (TRIA) increases the contents of total chlorophyll (Chl), Chla and Chl b by 25.1, 26.1, and 22.4%, respectively, after 4 h compared with the contents of control rice seedlings (Chen et al., 2003). It is a totally nontoxic, plant growth bio-regulator without any residual effect (Samui and Roy, 2007). TRIA is active at very low concentration on the cell membranes and acts in combination with other long chain alcohols to regulate the formation of TRIM, a putative secondary messenger(s) of TRIA and TRIM move rapidly throughout the plant resulting in dry matter increase (Ries and Wert, 1988). It produces stronger seedlings with better root system and finally developed into vigorous plants which produces better yield (Ahmed, 1990; De and Haquue, 1996). The most profound effects of TRIA are that it increases growth, biomass, and photosynthetic activity, as well as the free amino acid, reducing sugar, and soluble protein content (Muthuchelian et al., 1995). Furthermore, the foliar application of TRIA enhances crop production under conditions of abiotic stress, including water stress (Muthuchelian et al., 1997), salt stress (Perveen et al., 2013) and acidic mists (Muthuchelian et al., 2003).TRIA can increase the activities of nitrate reductase, amylase, peroxidase enzyme (Li et al., 2007) and promote carbon-nitrogen metabolism and increase the carbon-nitrogen ratio and the storage and accumulation of ATP to increase production (Wert, et al., 1977). Exogenous application of TRIA causes delay of senescence of many crops and improves freshness of the several vegetables and fruit crops.

Chemical properties of Tricontanol (TRIA)

TRIA is 30-C saturated long-chain primary fatty alcohol that is triacontane in which one of the terminal methyl hydrogen is replaced by a hydroxy group. It's general formula is $C_{30}H_{61}OH$ and molecular mass 438.81 g/mol, having density 0.777 g/ml at 95 °C and melting point is 87 °C (189 °F; 360 K). It was first isolated from shoots of alfalfa (*Medicago sativa* L.) (Ries et al., 1977). The chemical name is triacontanol-1 or n-triacontanol, referred to as triacontanol (TA or TRIA). It is also known as benzyl alcohol or melissyl alcohol or myricyl alcohol.

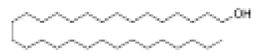

Figure 1. Structural formula of Triacontanol (TRIA)
[Source: https://en.wikipedia.org/wiki/1-Triacontanol. Last accessed on 19.09.2021

Function of TRIA in physiological growth regulation

Many researchers have been reported the TRIA-mediated growth responses in plant such as growth and yield

Table 1. Tricontanol (TRIA) mediated physiological growth responses in some crop species

Name of the crop	Physiological growth responses	Reference
Tomato (*Solanum lycopersicum* L.)	Plant height, number of leaves and branches, fresh and dry weights of the plant.	Khan et al., 2009
Coriander *(Coriandrum sativum* L.)	Shoot and root lengths, plant fresh and dry weights.	Idrees et al., 2010
Sadabahar (*Catharanthus roseus* L.)	Number of leaves per plant, average leaf-area and fresh and dry weights of plants, Net photosynthetic rate and stomatal conductance.	Naeem et al., 2019
Coffee senna *(Senna occidentalis* L.)	Fresh and dry weights of the plant, transpiration rate, Photosynthetic rate (P_{N}), stomatal conductance (gs).	Naeem et al., 2010
Opium poppy *(Papaver somniferum* L.)	Plant height, dry weight and number of branches.	Khan et al., 2007
Rice (*Oryza sativa* L.)	Leaf area index, Crop growth rate.	Pal et al., 2009
Rice (Machine-Transplanted)	Number of green leaves, stem diameter, dry weight.	Xiaochun et al., 2016
Sweet basil *(Ocimum basilicum* L.)	Shoot and root lengths, number of spikes per plant, total leaf area, plant fresh and dry weights.	Hashmi et al., 2011
Hyacinth bean *(Lablab purpureus* L.)	Plant fresh and dry weights, leaf-area per plant, number and dry weights of nodules, Photosynthetic rate (P_{N}), stomatal conductance (gs) and transpiration rate.	Naeem and Khan, 2005; Naeem et al. (2009)
Japanese mint *(Mentha arvensis* L.)	Plant height, leaf-area, leaf-yield, and plant fresh and dry weights.	Naeem et al., 2011
Artemisia *(Artemisia annua* L.)	Shoot and root lengths, plant fresh and dry weights, transpiration rate.	Aftab et al., 2010
Coriander (*Coriandrum sativum* L.)	Plant height at harvest, number of umbels per plant.	Parmar et. al., 2018
Bougainvillea (*Bougainvillea glabra* var. Elizabeth Angus)	Net photosynthetic rate, dry matter production and ethylene production rate, leaf area, shoot length, stomatal conductance.	Khandaker et al., 2013
Coriander *(Coriandrum sativum* L.)	Shoot fresh/dry weight.	Karam et al., 2017
Cocoa (*Theobroma cacao* L.)	Plant length and the leaf size, leaf number and stem diameter.	Rama et al., 2014
Mangrove *(Rhizophora apiculata*)	Increased root and shoot growth, length of roots, height and the biomass of the plant.	Moorthy and Kathiresan, 1993
Strawberry (Fragaria × ananassa)	Number of flowers and buds, inflorescence length, fruit number, fruit development and fruit ripening-related growth and development.	Pang et al., 2020
Green gram (*Vigna radiata* (L.) Wilczek)	Plant height, root and shoot length and their fresh mass.	Kumaravelu et al., 2000
Canola (*Brassica napus* L.)	Root-shoot fresh and dry weight, shoot length photosynthetic rate, transpiration rate, electron transport rate.	Shahbaz et al., 2013
Wheat (*Triticum aestivum* L.)	Root and shoot dry weight, total leaf area, root and shoot length, total Membrane Permeability (%), Relative Water Potential (%), Osmotic potential, Turgor potential.	Perveen et al., 2012
Okra (*Abelmoschus esculentus* L.)	Number of leaves per plant, number of internodesper plant, fresh and dry weight per plant.	Chowdhury, et al., 2014

