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Review Article

TRIAZOLES AS PLANT GROWTH REGULATORS AND STRESS PROTECTANTS IN FRUIT CROPS: A REVIEW

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This review provides a comprehensive overview of the basic and applied aspects of triazole growth regulators in regulation of plant growth and development. A brief summary of the morphological, physiological, and in vitro responses elicited by triazoles is given, followed by an updated synthesis of their mode of action. Because the unique role of triazoles as plant multi-protectants deserves special attention, an in-depth coverage has been attempted to highlight their role in the protection of plants from a variety of unrelated environmental stresses. The latter part of the review deals with their current and potential uses on various tropical and sub-tropical fruit crops.

Keywords: Triazole, Stress, PBZ, UNZ, GA, ABA, PGRs

INTRODUCTION

In the late 1960s, several compounds from the chemical class of 1-substituted imidazoles and 1, 2, 4-triazoles were commercially developed and successfully used for the treatment of plant and human fungal infections. These azole fungicides and antimycotics include the most active compounds known today for controlling plant diseases and human mycoses. The azole fungicides belong to the large group of ergosterol biosynthesis inhibitors that interfere with the biosynthesis of fungal steroids. Certain azole compounds interfere with the biosynthesis of gibberellins and influence the morphogenesis of plants, indicating their possible use as plant growth regulators. Hence, several triazole derivatives were developed and recommended for worldwide use as either fungicides or plant growth regulators (Table 1).

The triazoles are the largest and most important group of systemic compounds developed for the control of fungal diseases in plants and animals (Siegel, 1981). Commercial products have both fungitoxic and plant growth regulating properties, irrespective of whether they were released for one use or the other. They tend to be much more effective than many other PGRs, generally requiring relatively low rates of

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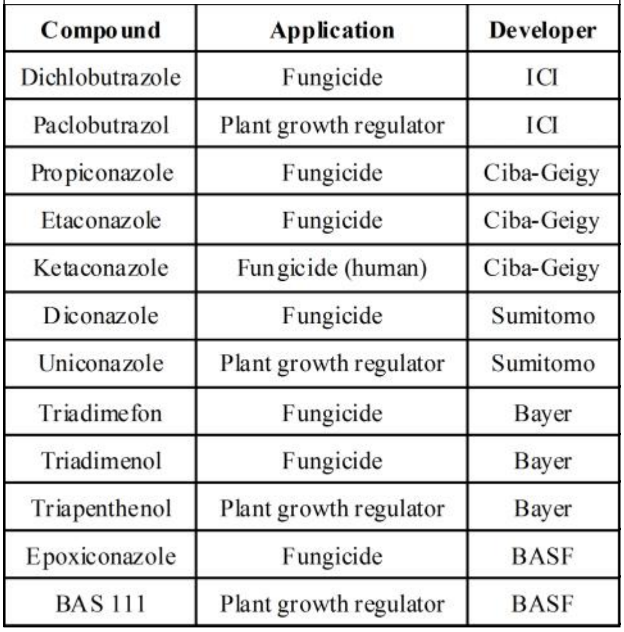
Table 1: Representative Examples of Triazole Compounds Recommended for Use as Fungicides or Plant Growth Regulators



Compound	Application	Developer
Dichlobutrazole	Fungicide	ICI
Paclobutrazol	Plant growth regulator	ICI
Propiconazole	Fungicide	Ciba-Geigy
Etaconazole	Fungicide	Ciba-Geigy
Ketaconazole	Fungicide (human)	Ciba-Geigy
Diconazole	Fungicide	Sumitomo
Uniconazole	Plant growth regulator	Sumitomo
Triadimefon	Fungicide	Bayer
Triadimenol	Fungicide	Bayer
Triapenthenol	Plant growth regulator	Bayer
Epoxiconazole	Fungicide	BASF
BAS 111	Plant growth regulator	BASF

application. Of the various triazoles, paclobutrazol (PBZ) and uniconazole (UNZ) thus far have been found to be the most active in retarding growth in both monocots and dicots (Gilley and Fletcher, 1997).

