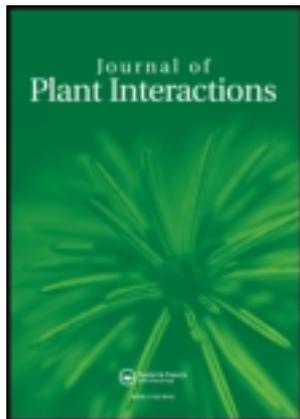


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Triacontanol: a potent plant growth regulator in agriculture

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REVIEW ARTICLE

Triacontanol: a potent plant growth regulator in agriculture

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Triacontanol (TRIA) is a natural plant growth regulator found in epicuticular waxes. It is used to enhance the crop production in millions of hectares, particularly in Asia. Quite a number of researchers have reported the TRIA-mediated improvement in growth, yield, photosynthesis, protein synthesis, uptake of water and nutrients, nitrogen-fixation, enzymes activities and contents of free amino acids, reducing sugars, soluble protein, and active constituents of essential oil in various crops. Expectedly, TRIA enhances the physiological efficiency of the cells and, thus, exploits the genetic potential of plant to a large extent. In fact, TRIA increased free amino acids, reducing sugars, and soluble protein of rice (*Oryza sativa* L.) and maize (*Zea mays* L.) within 5 min. TRIA elicited the appearance of L(+)-adenosine within 1 min in the roots of plants, the shoots of which were sprayed with nanomolar concentrations of TRIA. TRIA and octacosanol (OCTA), the primary alcohols, are ubiquitous in the environment. OCTA was reported to inhibit the activity of TRIA in the seedlings of rice (*Oryza sativa* L.) at equimolar concentrations; and both TRIA and OCTA elicited a second messenger, known as OCTAM and triacontanol second messenger (TRIM), respectively. TRIA rapidly increases the ratio of L(+)- to D(-)-adenosine, probably at the tonoplast. However, it is to be resolved as to how TRIA elicits L(+)-adenosine and what is the source of L(+)-adenosine in plants. Based on known metabolic processes, *de novo* synthesis of L(+)-adenosine is unlikely, because of the rapidity of the response. TRIA-mediated increase in dry matter production could influence the inter-relationship between primary and secondary metabolism, leading to increased biosynthesis of secondary products. Various studies present strong evidences that application of TRIA applied either to the root medium or to leaves enhanced the growth and yield of vegetables and other crops, including agronomic and horticultural crops as well as medicinal and aromatic crop plants under normal and adverse conditions. However, further investigations are required to elucidate the possible role of TRIA on plant growth regulation, physiological activities and secondary metabolite biosynthesis regarding medicinal and aromatic plants subjected to abiotic stress. The present review covers the pivotal role of TRIA in plant growth and development, its mode of action and its significance in improving the crop productivity and quality of agricultural crops.

Keywords: medicinal and aromatic crops; plant growth; crop yield; bioactive constituents; triacontanol

Introduction

The plant growth regulatory activity of triacontanol (TRIA) was first discovered by Ries et al. (1977) in alfalfa (*Medicago sativa* L.). According to Mandava (1979), TRIA is a secondary plant growth substance and cannot be considered as a phytohormone. Such types of growth regulators enhance the physiological efficiency of the cells and, thus, exploit the plant genetic potential to a large extent. Earlier studies have given sound evidences regarding distribution of TRIA in the epicuticular waxes in widely diverse genera, such as California Croton (*Croton californicus*), blueberry (*Vaccinium ashei*), Brazilian palm (*Copernicia cerifera*), runner bean (*Phaseolus multiflorus*), white clover (*Trifolium repens*), alfalfa (*Medicago sativa*), and in physic nut (*Jatropha curcas*) (Hufford and Oguntimein 1978; Luzbetak et al. 1978; Freeman et al. 1979; Lee et al. 1979). TRIA is considered to be the only primary alcohol (Figure 1) found in the wax of the rice leaves (Uchiyama and

Ogasawara 1981). The callus tissue contained a homologous series of alkanes, namely, n-C₂₃H₄₈, n-C₂₅H₅₂, and n-C₂₇H₅₆ compared to n-C₂₇H₅₆, n-C₂₉H₆₀, and n-C₃₁H₆₄ found in the rice leaves. This observation might explain as to why TRIA could enhance callus growth in cultures of different species (Hangarter et al. 1978).

Many researchers have reported the positive role of TRIA in enhancing growth, yield, photosynthesis, nitrogen fixation, enzymes activities, free amino acids, reducing sugars, and soluble protein of plants (Ries 1991; Ries et al. 1993; Nagoshi and Kawashima 1996; Borowski et al. 2000; Naeem et al. 2009; Aftab et al. 2010; Idrees et al. 2010; Naeem et al. 2010, Naeem et al. 2011). Muthuchelian et al. (1997, 2003) investigated the significant effect of TRIA on acid mist-treated *Erythrina variegata* L. seedlings with particular emphasis on growth, photosynthetic pigments, ribulose-1,5-bisphosphate (RuBPC), and photosynthetic activity. Kumaravelu et al. (2000)

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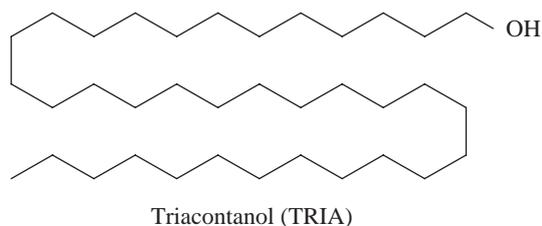


Figure 1. Structural formula of triacontanol (TRIA).

reported the ameliorating effect of TRIA applied at 0.5 mg dm^{-3} on growth and yield attributes, photosynthetic pigments, nitrate reductase (NR) activity and contents of nitrate, protein, starch, amino acids, and total phenols in green gram (*Vigna radiata* L.). TRIA application increased the plant dry weight, protein, and chlorophyll contents and net photosynthetic rate in rice (*Oryza sativa* L.) (Chen et al. 2002). Similarly, exogenous application of TRIA showed positive effect on growth, chlorophyll content, efficiency of photosystem-II (PS-II) and gas exchange characteristics in the seedlings of rice (Muthuchelian et al. 1995; Kumaravelu et al. 2000), maize (Ries 1991), and wheat (Ries 1991). Increase in plant growth could mainly be due to an abrupt TRIA-induced increase in photosynthesis as TRIA has been reported to be involved in the up-regulation of many genes involved in the photosynthetic process (Chen et al. 2002, 2003).

The present review emphasizes the role of TRIA in enhancing growth, yield, and quality of crop plants as well as in improving physiological and biochemical attributes and active constituents of medicinal and aromatic plants under normal and stressful conditions.