Table 2. Tricontanol (TRIA) mediated biochemical growth responses in some crop species

Name of the crop	Biochemical growth responses	References
Tomato (*Solanum lycopersicum* L.)	Total chlorophyll, and β-carotenoids content, free amino acids, reducing sugar and soluble protein, N, P, and K contents in the leaves, lipid peroxidation and acting as an antioxidant compound.	Khan et al., 2009
Coffee senna *(Senna occidentalis* L.)	Total chlorophyll and carotenoid content, nitrate reductase and carbonic anhydrase activities, N, P, K and Ca content in leaf.	Naeem et al., 2010
Coriander *(Coriandrum sativum* L.)	Phenolic compounds and anthocyanin, carotenoid, ascorbate, dehydroascorbate (DHA) and GSH content, protein content, Phenylalanine ammonia lyase enzyme (PAL) assay, Electrolyte leakage, MDA (malondialdehyde), lipid peroxidation and H_2O_2 assay.	Karam et al., 2017
Bougainvillea (*Bougainvillea glabra* var. Elizabeth Angus)	Leaf sugar content, soluble protein, TSS, and antioxidant activities, mineral content (N, P, and K), Chlorophyll a, b and total chlorophyll, sucrose phosphate synthase (SPS) activity.	Khandaker et al., 2013
Japanese mint *(Mentha arvensis* L.)	Total chlorophyll and carotenoid contents, activities of nitrate reductase and carbonic anhydrase, N, P, and K contents in leaf, total phenol.	Naeem et al., 2011
Hyacinth bean *(Lablab purpureus* L.)	Total chlorophyll and carotenoid content, *nitrate reductase and carbonic anhydrase* activities, N,P, K and Ca content in leaf, nodule-N and leghemoglobin contents.	Naeem and Khan, 2005; Naeem et al., 2009
Artemisia *(Artemisia annua* L.)	Total chlorophyll and carotenoid content, *nitrate reductase*and *carbonic anhydrase* activities, N, P and K content in leaf	Aftab et al., 2010
Coriander *(Coriandrum sativum* L.)	Total chlorophyll and carotenoids content, *nitrate reductase*and *carbonic anhydrase* activities, N, P and K content in leaf	Idrees et al., 2010
Opium poppy *(Papaver somniferum* L.)	Chl *a*, Chl *b* and total Chlorophyll.	Khan et al., 2007
Sweet basil *(Ocimum basilicum* L.)	Chl *a,* Chl *b*, total Chl, and carotenoid contents, activities of *nitrate reductase* and *carbonic anhydrase*, N,P, and K contents in leaf.	Hashmi et al., 2011
Rice (Machine-Transplanted)	Total chlorophyll content, activities of APX, CAT, POD, and GR, sucrose content, ROS production and membrane damage.	Xiaochun et al., 2016
Sadabahar (*Catharanthus roseus* L.)	Total chlorophyll and total carotenoids contents, activities of nitrate reductase, carbonic anhydrase and tryptophan decarboxylase.	Naeem et al., 2019
Rhizophora apiculata (Mangrove)	Reduction of *nitrate reductase* as well as increase amount of chlorophylls in the photosystem I and II.	Moorthy and Kathiresan, 1993
Coriander (*Coriamdrum sativum* L.)	Hydrogen peroxide content and levels of lipid peroxidation in terms of malondialdehyde content, antioxidant enzymes activities such as *superoxide dismutase, catalase, ascorbate peroxidase*and *peroxidase*.	Karam and Keramat, 2017
Ground nut (*Arachis hypogaea* L.)	Total chlorophyll content, total soluble sugars, total soluble proteins and *ascorbate peroxidase, catalase, Peroxidase a*nd *polyphenol oxidase* activities, lipid peroxidation, Malondialdehyde (MDA) content.	Verma et al., 2011
Strawberry (Fragaria × ananassa)	Chlorophyll content, Vit c, TSS, ABA, IAA, Ethylene content, protein content, fruit sugar content and anthocyanin content, flavonoid synthesis, SOD *(Superoxide dismutase),* POD *(Peroxidase), CAT (Catalase),* PPO *(Polyphenol oxidase),* MDA (malondialdehyde) and Proline content.	Pang et al., 2020
Green gram (*Vigna radiata* (L.) Wilczek)	Contents of chlorophylls, saccharides, starch, soluble proteins, amino acid and total phenols, leaf nitrate content, and *nitrate reductase* activity.	Kumaravelu et al., 2000
Canola (*Brassica napus* L.)	Ratio of chlorophyll a/b, free proline and glycine betaine contents, shoot and root K contents.	Shahbaz et al., 2013
Wheat (*Triticum aestivum* L.)	Total phenolics, amino acids, leaf free prolineand glycinebetaine content.	Perveen et al., 2012