All triazole compounds are characterized by a ring structure containing three nitrogen atoms, a chlorophenyl, and a carbon side chain (Fletcher *et al*., 1986). Effectiveness as a fungicide or PGR is determined by the stereochemical configuration of the substituents on the carbon chain (Fletcher and Hofstra, 1988). Paclobutrazol and triadimenol, for example, have four enantiomers, which differ in their relative activity as fungicides or inhibitors of gibberellins and sterol biosynthesis (Burden *et al*., 1987). There are indications that an R configuration at the chiral carbon bearing the hydroxyl group is the prime determinant for fungitoxicity, whereas enantiomers having an S configuration at this carbon atom are inhibitors of gibberellins biosynthesis and more effective as PGRs.

Translocation

Triazoles are primarily believed to be transported acropetally in the xylem (Davis *et al*., 1988). However, recent findings show that PBZ is not exclusively xylem mobile as previously believed. In some plants (e.g., *Pistachia chinensis* Bunge, *Ricinus communis* L.), PBZ has been detected both in xylem and phloem sap (Witchard, 1997), indicating that xylem is not the only route for translocation of triazoles.

The metabolic fate of applied triazoles has not been studied thoroughly, though most have a high chemical stability and thus tend to be catabolized by plants at a very slow rate. It has been suggested that a strong correlation may exist between persistence of a triazole and its efficacy as a PGR. Two of the most active triazoles, PBZ and UNZ, are comparatively resistant to degradation and this may limit their widespread use on food crops.

Mode of Action

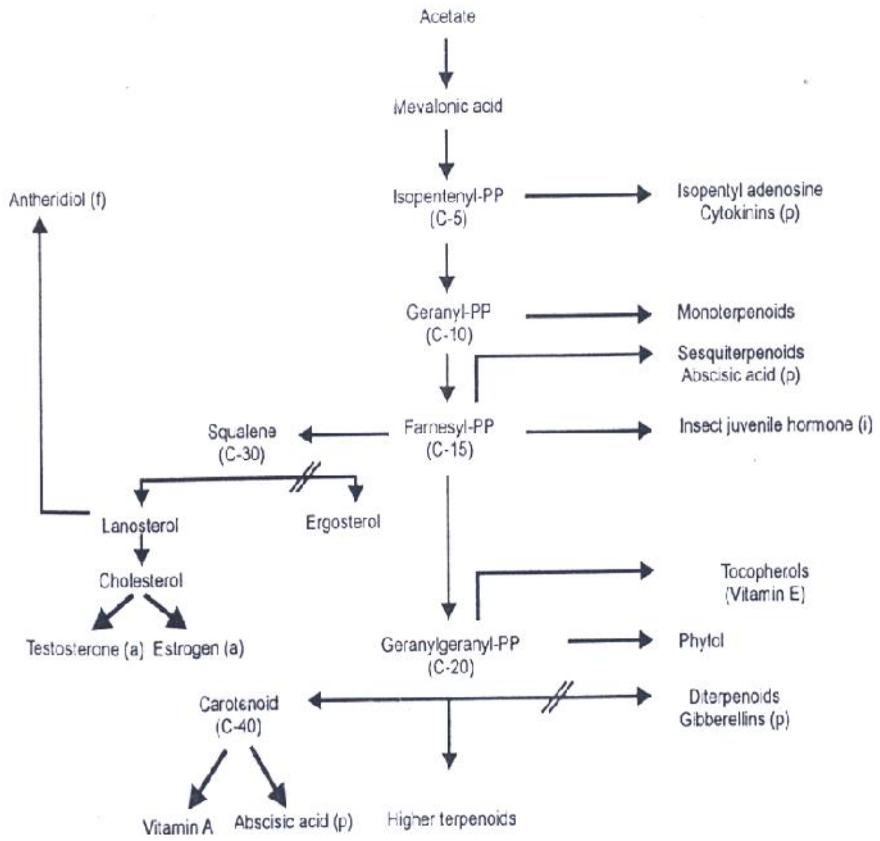
The triazoles are characterized by a lone pair of electrons on the Sp^2-hybridized nitrogen atom in the heterocycle. This pair of electrons occurs on the periphery of the molecule, enabling it to interact with cytochrome P-450 dependent monooxygenases. As the 6th ligand, it bonds to the protoheme iron of cytochrome P-450, thereby displacing oxygen required for catalytic reactions (Grossmann, 1990). In most fungi ergosterol is an indispensable component of fungal membranes and inhibition of this sterol leads to a loss of membrane integrity and ultimate cell death. The demethylation of the ergosterol precursor at the C-14 position of 24-methylene dihydro lanosterol proceeds via several oxidation steps catalyzed by a cytochrome-P450 mixed function oxygenase. The relative activity of enantiomeric forms of a triazole fungicide has been correlated to their affinity with this target enzyme. In plants, triazole compounds interfere with the biosynthesis of gibberellin by inhibiting the oxidation of ent-kaurene to ent-kaurenoic acid.