Physiological activity of TRIA at low concentrations

According to Ries and Houtz (1983), the low concentrations of TRIA might be biologically active because of the sensitivity of the plants to its extremely low doses. The physiological activity of TRIA in maize (*Zea mays*) and rice (*Oryza sativa*) seedlings has been improved consistently by increasing the purity of TRIA to 99.7% (Ries and Wert 1982). As per earlier studies of Ries and Wert (1977), TRIA is active at concentrations as low as $10 \mu\text{g L}^{-1}$ (2.3×10^{-8} M) when applied either to shoots or roots of a crop. Since TRIA is extremely insoluble in water (2×10^{-16} M or 9×10^{-14} g L⁻¹), the solution of TRIA has been formulated as a stable colloidal dispersion of fine crystalline particles in water (Laughlin et al. 1983). This formulation indicates accurate quantification of the application rate and a smooth dose-response curve for dry weight gain of corn as a result of TRIA application. The TRIA, applied at $10 \mu\text{g L}^{-1}$, increased the dry weight and leaf area of rice plants in nutrient cultures (Ries and Wert 1977). Similarly, Hangarter et al. (1978) found that TRIA, isolated from alfalfa or the one synthesized artificially (Ana-

labs), were active at extremely low concentrations (23 nM). TRIA also promoted growth of tobacco callus at concentrations as low as $0.01 \mu\text{g}$ per Petri dish when applied to either roots or shoots (Ries and Wert 1977). As suggested by Jones et al. (1979) and Ries and Houtz (1983), there are possibilities that impurities in TRIA might inhibit the physiological effect of TRIA at higher levels. Application of even pico mole quantities of (+)-adenosine (a precursor in TRIA biosynthesis and a plant growth-promoting second messenger) to the foliage of tomato (*Lycopersicon esculentum* Mill.), maize (*Zea mays* L.), and cucumber (*Cucumis sativa* L.) increased the concentrations of Ca^{2+} , Mg^{2+} , and K^{+} by 20–60% in the exudates obtained from the stumps of excised plants within 5 seconds of TRIA application (Ries et al. 1993).

Mode of TRIA action

Many investigators have explored the effects of TRIA on several basic metabolic processes including photosynthesis, nutrient uptake, and enzyme activities. Several efforts have been made to elucidate the mechanism of TRIA action (Ries and Houtz 1983; Ries 1991; Ries et al. 1993). Assumption of a cascade effect led to the identification of 9-β-L (+)-adenosine as a second messenger of TRIA (Ries 1991; Ries et al. 1993). TRIA rapidly elicits the second messenger (TRIM) in rice (*Oryza sativa* L.), which at nanomolar concentrations causes the plants to respond in a manner similar to TRIA (Ries 1991). TRIM has been identified as 9-β-L (+)-adenosine (9H-purin-6-amine, 9-β-L-ribofuranosyl) as depicted in Figure 2. TRIA enhanced the formation or release of L(+)-adenosine in the root tissue of rice seedlings within one min of TRIA application to the shoots, which might have elucidated the first step in the mode of TRIA action (Ries et al. 1990). It is already reported that TRIA rapidly increases the ratio of l(+)-adenosine to d(-)-adenosine, probably at the tonoplast (Ries 1991). There remains the problem of how TRIA elicits l(+)-adenosine and what is the source of l(+)-adenosine in plants. Based on known metabolic processes, *de novo* synthesis of l(+)-adenosine is unlikely, because of the rapidity of the response. The most probable source of adenosine is AMP derived from ADP and ATP (Olsson and Pearson 1990). In TRIA treated plants,

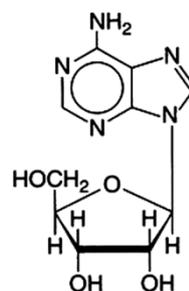


Figure 2. Structural formula of adenosine.

the nonracemic L(-)-adenosine (-11%) is released to affect plant processes (Ries 1991).

Ries et al. (1993) in their study, noticed that more information is needed regarding protocols that will ensure consistent results with both TRIA and L(+)-adenosine in growth chamber, greenhouse, and field studies. However, the strong evidence is overwhelming that TRIA applied at nanomolar concentrations might increase the yield or improve the quality of various plant species. TRIA increased the dry weight as well as content of free amino acids, reducing sugars, and soluble protein of rice (*Oryza sativa* L.) and maize (*Zea mays* L.) plants within 5 min (Ries 1991). TRIA also elicited the appearance of L(+)-adenosine in the roots of plants whose shoots were sprayed with its nanomolar concentrations within 1 min (Ries and Wert 1988). This was the first evidence that L(+)-adenosine occurred in nature. Synthetic L(+)-adenosine increased the rate of growth of rice seedlings, as measured by total dry weight gain of more than 50% within 24 h at foliar application rate of 0.01–100.0 $\mu\text{g L}^{-1}$ (3.7×10^{-11} to 10^{-7} M); whereas, D(-)-adenosine did not affect the plant growth at all (Ries 1991). In relation to the mode of action of exogenously applied TRIA and L(+)-adenosine, it is postulated that both of the compounds move rapidly through the leaf cuticle to the plasma membrane of epidermal cells of tomato (*Lycopersicon esculentum* Mill.), maize (*Zea mays* L.), and cucumber (*Cucumis sativa* L.). TRIA then elicits the formation of l(+)-adenosine. The study suggested that L(+)-adenosine triggered a rapidly transmitted signal within whole plants that resulted in a transient increase in apoplastic ion concentration within stem tissue (Ries et al. 1993).

Thus, it is also a significant challenge to discover as to how both TRIA and L(+)-adenosine enhance plant metabolism and how TRIA elicits L(+)-adenosine. Further, identification of octacosanol second messenger (OCTAM) and the determination of how it inhibits the activity of TRIA may lead to discovery of the site of TRIA and/or L(+)-adenosine action (Ries 1991; Ries et al. 1993).

TRIA elicits L(+)-adenosine

Adenosine (abbreviated as TRIM) was found to be a naturally occurring plant growth substance elicited by TRIA (Ries et al. 1990). The adenosine from TRIA-treated plants was identical to the adenosine obtained from control plants as determined by melting point, IR and MS, and from proton and carbon NMR analysis (Ries et al. 1990). However, only the pure adenosine obtained from TRIA-treated plants could stimulate the plant growth. Other forms of adenosine, including d(-)-adenosine, did not stimulate growth at similar concentrations. Thus, it was postulated that the adenosine from TRIA-treated plants was L(+)-adenosine, the enantiomer of d(-)-adenosine. In addition, TRIA caused simultaneous increases in

soluble proteins, reducing sugars, and free amino acids (Ries 1985, 1991). Similar increases in these metabolic constituents occurred in the cell-free extracts of maize leaves treated with TRIA, although the response was less rapid (Ries 1985). The rapid increase in total nitrogen by TRIA treatment is also difficult to explain. This increase, whether expressed in total N or as soluble N and insoluble N, was magnified when there was an accompanying increase in dry weight of TRIA treated plants (Knowles and Ries 1981). A hypothesis is that plant metabolism is altered by TRIA or its second messenger L(+)-adenosine, leading to expected compositional or chemical changes (Diehi 1974; Knowles and Ries 1981). The elicitation of the second messenger of TRIA (L(+)-adenosine) in the roots within 1 min after TRIA application to the foliage is also difficult to explain based on our current knowledge of translocation of substances and enzyme kinetics. The L(+)-adenosine had the same effect on plants as TRIA, and apparently it did not elicit any other chemical compound which stimulated the plant growth (Ries et al. 1990, 1993).