improvement, photosynthetic activities, transpiration, stomatal conductance, water uptake as well as mineral nutrient acquisition, nitrogen-fixation etc., in various agricultural and horticultural crops. It has been reported that exogenous application of TRIA when applied initially, it moves rapidly in plants and directly or indirectly regulates several

Table 3. Tricontanol (TRIA) mediated yield and quality attributing growth responses in some crop species

Name of the crop	Yield attributing growth responses	Quality attributing growth responses	References
Coriander *(Coriandrum sativum* L.)	Number umbels per plant, Fruits per umbel.	Essential oil content	Idrees et al., 2010
Tomato (*Solanum lycopersicum* L.)	Number of fruits per plant, weight per fruit and fruit yield per plant.	Fruit ascorbic acid and lycopene contents.	Khan et al., 2009
Bougainvillea (*Bougainvillea glabra* var. Elizabeth Angus)	Blooming rate, floral buds formation and bract growth, number of flowers/branch.	Flower longevity and quality of flowers, phytochemical levels (Phenol, carotenoids, Flavonoid), flowers fresh weight and leaf drop.	Khandaker et al., 2013
Japanese mint *(Mentha arvensis* L.)	Herbage yield, essential oil yield.	Essential oil content, menthol, L-menthone, isomenthone, and menthylaceteate contents.	Naeem et al., 2011
Hyacinth bean *(Lablab purpureus* L.)	Number of pods per plant, number of seeds per pod, 100-seed weight and seed-yield per plant.	Seed-protein content, total carbohydrate content, and tyrosinase activity.	Naeem and Khan, 2005; Naeem et al., 2009
Opium poppy *(Papaver somniferum* L.)	Number of capsules, seed yield per plant, and crude opium yield per plant.	Morphine content and morphine yield per plant.	Khan et al., 2007
Coffee senna *(Senna occidentalis* L.)	Number of pods per plant, number of seeds per pod, 100-seed weight and seed yield per plant.	Total anthraquinone and sennoside contents and seed-protein content.	Naeem et al., 2010
Sweet basil *(Ocimum basilicum* L.)	Essential oil yield.	Leaf-protein and carbohydrate contents, essential oil content, linalool, methyl eugenol, and eugenol contents.	Hashmi et al., 2011
Coriander (*Coriandrum sativum* L.)	Seed yield, stover yield.	-	Parmar et al., 2018
Rice (*Oryza sativa* L.)	Panicle length, harvest index, number of filled grain/panicle, Straw yield, test weight.	-	Pal et al., 2009
Artemisia *(Artemisia annua* L.)	Artemisinin yield.	Essential oil content, artemisinin content.	Aftab et al., 2010
Rice (Machine-Transplanted)	Number of tillers, grain filling and grain yield per hill at maturity.	-	Xiaochun et al., 2016
Sadabahar (*Catharanthus roseus* L.)	Leaf yield and herbage yield.	Essential oil content.	Naeem et al., 2019
Green gram (*Vigna radiata* (L.) Wilczek)	Early flowering, pod production and retention, number of pods and seeds per plant, seed and pod weight and seed yield.	-	Kumaravelu et al., 2000
Canola (*Brassica napus* L.)	Number of seeds per plant, Yield per plant, 100-Seed weight, number of seeds/plant.	-	Shahbaz et al., 2013
Wheat (*Triticum aestivum* L.)	100-Seed weight, number of grain per plant, number of fertile tillers per plant, grain yield per plant.	-	Perveen et al., 2012
Tomato (*Lycopersicon esculentum* MIill.)	Number of branches per plant, No. of fruits per plant, Average fruit weight, Fruit diameter, early yield per plant Total yield per plant.	-	Dhall and Ahuja, 2004
Okra (*Abelmoschus esculentus* L.)	Days required for 50% flowering, flower buds per plant, number of pods per plant, pod length (cm), pod diameter (cm), yield (t/h).	-	Chowdhury et al., 2014