The isoprenoid pathway contains polymers derived from a basic five carbon isoprene unit. The pathway generates animal, fungal, insect, and plant hormones as well as other metabolites, including vitamins A and E, phytoalexins, steroids, allelopathic compounds, and insect antifeedants. Specific products of the isoprenoid pathway that are inhibited by the triazoles are ergosterol in fungi and gibberellins in plants (Figure 1). It has been suggested (Fletcher and Hofstra, 1985) that the PGR properties of triazoles are mediated by interfering with the isoprenoid pathway and thus modulating the balance of important plant hormones, including GA, ABA, and cytokinins. The ultimate effect, therefore, would be dependent on the dynamic equilibrium of these hormones at a specific stage of plant growth and development.

General Plant Responses to Triazoles

1. Morphological changes
   - Reduction in plant height and spread
   - Higher root to shoot ratio
   - Modified leaf morphology
2. Physiological changes
   - Improved water uptake
   - Enhanced flowering
   - Protection from biotic and abiotic stresses

Figure 1: Isoprenoid Pathway



3. Biochemical changes
   - Enhanced activity of anti-oxidant systems
   - Activated free radical scavenging systens
4. *in-vitro* responses
   - *in-vitro* production of roots, shoots and micro shoots
   - *in-vitro* hardening and production of somatic embryos and their germination
   - Reduction in hyperhydricity