Response of plants to TRIA

Growth attributes

Various studies provided strong evidence that application of TRIA, applied either through the root medium or to the leaves, enhanced the growth and yield of vegetables and cereal crops (Ries et al. 1977, 1978). TRIA has shown to increase the growth and/or yield of most of the major annual vegetables, agronomic and horticultural crops as well as forest species (Ries 1985, 1991; Kawashima et al. 1987; Kapitsimadi and Vioryl 1995). The increase in yield is due to the rapid increase in the net assimilation rate as observed in tomato after TRIA spray (Ries 1985, 1991). In greenhouse studies, foliar applications of 1.0–100 $\mu\text{g L}^{-1}$ of L(+)-adenosine increased the growth of tomato (*Lycopersicon esculentum* Mill.), maize (*Zea mays* L.), cucumber (*Cucumis sativus* L.), and carrot (*Daucus carota* L.) (Ries et al. 1990). Further, in controlled environment studies, Eriksen et al. (1982) noticed a TRIA-mediated increase in the dry weight of tomato (*Lycopersicon esculentum*) seedlings; but, such a dry weight increase was not observed in maize seedlings. TRIA showed no effect on seed germination or on early growth of several species when seeds were treated with it (Hoagland 1980), but significant effect of TRIA was reported in increasing the rate of germination of cotton (*Gossypium hirsutum*) (Zerong et al. 1981) and leguminous crops (Janardhan 1992). Skogen et al. (1982) reported increases in growth, number of inflorescences, and quality of flowers treated with TRIA in chrysanthemum (*Chrysanthemum morifolium*). Foliar spray of TRIA increased the dry weight of rice seedlings grown in nutrient medium

and that of the plants of corn, barley, and tomato (Ries et al. 1977). The growth promoting effects of TRIA on various attributes, especially on plant height, fresh and dry weights, leaf-area and root nodulation, have been explored in various medicinal crops by various researchers (Srivastava and Sharma 1990; Misra and Srivastava 1991; Shukla et al. 1992; Muthuchelian et al. 2003; Giridhar et al. 2005; Chaudhary et al. 2006). TRIA improved fresh and dry weights, leaf area, and the number and dry weight of nodules in case of hyacinth bean (*Lablab purpureus* L.) (Naeem and Khan 2005; Naeem et al. 2010). Furthermore, the effect of foliar spray of GA₃, TRIA, and that of their combination (GA₃+TRIA) was found to be significant for plant height and dry weight of opium poppy (Khan et al. 2007). Application of TRIA alone and in combination with potassium enhanced the plant height, fresh and dry weights and area per leaf of tomato (Khan et al. 2009).

Various studies, conducted on the medicinal and aromatic plants (Table 1), revealed that foliar sprays of TRIA significantly stimulated the growth attributes of turmeric (*Curcuma longa* L.), hyacinth bean (*Lablab purpureus* L.), ashwagandha (*Withania somnifera* L.), artemisia (*Artemisia annua* L.), coriander (*Coriandrum sativum* L.), coffee senna (*Senna occidentalis* L.), mint (*Mentha arvensis* L.), and ginger (*Zingiber officinale* Rosc.) (Singh 2008; Naeem et al. 2009; Nasir 2009; Aftab et al. 2010; Idrees et al. 2010; Naeem et al. 2010, Naeem et al. 2011; Singh et al. 2011).

Physiological and biochemical attributes

Exogenous application of TRIA has been reported to regulate directly or indirectly several physiological and biochemical processes (Ries and Houtz 1983; Ries 1991; Ries et al. 1993; Naeem et al. 2009, 2010, 2011). Application of TRIA to barley roots resulted in a rapid stimulation of membrane associated Ca²⁺/Mg²⁺ dependent ATPase activity (Lesniak et al. 1986) in a calmodulin-dependent manner. Besides, activity of NADPH oxidase of the plasma membrane is potentiated by TRIA application (Moore et al. 1991). 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). A large number of the TRIA responsive genes were associated with photosynthesis. These genes were upregulated and the stress related genes were down regulated by TRIA. Chen et al. (2002) reported that higher *rbcs* gene levels were associated with improved photosynthetic activity in TRIA-treated plants. They also illustrated 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 (Chen et al. 2003).

Triacantanol increased the minimal fluorescence and the maximal fluorescence (*F_o* and *F_m*) in rice plants, as revealed by Chen et al. (2003). They explained that increased *F_o* value indicated that TRIA increased the antenna pigment level or the efficiency of excitation trapping at the active centers of PS-II. These data were similar with those obtained in tomato (Borowski et al. 2000). They further reported a quantitative increase (30% increase over the control) in RuBisCO as a result of TRIA application. Other proteins were unaffected quantitatively by TRIA treatment.

Photosynthesis has been implicated as an important plant response to TRIA (Eriksen et al. 1981) and the increased growth and dry weight of plants were attributed to improved photosynthesis and enhanced accumulation of photosynthates. A number of studies have demonstrated an increased rate of CO₂ fixation in a variety of plant species when the TRIA was applied in nanomolar concentrations (Haugstad et al. 1983; Popova et al. 1989; Srivastava and Sharma 1990; Misra and Srivastava 1991). Houtz et al. (1985b) suggested a TRIA-stimulated increase in the specific activity of the enzymes RuBisCO and phosphoenolpyruvate carboxylase. Moreover, TRIA affected several other enzyme systems especially the membrane bound Ca²⁺/Mg²⁺ dependent ATPase (Lesniak et al. 1986, 1989). TRIA also increased the activity of the key respiratory enzyme malate dehydrogenase (Savithiry et al. 1992). Ries and Houtz (1983) suggested that the hormonal effects of TRIA might be due to TRIA-induced alterations at the membrane level. TRIA-mediated activation of a number of membrane bound enzymes supports this assumption (Ries and Wert 1988; Ries 1991; Savithiry et al. 1992). As per Ries et al. (1990), TRIA treatment causes rapid elicitation of a specific second messenger, 9-β-L(+) adenosine, which could induce extremely rapid physiological responses.