physiological processes in plants. TRIA also play a significant role in plant metabolism like photosynthetic activities, increases growth of root, shoot and flower production. Several enzymes relating to carbohydrate metabolism increase in activity following TRIA treatment and better plant response have been occurred when foliar applications at warm temperatures. TRIA-mediated increase in dry matter accumulation in plants could persuade the inter-relationship between primary and secondary metabolism that leads to augment the biosynthesis of secondary metabolites having diverse biological functioning. Furthermore, TRIA contributes a significant role in ameliorating the stress-accrued alterations by both biotic as well as abiotic in plants via modulating the activation of the stress tolerance mechanisms. TRIA efficiently reduces the negative effects of salinity stress, and improves the photosynthetic rate, the transpiration rate, and the chlorophyll contents (Perveen et al., 2013). Chen et al., 2003 reported that TRIA affected the photosynthesis by increasing the level and activity of ribulose-1, 5-bisphosphate carboxylase oxygenase (RuBisCO) and by improving the status of photosystems. Ries and Houtz, 1983 suggested for the first time that the growth stimulating effects of TRIA might be due to certain alterations at the cell membrane level and net photosynthesis was stimulated to a greater extent in isolated protoplast preparations, supporting the suggestion that the putative initial site of TRIA action could be localized at the level of plasma membranes. Some of the possible TRIA-mediated physiological growth responses in various plant species are briefly discussed in Table 1.

Function of TRIA in biochemical growth regulation

It has also been suggested that TRIA increased free amino acids, reducing sugars, and soluble protein of rice (*Oryza sativa* L.) and maize (*Zea mays* L.) within 5 minutes. Exogenous application of TRIA promotes the protein synthesis and enzymes activities (*peroxidase, nitrate reductase, carbonic anhydrase*) and alters the contents of free amino acids, reducing sugars, soluble protein and active constituents of essential oil. There are strong evidences established from various experiments that exogenous application of TRIA mediated several physio-biochemical attributes especially oxidative stress, antioxidant systems, compatible solutes and its mode of action in plants under salinity conditions. Foliar application of TRIA, at a concentration of 0.5 mg dm^3, significantly promoted the contents of saccharides, starch, soluble proteins, amino acids, and phenols in green gram (Kumaravelu et al., 2000). TRIA application also improved the contents of soluble protein, starch, sugars, and free amino acids in the leaves of *Oryza sativa* and *Zea mays* (Kim et al., 1989). Some of the possible TRIA-mediated biochemical growth responses in various plant species are briefly discussed in Table 2. Since MaYMV is a newly emerged disease, despite its potential impact, much is not known about its epidemiology and control measures. Adequate field and laboratory research-based information will be required including more assessments of alternative hosts that the virus overwintering, insect vectors that transmitting the virus from plant to plant and associated factors that contribute to MaYMV disease epidemics including cropping system, cultural practices and environmental condition. Plant virus diseases including MaYMV are intrinsically difficult to manage directly by use of chemical pesticides; however, integrated management methods which include cultural practices such as removal of infection sources, field sanitation, removal of alternative hosts, use of healthy seed (virus-free seeds); chemical pesticides to control insect vectors indirectly through seed treatment and foliar spray are the most possible management measures of plant viral diseases. For such an approach to succeed, the epidemiology and associated factors influencing the geographical spread of the disease should have to be studied.