PRIMARY AND SECONDARY EFFECTS OF TRIAZOLES

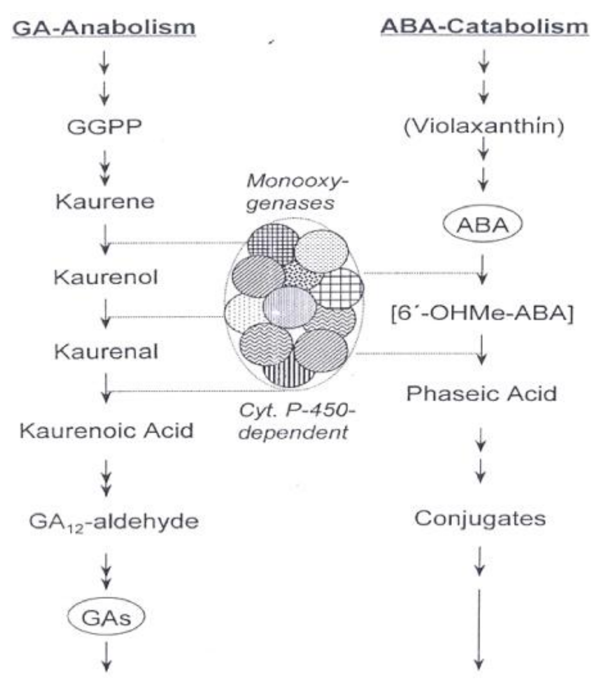
Primary Effects

Gibberellins

Triazoles interfere with the first three steps in the pathway of ent-kaurene oxidation and thus the formation of ent-kaurenol, ent-kaurenal, and ent-kaurenoic acid are inhibited, whereas steps following ent-kaurenoic acid in the pathway are not affected (Izumi *et al*. 1985; and Graebe, 1987). These microsomal oxidation reactions are catalyzed by kaurene oxidase, a cytochrome P-450 hydroxylase. Interference with the different isoforms of this enzyme could lead to inhibition of GA biosynthesis and abscissic acid (ABA) catabolism as shown in Figure 2 (Rademacher, 1997). Inhibition of GA biosynthesis as the primary effect of the triazole PGRs is supported by the evidence that triazole treated plants have lower concentrations of GA-like substances and that the PGR and stress protective properties of triazoles could be reversed with the application of GA. The effects of triazoles and GA are mutually antagonistic, as seen in examples of inhibition of triazole-induced physiological and biochemical processes.

Based on the interactions of triazoles and GA, it is logical to conclude that the PGR and stress protective effects of the triazoles are a consequence of their primary action as inhibitors of GA biosynthesis.

Figure 2: Interference of Different Isoforms of Cytochrome P_{450} Dependent Monooxygenases in GA and ABA Metabolism



Sterols

The fungicidal effects of triazoles can be attributed to their interference with the biosynthesis of ergosterol, resulting in depletion of the major sterol and an accumulation of 14-methyl sterols (Siegel, 1981; and Koller, 1987). There is evidence that suggests that certain triazole isomers interfere with sterol synthesis in plants. Although the involvement of sterols in plant growth and development is not well established, it has been suggested that the PGR effect of triazole compounds may be related to their effects on sterol biosynthesis (Davis and Curry, 1991).

Abscissic Acid

ABA, commonly considered a “stress hormone” (Zeevart and Creelman, 1988). has been

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implicated in plant acclimation and protection against various environmental stresses such as heat, chilling, drought and flooding (Mackay *et al*., 1990). ABA can be derived directly from farliesyl-P-P or indirectly from carotenoids, more specifically from xanthoxin. Although experimental evidence favors the indirect pathway, in either case mevalonic acid is the precursor. In bean plants, the triazole fungicide, TRIAD, induced a transient rise in ABA levels, reduced transpiration and protected the plants from drought.

Increases in the levels of ABA have also been associated with triazole induced cold hardiness (Tafazoli and Beyl, 1993). There is evidence to suggest (Hauser *et al.,* 1990) that the increase in ABA levels by triazoles is due to prevention of its catabolism to phaseic acid (Figure 2), an enzymatic step that is catalyzed by a cytochrome P-450-dependent monooxygenase. These apparent discrepancies may be ascribed to the use of different growth conditions, application methods, plant species, developmental Stage, and the concentration of triazole used. Because the hormonal balance of plants is in a dynamic state, the estimated ABA levels could also depend on the time of analysis after triazole treatment. Since increases in ABA levels have been associated with plant stress protection (Zeevaart and Creelman, 1988), it is suggested that triazole induced stress protection could be mediated at least partially, via its effects on ABA levels (Fletcher and Hofstra, 1988).

Secondary Effects

Cytokinins

Cytokinins stimulate cell division, and it is now widely accepted that cytokinins produced in roots move in the xylem to the shoot where they regulate both development and senescence (Letham and Palni, 1983). TRIAD and triadimenol delayed leaf senescence and it has been suggested that they had cytokinin-like properties (Buchenauer and Rohner, 1981). It has been suggested that the enhanced levels of cytokinins found in the roots of plant seedlings after treatment with various retardants, including BAS 111, could be due to either a stimulated synthesis of cytokinins that are transported to the shoot or prevention of cytokinin degradation and the increased cytokinins were identified as trans zeatin, dihydrozeatin, and its ribosides.

Ethylene

In several plant species, triazoles reduce ethylene formation. They inhibit ethylene synthesis by interfering with the conversion of ACC to ethylene by ACC oxidase. Subsequent studies with ACC oxidase suggest that cytochrome P-450 monooxygenase reactions may be involved in the conversion of ACC to ethylene (Kraus *et al*., 1992). The proposal that the effects of triazoles are mediated by a change in hormonal balance is accompanied by an increase in cytokinins and a decrease in abscissic acid and ethylene levels (Grossmann *et al*., 1994).