Ivanov and Angelov (1997) observed a significant increase of the net CO₂ uptake to 109% and 119%, when the TRIA was applied to pea plants at 10⁻⁸ and 10⁻⁶ M, respectively. Besides, they noted that treatments with octacosanol (OCTA) under the same experimental conditions and concentrations did not elicit any changes in photosynthesis over the same time range (30 and 60 min). Ries and Houtz (1983) suggested for the first time that the growth stimulating or hormonal effects of TRIA might be due to certain alterations at the cell membrane level. They demonstrated that 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. As per their study, Ivanov and Angelo (1997) suggested that TRIA-induced increase in the content of pyrene excimer (excitation light beam [steady state fluorescence spectra]) was due to the molecular dynamics and/or fluidity of protoplast and

Table 1 Positive response of various plant species to foliar application of triacontanol.

Name of plant	Botanical name	Family name	Growth attributes	Yield attributes	Biochemical attributes	Quality attributes	Reference citation
Opium poppy	<i>Papaver somniferum</i> L.	Papaveraceae	Plant height, dry weight and number of branches	Number of capsules, seed yield per plant, and crude opium yield per plant	Chl <i>a</i> , Chl <i>b</i> , and total content	Morphine content and morphine yield per plant	Khan et al. (2007)
Tomato	<i>Solanum lycopersicum</i> L.	Solanaceae	Height per plant, number of leaves and plant fresh and dry weights	Number of fruits per plant, weight per fruit and fruit yield per plant	Total chl and carotenoids content, leaf-N, -P, and -K contents	Fruit ascorbic acid and lycopene contents	Khan et al. (2009)
Hyacinth bean	<i>Lablab purpureus</i> L.	Fabaceae	Plant fresh and dry weights, leaf-area per plant, number and dry weights of nodules	Number of pods per plant, number of seeds per pod, 100-seed weight and seed-yield per plant	Photosynthetic rate (P_N), stomatal conductance (gs) and transpiration rate, total chl and carotenoid content, NR and CA activities, leaf-N, -P, -K, and -Ca content, nodule-N and leghemoglobin contents	Seed-protein content, total carbohydrate content, and tyrosinase activity	Naeem and Khan (2005), Naeem et al. (2009)
Artemisia	<i>Artemisia annua</i> L.	Asteraceae	Shoot and root lengths, plant fresh and dry weights	Artemisinin yield	P_N , gs and transpiration rate, total chl and carotenoid content, NR and CA activities, leaf-N, -P, and -K content	Essential oil content, artemisinin content	Aftab et al. (2010)
Coriander	<i>Coriandrum sativum</i> L.	Umbelliferae	Shoot and root lengths, plant fresh and dry weights		Total chl and carotenoids content, NR and CA activities, leaf-N, -P, and -K content	Essential oil content	Idrees et al. (2010)
Coffee senna	<i>Senna occidentalis</i> L.	Fabaceae	Plant fresh and dry weights	Number of pods per plant, number of seeds per pod, 100-seed weight and seed yield per plant	P_N , gs and transpiration rate, total chl and carotenoid content, NR and CA activities, leaf-N, -P, -K, and -Ca content	Total anthraquinone and sennoside contents, and seed-protein content	Naeem et al. (2010)
Sweet basil	<i>Ocimum basilicum</i> L.	Labiatae	Shoot and root lengths, number of spikes per plant, total leaf area, plant fresh and dry weights	Essential oil yield	Chl <i>a</i> , Chl <i>b</i> , total Chl, and carotenoid contents, activities of NR and CA, leaf-N, -P, and -K contents	Leaf-protein and carbohydrate contents, essential oil content, linalool, methyl eugenol, and eugenol contents	Hashmi et al. (2011)
Japanese mint	<i>Mentha arvensis</i> L.	Lamiaceae	Plant height, leaf-area, leaf-yield, and plant fresh and dry weights	Herbage yield, essential oil yield	Total chl and carotenoid contents, activities of NR and CA, leaf-N, -P, and -K contents, total phenol	Essential oil content, menthol, L-menthone, isomenthone, and menthyl acetate contents	Naeem et al. (2011)

Abbreviation: Chl, Chlorophyll; NR, Nitrate reductase; CA, Carbonic anhydrase.

chloroplast membranes that were markedly enhanced as a result of TRIA application. Furthermore, they noted that the concentration range of TRIA, effective in the enhancement of photosynthesis, corresponded well to the TRIA concentrations influencing membrane dynamic properties; this indicated a good correlation between the two phenomena. They also demonstrated that the incubation of both protoplast and chloroplasts with TRIA resulted in a rise of the excimer/monomer (I_E/I_M) ratio of pyrene fluorescence. These results are discussed in terms of specific concentration-dependent TRIA-induced alterations of the dynamic properties of protoplast and chloroplast membranes and their possible involvement in the initiator and integral physiological response to exogenous application of TRIA (Ivanov and Angelov 1997). In a study, Borowski et al. (2000) revealed that the maximum efficiency of PS-II in the dark (F_v/F_m) was clearly increased by the applied TRIA, and the efficiency of excitation-capture by PS-II reaction centers (F_v/F_m) were even much increased.

In fact, a number of studies have demonstrated an increased rate of CO_2 fixation and photosynthesis in a variety of plant species as a result of TRIA application in nanomolar concentrations (Houtz et al. 1985a; Ivanov and Angelov 1997). Srivastava and Sharma (1990) and Misra and Srivastava (1991) reported significant improvement in the rate of CO_2 fixation and net photosynthesis in opium poppy (*Papaver somniferum* L.) and lemongrass (*Cymbopogon flexuosus* Steud. Wats.), respectively. According to Muthuchelian et al. (2003), when the seedlings of *Erythrina variegata* L. were sprayed with TRIA, the harmful effect of acidic mist on photosynthesis machinery was partially or completely reversed, indicating that TRIA might protect plants from acid rain. TRIA application also improved the photosynthesis in rice in normal conditions (Chen et al. 2002). Similarly, TRIA alone or in combination with gibberellic acid (1.5 mg L^{-1} of TRIA + 75 mg L^{-1} of GA_3) significantly increased the net photosynthetic rate, stomatal conductance and internal CO_2 concentration in *Artemisia annua* (Aftab et al. 2010). Moreover, Naeem et al. (2009, 2010, 2011) also found the significant effect of TRIA on photosynthetic parameters regarding hyacinth bean (*Lablab purpureus* L.), coffee senna (*Senna occidentalis* L.), and Japanese mint (*Mentha arvensis* L.).

In addition, the contents of photosynthetic pigments were significantly influenced by exogenous application of TRIA. The content of the pigments in TRIA-treated leaves could presumably be attributed to the increase in the number and size of chloroplasts as revealed by Ivanov and Angelov (1997), Chen et al. (2003), and Muthuchelian et al. (2003). Significant effects of TRIA on photosynthetic pigments were also reported in opium poppy and Japanese mint (Srivastava and Sharma 1990, 1991), lemongrass (Misra and Srivastava 1991), opium

poppy (Khan et al. 2007), hyacinth bean (Naeem et al. 2009), artemisia (Aftab et al. 2010), coriander (Idrees et al. 2010), and coffee senna and mint (Naeem et al. 2010, 2011).