Function of TRIA in yield and quality attributing traits regulation

Average yield and quality attributing traits are enhanced by TRIA application at a very low concentration in several vegetable crops (tomato, eggplant, cabbage, chilli, cucumber, potato and bean etc) have already been reported. TRIA can promote the plant growth in both laboratories as well as in greenhouse conditions; however, results obtained in the field study were not encouraging (Ries and Houtz, 1983). TRIA-mediated improvement in grain weight, test weight as well as harvest index and ultimately quality of some cereal crops like wheat, rice etc. Foliar spray of 0.5 mg dm^3 of TRIA significantly promoted the onset of flowering and increased the pod production pod number, seed number, mass per plant, and mass per pod in green gram plants exposed to TRIA at 0.5 mg dm^3 (Kumaravelu et al., 2000). Eriksen et al., 1982 noticed a significant increase in total as well as per plant yield of tomato, when TRIA was applied as foliar sprays; but when TRIA was added to the growth medium, only a temporary increase in yield and number of fruits was observed. Idrees et al., 2010 were recorded the highest values regarding the number of umbels, fruits per umbel, 100 seed weight, and

Table 4. Tricontanol (TRIA) mediated molecular responses in some crop species

Name of the crop	Molecular growth responses	References
Variety of plant species like rice, wheat, corn, maize, cucumber etc.	Increases cell number and growth *in vitro* culture, increase protein formation and rapid cell division.	Roger et al., 1978
Coffea arabica L. and *Coffea canephora* P. ex Fr.	Induced embryo formation (somatic embryogenesis) from *in vitro* stem segment callus tissues along with multiplication of primary embryos into secondary embryos.	Ciridhar et al., 2004
Groundnut (*Arachis hypogaea* L.)	*In vitro* shoot multiplication potentiality (multiple shoots, auxiliary branches and shoot buds) per explants as well as *in vitro* shoot establishment.	Verma et al., 2011
Strawberry (Fragaria × ananassa)	Transcriptome analysis, differentially expressed genes (DEGs) genes of up- and down-regulating enzyme related to fruit softening and coloring and Relative gene expression, DNA metabolic processes.	Pang et al., 2020
Tufted bamboo (*Dendrocalamus strictus*)	*In vitro* shoot multiplication rate, adventitious rhizogenesis (%).	Mishra et al., 2001

seed yield, when the TRIA was applied together with GA3 to coriander crop. Some of the possible TRIA-mediated yield and quality attributing growth responses in various plant species are briefly discussed in Table 3.

Function of TRIA in molecular growth regulation

TRIA exploits the molecular potentiality of the crop to a large extent by enhancing the physio-biochemical efficiency of the plant cells.TRIA enhances the elongation of multiple shoots and micro-propagated plantlets in ornamentals, herbaceous and other woody plants. Hangarter et al., 1978 demonstrated the favorable effect of TRIA in an in vitro study on *Nicotiana tabacum, L. esculentum, Solanum tuberosum, Phaseolus vulgaris*, and a barley hybrid (*Hordeum vulgare*x *H. jubatum*). TRIA has a positive effect on in vitro shoot multiplication, biosynthesis of secondary metabolites. Isolation and characterization of TRIA-regulated genes was the first step toward understanding the TRIA action, since it gave clues to the biochemical pathways and physiological processes that regulate, and reveal the components involved in TRIA signaling (Chen et al., 2002). Chen et al., 2002 reported that higher rbcS gene levels were associated with improved photosynthetic activity in TRIA-treated plants. Recently, compiled microarray data bases provide information about the expression profile of any gene that focuses on hormone-related gene expression. Microarray data suggest that almost all hormone-responsive signal transduction pathways appear to interact with each other during growth and development. Some of the possible TRIA-mediated molecular growth responses in various plant species are briefly discussed in Table 4.

CONCLUSION

Foliar and soil application of triacontanol is very effective in improving plant response to various physio-biochemical, yield and quality attributing and molecular growth regulation. A conclusion may be drawn from the overall discussion of the above review that exogenous traicontanol application at nanomolar concentrations, improves the growth and productivity of many crops of agricultural, horticultural and medicinal and aromatic plants, woody plants and trees etc. TRIA modulates the enhancement of dry matter leads to increase in secondary metabolites including essential oils, crude substances etc and active photochemical of medicinal and aromatic plants. However, further studies are required to elucidate the possible role of triacontanol on the up-regulation of plant growth and development at physiological, biochemical and molecular level. Further understanding of molecular mechanisms of growth regulator biosynthesis, perception and response has to be improved considerably. Integrated approaches for future investigations to be undertaken for successful implementation of TRIA in plant growth regulation.

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