Triacetonol application caused an increase in peroxidase activity in 'Little Marvel dwarf' (LM) and 'Alaska' peas (AP) plants compared to the untreated controls. The effects of TRIA on root and stem growth, peroxidase activity, and auxin-destruction appeared to be cultivar-specific, with respect to LM and AP varieties of peas (Henry and Gordon 1980). As a result of foliar spray of TRIA at early vegetative stages, Naeem et al. (2009) reported an increase in the nodule-nitrogen and leghemoglobin contents of hyacinth bean (*Lablab purpureus* L.) at 60 days after sowing (DAS) followed by that at 90 DAS. The TRIA applied at 10^{-6} concentration surpassed the control by 5.4% in nodule-nitrogen content and by 14.1% in leghemoglobin content at 60 DAS. However, the plants gave negative response to 10^{-5} M of TRIA both for nodule-nitrogen and leghemoglobin contents in comparison to 10^{-6} M of TRIA.

The significant effect of TRIA on activities of NR and carbonic anhydrase (CA) has been reported by Kumaravelu et al. (2000), Muthuchelian et al. (2003), and Nasir (2009). The TRIA alone or in combination with gibberellic acid significantly enhanced the activities of NR and CA in artemisia (Aftab et al. 2010) and coriander (Idrees et al. 2010). Moreover, a remarkable enhancement in the activities of NR and CA in hyacinth bean, coffee senna and mint was reported by Naeem et al. (2009, 2010, 2011) as a result of TRIA application.

Naeem et al. (2009) reported significant effect of foliar application of TRIA on N, P, K, and Ca content of leaves in hyacinth bean. The concentrations of these leaf-nutrients were found significantly higher at 10^{-6} M of TRIA over the control. Thereafter, at 10^{-5} M of TRIA, the tissue concentrations of these elements decreased. A positive effect of TRIA on total leaf-nitrogen content was earlier revealed by Knowles and Ries (1981) and Ries and Houtz (1983) in the case of rice and maize, respectively. Knowles and Ries (1981) clarified that enhancement in leaf-nutrients, particularly that in nitrogen, due to TRIA application could be attributed to the compositional or chemical change in plants leading to alterations in leaf-nitrogen concentration. In contrast, TRIA applied at 0.5 and 1.0 mg dm^{-3} , reduced the leaf nitrate content in green gram (Kumaravelu et al. 2000). A significant improvement in leaf-nutrient content of tomato, opium poppy, artemisia, coriander, and ginger was observed by Khan et al. (2006, 2007, 2009), Aftab et al. (2010), Idrees et al. (2010), and Singh et al. (2011) as a result of TRIA application alone or in combination with GA_3 . TRIA application at 10^{-6} M alleviated the leaf-N, -P, and -K contents in the case of coffee senna and mint, respectively (Naeem et al. 2010, 2011). Sharma et al. (2002)

suggested that a higher content of leaf-nutrients in TRIA treated plants could be attributed to the higher metabolic activity and increased dry matter production that might result in enhanced water and nutrient uptake from soil subsequently.

Yield and quality attributes

Past decades have witnessed much success in increasing the yield of food crops and vegetables using TRIA (Bouwkamp and McArdle 1980; Eriksen et al. 1981; Ries and Houtz 1983; Hashim and Lundergan 1985; Ries 1985; Stoutemyer and Cooke 1987; Borowski et al. 2000; Muralidharan et al. 2000). The first published report on TRIA showed a significant increase in yield on several crops including dry beans, sweet corn, and cucumbers (Ries et al. 1978; Ries and Houtz 1983). TRIA, applied through soil drenching, has been shown to be effective in promoting the growth and development of tabasco pepper both in greenhouse and field conditions (Mamat et al. 1983). Bhalla (1981) reported the TRIA-enhanced growth of maize and tomato plants grown in the greenhouse. The results of 46 field experiments, conducted in several parts of the world, generally showed no significant increases in crop yield, except one study conducted in Japan, where the yield of rice was increased by 17–21% on account of soil applications of TRIA at 0.057–4.0 g ha⁻¹. However, foliar and seed treatment with TRIA at 0.05 and 0.10 mg L⁻¹ increased the yield of cotton by 12 and 31%, respectively (Sheng 1981). The average yield of winter wheat was increased by 12% due to foliar application of TRIA at 0.1 and 0.5 mg L⁻¹ (Chen et al. 1980). As per an extensive study in China conducted in a three-year period, several vegetable crops (tomato, egg-plant, cabbage, and winged bean) responded positively to 0.1–1.0 mg L⁻¹ of TRIA. However, in the USA, TRIA increased the plant growth in laboratory-study as well as in greenhouse-study; however, results obtained in the field study were not encouraging (Ries and Houtz 1983).

In brown rice, Nagoshi and Kawashima (1996) reported a TRIA-mediated improvement in heading and percentage of ripened grain at harvesting time that led to the enhancement in the individual grain weight and 1000-grain weight. Chowdhury et al. (2009) found the beneficial effect of TRIA in improving fruit quality and economic yield of different cultivars of water chestnut (*Trapa bispinosa*); TRIA application increased the fresh fruit yield by 32% in green cultivars and by 31% in red cultivars. 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). Improvement in yields of several important food crops have been recorded by several researchers as a result of TRIA application (Ries et al. 1978; Ries 1985;

Kawashima et al. 1987). Borowski et al. (2000) reported significant increase in tomato yield as result of TRIA application at 0.3 and 3.0 mg L⁻¹. Similar results have been reported by Asane et al. (1998), Barus (1998), and Blamowski et al. (1998) on peas, plum, and radish, respectively. In another study, 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. Further, they found no effect of TRIA on maize yield, whether the TRIA was applied to the leaves or it was added to the growth substrate. Verma et al. (2009) maintained that TRIA did not induce enhancement in pod yield, number of pods per plant, pod weight per plant, and shelling percentage of groundnut. There were recorded the highest values regarding the number of umbels, fruits per umbel, 100 seed weight, and seed yield, when the TRIA was applied together with GA₃ to coriander crop (Idrees et al. 2010)

Naeem et al. (2009, 2010) reported a favorable effect of TRIA on the yield and yield attributes (number of pods and seed yield per plant) of hyacinth bean and coffee senna; the highest values were recorded when the TRIA was applied at a 10⁻⁶ M concentration. Ivanov and Angelov (1997), Borowski et al. (2000), Kumaravelu et al. (2000), Chaudhary et al. (2006), Sharma et al. (2006), and Nogalska et al. (2008) reported the significant effect of TRIA on the yield and yield attributes of pea, tomato, green gram, water chestnut, tomato, and soybean, respectively. A significant improvement in fruit-yield of tomato (Khan et al. 2006, 2009) and crude opium-yield, and seed yield of opium (Khan et al. 2007) has also been reported as a result of TRIA application carried out alone or in combination with GA₃. Foliar application of TRIA at 10⁻⁶ M significantly enhanced the crop herbage yield and the yield of essential oil in mint (Naeem et al. 2011). Application of TRIA (at 10⁻⁶ M) also improved the values of primary and secondary fingers and rhizome yield per plant in turmeric and ginger (Singh 2008; Singh et al. 2011). According to Nasir (2009), TRIA combined with N and P fertilizers (10^{-6.5} M of TRIA + N₆₀P₄₀) significantly increased the capsules per plant and seed yield of datura (*Datura innoxia* Mill.). The application of TRIA in combination with N and P (10^{-6.5} M of TRIA + N₄₅P₂₆) also increased the seed yield and root yield of withania (*Withania somnifera* L.) (Nasir 2009).

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), *Acacia catechu* (Thakur and Thakur 1992), and

Erythrina variegata (Muthuchelian et al. 1995). Moreover, Naeem et al. (2009, 2010) reported a significant positive effect of TRIA on the seed-content of protein and carbohydrate in hyacinth bean. Similarly, carbohydrate and protein contents in turmeric (*Curcuma longa* L.) and ginger (*Zingiber officinale* Rosc.) were significantly improved by the foliar spray of TRIA (Singh 2008; Singh et al. 2011).

Active constituents of plants

Khan et al. (2007) found a significant positive effect of cumulative application of TRIA and GA₃ on the yield of opium and its morphine content. The crude-opium production of opium poppy (*Papaver somniferum* L.) was also enhanced due to the combined application of TRIA and GA₃ (Khan et al. 2007). Srivastava and Sharma (1990) also examined the effect of TRIA on alkaloid-biosynthesis as well as on the relationship between alkaloid production and physiological parameters in opium poppy. They reported a significant increase in capsule number and morphine content of the plant owing to foliar application of TRIA at concentration of 0.01 mg L⁻¹; whereas, there was no effect of TRIA on thebaine and codine contents of opium poppy. As reported by Henry and Primo (1979), they observed a greater polyphenol oxidase activity in the leaf tissue of lettuce treated with foliar spray of TRIA in comparison to the control. In an *in vitro* cell free system, the activities of starch phosphorylase and phosphoenol pyruvate carboxylase (PEPCase) were increased up to 40% in the supernatant obtained from maize leaves, 20 min after leaf treatment with TRIA (Houtz and Ries 1983).

Both *in vitro* and *in vivo* studies, conducted on rice and maize, revealed a promotive effect of TRIA on the content of reducing sugars, amino acids, and soluble protein in (Knowles and Ries 1981; Ries and Wert 1982). Misra and Srivastava (1991) reported a significant effect of a TRIA formulation, Miraculan, on essential oil yield of lemongrass. They stated that Miraculan-spray at concentration of 0.4 mg L⁻¹

significantly improved the accumulation of essential oil and its components, particularly that of citral-*a* and citral-*b*; whereas, TRIA had no effect on the geraniol content of the oil. As a result of foliage-applied TRIA, Farooqi and Sharma (1988) found an increase in the essential oil yield in *Mentha arvensis*. Srivastava and Sharma (1991) reported an improved content of menthol and yield of essential oil in TRIA-treated *M. arvensis* plants. Aftab et al. (2010) noted a significant enhancement in the content of *Artemisia annua*, registering a simultaneous increase in the content and yield of artemisinin in the leaves (Figure 3). Similarly, Idrees et al. (2010) revealed the significant positive effect of combined application of TRIA and GA₃ on the essential oil content of coriander (Figure 4). Moreover, Naeem et al. (2010) recorded a TRIA-mediated improvement in the level of anthraquinone and sennoside content in coffee senna (Figure 5). In addition, Naeem et al. (2011) recorded a TRIA-mediated improvement in the contents of components of essential oil (menthol, l-methone, isomenthone, and menthyl acetate) of *Mentha arvensis* L. (Figure 6). Total alkaloid content in withania (*Withania somnifera* L.) and datura (*Datura innoxia* Mill.) and curcumin content of turmeric (*Curcuma longa* L.) was also successfully enhanced by foliar application of TRIA (Singh 2008; Nasir 2009; Singh et al. 2011).

Role of TRIA in *in vitro* studies

Generally, TRIA enhances the elongation of multiple shoots and micropropagated plantlets, although such an effect of TRIA has not been observed on the woody plants (Tantos et al. 2001). The TRIA, applied at 10 µg L⁻¹, increased the fresh and dry weight of shoots by 20–25% in *Salvia officinalis*. The promotive effect of TRIA was also reported in micropropagation of ornamentals and other plants (Kissimon et al. 1999; Reddy et al. 2002). In an *in vitro* study, Hangarter et al. (1978), demonstrated the favorable effect of TRIA on *Nicotiana tabacum*, *L. esculentum*,

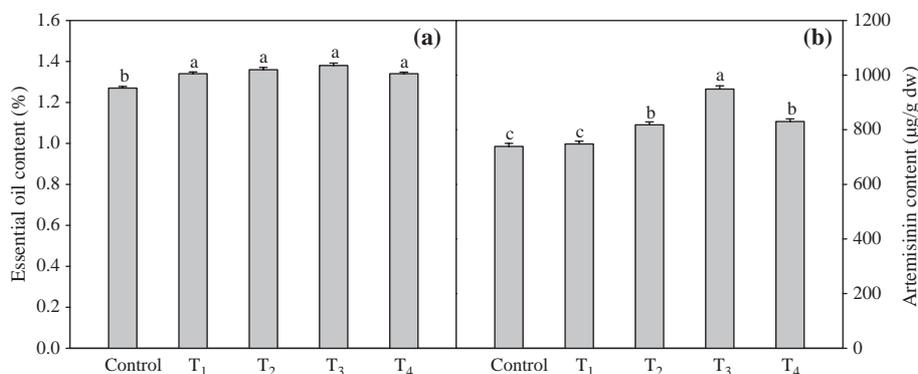


Figure 3. Effect of foliar sprays of different concentrations of triacontanol (TRIA) and GA₃ viz. Control, 1.5 mg TRIA (T₁), 1.5 mg L⁻¹ TRIA + 50 mg L⁻¹ GA₃ (T₂), 1.5 mg L⁻¹ TRIA + 75 mg L⁻¹ GA₃ (T₃), and 1.5 mg L⁻¹ TRIA + 100 mg L⁻¹ GA₃ (T₄) on essential oil content (a), artemisinin content (b) of *Artemisia annua* L. Bars showing the same letter(s) are not significantly different at $p = 0.05$ as determined by Duncan's multiple range test. Error bars (-) show SE (Aftab et al. 2010).

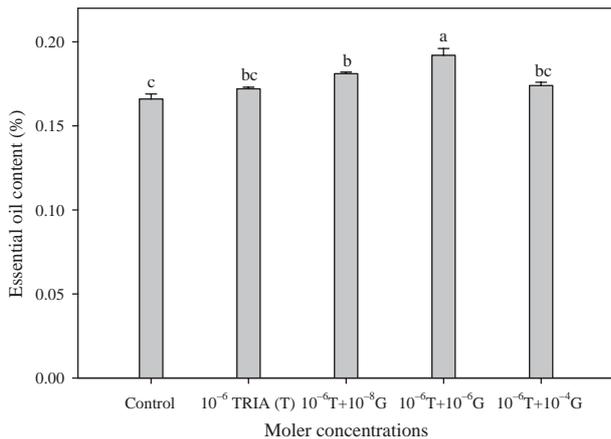


Figure 4. Effect of spray of triacontanol (TRIA) alone or in combination of GA₃ on essential oil content of coriander. Means within a column followed by the same letter(s) are not significantly different ($p = 0.05$). The data shown are means of four replicates \pm SE (Idrees et al. 2010).

Solanum tuberosum, *Phaseolus vulgaris*, and a barley hybrid (*Hordeum vulgare* \times *H. jubatum*). In addition, encouraging results have been obtained with regard to TRIA-mediated growth improvement in *O. sativa* (Yun and Kim 1986), *Malus domestica* (Ma et al. 1990), *Melissa officinalis* (Tantos et al. 1999), woody plants (Tantos et al. 2001), *Bupleurum fruticosum* (Fraternal et al. 2002), *Capsicum frutescens* and *Decalepis hamiltonii* (Reddy et al. 2002), and *Thymus mastichina* (Fraternal et al. 2003). Fraternal et al. (2003) recorded a TRIA-mediated enhancement in shoot growth of *T. mastichina* at 10 and 20 mg L⁻¹ of TRIA. Application of TRIA at a similar range of concentrations produced improved number of nodes and shoot length as reported by others on micropropagation of herbaceous and woody plants (Tantos et al. 1999, 2001; Fraternal et al. 2002; Reddy et al. 2002). Fraternal et al. (2003) reported that TRIA applied at 10 and 20 μ g L⁻¹, enhanced the essential oil yield of *Thymus mastichina* L. (about 33%) as compared to control. However, such an effect was not detectable when TRIA was applied with auxin and/or cytokinin. Furthermore, they observed that TRIA applied at 10 and 20 μ g L⁻¹ to the control plants induced a decrease in the number of glands at post-secreted stage (corresponding to an increase of glands in secretory stage), and an increase in the essential oil yield (about 67% increase in glands in secretory-stage corresponding to about 47% increase in the oil yield).

The biosynthesis of secondary metabolites in *in vitro* culture studies is also affected by TRIA, like by other plant growth regulators. TRIA has been reported to enhance the production of secondary metabolites in *Artemisia annua* (Yaseen and Tajuddin 1998). TRIA, applied at 5 μ g L⁻¹ enhanced the content of diterpenoids in the shoots of *Salvia officianlis* to the highest extent (Grzegorzczuk et al. 2005). However, the use of TRIA concentrations (10

or 20 μ g L⁻¹) did not induce further increase in the diterpenoid yield of sage (*Salvia officianlis*) shoots. Grzegorzczuk et al. (2006) observed a positive effect of TRIA on shoot multiplication, production of biochemical compounds, and antioxidant capacity of *S. officianlis*. Moreover, TRIA also increased carnosol content in sage shoots, with a little influences on carnosic acid. The ability of TRIA to increase diterpenoid production may be ascribed to the biosynthesis of the compounds that is probably localized in the chloroplasts (Munne-Bosch and Alegre 2001), the TRIA-mediated increase in chlorophyll content in many plants being one of the strong evidences in this regard (Ries 1985).

Role of TRIA under abiotic stresses

Muthuchelian et al. (2003) reported a TRIA-mediated increase in root and shoot, leaf density and area, and fresh and dry biomass accumulation of acidic-mist-treated *Erythrina variegata* plants. Their studies suggested that lipophilic TRIA might act on cell membranes to produce 9- β -L(+) adenosine. In fact, this substance is rapidly translocated throughout the plant causing a cascade of metabolic events and, thus, resulting in significant increases in growth and dry matter of plant (Ries and Wert 1992).

Application of TRIA increased ¹⁴CO₂ fixation, enzyme activities, synthesis of chl *a*, chl *b*, carotenoids, starch, and sugars in *E. variegata* seedlings under flooded and acid mist conditions as well as under salt and cadmium stressed conditions (Muthuchelian et al. 1992, 1994, 1995, 1996, 1997, 2001, 2003). Muthuchelian et al. (2003) suggested that the TRIA-enhanced growth of plants might result from an increase in effective leaf area, stimulation of photosynthesis and increase in the activities of RuBisCO and NR. Reductions in shoot growth rate, leaf area index (LAI), and relative growth rate

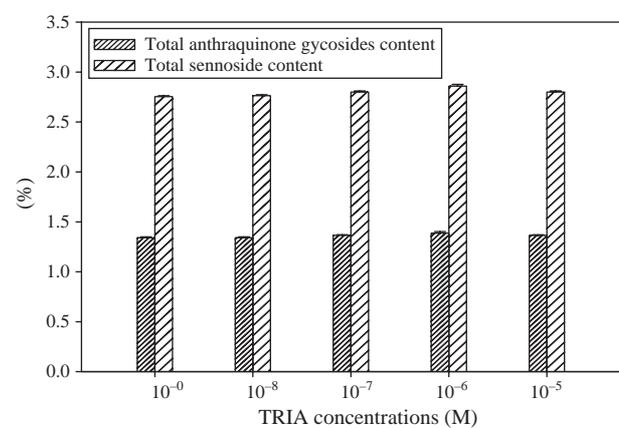


Figure 5. Effect of five concentrations of triacontanol (TRIA) (10⁻⁰, 10⁻⁸, 10⁻⁷, 10⁻⁶, and 10⁻⁵ M) on total anthraquinone glycosides content and sennoside content of coffee senna (*Senna occidentalis* L.) studied at 300 DAS (Means of three replicates). Error bars (-) show SE (Naem et al. 2010).

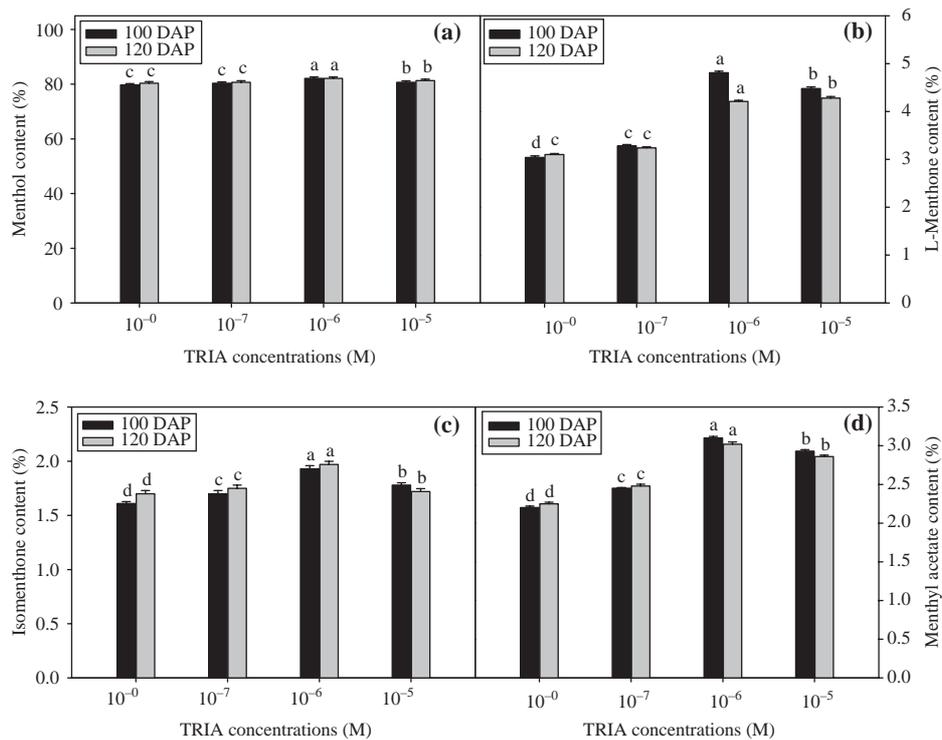


Figure 6. Effect of four concentrations of foliar sprays of triacontanol (TRIA) (10^0 , 10^{-7} , 10^{-6} , and 10^{-5} M) on menthol content (a), L-menthone content (b), isomenthone content (c), and menthyl acetate content (d) of mint (*Mentha arvensis* L.) studied at 100 and 120 DAP. Means within a column followed by the same letter(s) are not significantly different ($p = 0.05$). Error bars (-) show SE (Naeem et al. 2011).

(RGR) were improved by TRIA application in water stressed seedlings of *E. variegata* sprayed. Similar results have been reported by Muthuchelian et al. (1995) in *E. variegata* and by Srivastava and Sharma (1991) in *Papaver somniferum* L. The reduction in the contents of chlorophyll and carotenoids as well as that in chlorophyll fluorescence was also improved by TRIA in salt-stressed *E. variegata* seedlings (Muthuchelian et al. 1996) and *Triticum aestivum* plants. (Perveen et al. 2010). Thakur and Thakur (1993) reported that application of TRIA and mixtalol overcame the adverse effects of moisture stress in *Lycopersicon esculentum* cultivars. According to Muthuchian et al. (1994, 1997), TRIA application reduced the inhibition of PS-II activity to about 22% in water stressed plants of *E. variegata*; the reduction in RuBisCO activity underwater stress was also improved by TRIA spray. They also reported a TRIA-mediated maintenance in the photosynthetic machinery and a significant delay in the leaf-senescence in water stressed plants. By means of TRIA application, Krishnan and Kumari (2008) reported a successful amelioration of salt stress in soybean plants in terms of leaf weight ratio, relative water content, chlorophyll pigments, nucleic acids, soluble sugars, and soluble proteins.

By TRIA application, Rajasekaran and Blake (1999) reversed the damaging effect of drought-stress in terms of membrane leakage on Jack pine seedlings. The study of Borowski and Blamowski (2009) showed that periodic chilling decreased the value of all the

growth, yield, and physiological parameters in the plants to a significant degree, with the exception of electrolyte leakage, water saturation deficit and proline content, whose values under these conditions was increased using TRIA. TRIA favorably influenced both treated and untreated plants with periodic chilling. Besides, a negative influence of chilling on the growth and yield of *Ocimum basilicum* L. was decreased by TRIA applied at 0.10 mg dm^{-3} .

Further studies and future prospects

TRIA being a plant growth promoter plays pivotal role in the up-regulation of many biochemical and physiological processes in plants, including photosynthesis. This leads to maximize the growth, yield and quality of several crops and helps improve the active constituents of medicinal and aromatic plants under normal and abiotic stress conditions. The application of TRIA may be successfully employed in future to enhance the productivity, quality, and production of essential oil and other active constituents of medicinal and aromatic plants. However, further investigations are required to elucidate the possible regulatory role of TRIA on plant growth, physiological activities, and biosynthesis of secondary metabolite in medicinal and aromatic plants subjected to abiotic stresses. Intense efforts are still required in order to design the protocols to ensure the consistent results regarding response of plants to application of TRIA and l(+)-adenosine in the growth chambers,

greenhouses, hydroponics systems, and field studies. It is also a significant challenge to discover as to how both TRIA and I(+)-adenosine rapidly increase the plant metabolism and how TRIA elicits the synthesis of I(+)-adenosine. Identification of OCTAM and determining as to how it inhibits the activity of TRIA may lead to the discovery of the site of TRIA and/or I(+)-adenosine action (Ries et al. 1993).

Since the PGRs that boost up crop productivity are normally expensive, it is always desirable to find out the low-cost PGRs. The TRIA fulfills this requirement as it is extraordinarily cheap to afford. In future studies, it could also be explored if TRIA, in combination with other inexpensive PGRs, could further enhance the performance of crop plants at a desirable extent. The secondary messengers, which are produced by TRIA and other growth promoting substances, and the mechanism of TRIA-mediated elicitation of plants metabolism could also be worked out in future studies. In addition, the research work regarding combined application of TRIA and other PGRs would enable one to explore the economically and ergonomically feasible agronomic solutions to increase the essential oil and the medicinally important active constituents in medicinal and aromatic plants, the production of which is far short than it is unanticipated high demand in the global market.

Conclusions

The evidence is overwhelming that TRIA applied at nanomolar concentrations improves the plant growth and physiological activities in diverse groups of plants. Foliar application of TRIA has been proved to be a successful technique to improve the growth, yield, and quality of various crops, including vegetables, horticultural crops, and medicinal and aromatic plants. TRIA-mediated increase in dry matter leads to increased biosynthesis of secondary plant products as well, including essential oil and active constituents of medicinal and aromatic plants. However, further studies are required to reveal the possible role of TRIA on the regulation of plant growth and metabolism in terms of regulation of gene expression.

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