Polyamines

S-adenosylmethionine (SAM) is the shared common precursor for both ethylene and polyamine biosynthesis (Yang and Hoffman, 1984). Inhibition of ethylene biosynthesis should therefore affect polyamine metabolism. Increases in the levels of spermidine and spermine have been reported after treatment with PBZ and UNZ in several crops. Consequently, free putrescine in the cells, the direct precursor of these biologically more active polyamines, simultaneously decreased. The increased polyamine levels observed after triazole treatment may in part account for some of the senescence and root-promoting effects observed after triazole treatment (Fletcher and Hofstra, 1988).

Stress Protection in Plants

Crop plants are often subjected to environmental stresses that interfere with their normal physiological processes, affecting growth, development and, ultimately, crop yield. In addition to their growth regulatory and fungicidal effects, triazoles have been found to be highly effective in protecting plants from various environmental stresses (Davis *et al*., 1988; and Fletcher and Hofstra, 1988).

They are highly active against several economically important fungal diseases, including powdery mildew, smut, bunt, and rust. In addition to its fungicidal action, it was demonstrated that these triazoles protected plants from injury due to biotic and abiotic stresses, including powdery mildew, drought, chilling, ozone, heat, and air pollutants. Hence, the triazoles were referred to as plant multi-protectants.

Drought

Reduction of transpiration and protection from drought by triazoles was associated with a reduction in shoot weight and length, leaf area, and increased diffusive resistance, indicating partial closure of stomata and a transient rise in ABA levels. Triazole treated plants characteristically use less water and may be able to withstand drought better than untreated plants (Davis *et al*. 1988). Water use by triazole treated plants was reduced by 35% due to reduction in leaf area and lower stomatal conductance. Due to the beneficial effects of triazoles in water conservation, their use in plant micropropagation has increased. PBZ and UNZ added to culture media reduced water loss and increased survival of in vitro plants.

Low Temperature

Protection against cold injury is attributed to an inhibition of chilling induced degradation of membrane lipids (Whitaker and Wang, 1987). Triazole treated plants did not influence fatty acid saturation but, instead, prevented the loss of phospholipids and accumulation of free fatty acids that were characteristic of the controls. They also increased the levels of the antioxidants, tocopherol, and ascorbic acid in treated plants and it has been suggested that membrane damage is the result of oxygen free radicals generated by low temperatures and that triazoles protect membranes by preventing or reducing oxidative injury. Therefore the ability of triazole compounds to alter the ABA balance may play a role in protection from low temperature stress.

High Temperature

High temperatures can induce numerous physiological and biochemical effects in plants, including protein denaturation, enzyme inactivation altered metabolic rates, membrane damage and reduced chloroplast biochemical activity. These effects of heat stress are often confounded with those of water stress. Since high temperatures are accompanied by increases in transpiration rate and dehydration.

One of the major sites of heat stress damage is the chloroplast and, therefore reduced leaf temperature may be important in maintaining a functional photosynthetic system (Booker *et al*., 1991). Triazoles were also effective in protecting plants from a combination of heat and drought.

Evidence also indicates that protection of several plant seedlings from high temperature damage by triazole compounds may be related to increases in the activities of important antioxidant enzymes such as superoxide dismutase, ascorbate peroxidase, glutathione reductase, peroxidase, and catalase. Thus, triazole induced protection from heat stress may be related to a more efficient free radical scavenging system.

Environmental Pollutants and Other Stresses

Triazoles have been shown to decrease injury due to air pollutants. Ozone injuries in leaves are chlorosis, necrotic lesions, solute leakage, reduced Hill activity, a decrease in phospholipids and a concomitant increase in free fatty acids indicative of free radical damage. These phytotoxic symptoms caused by ozone, UVB radiation, sulphur dioxide and other harmful pollutant injuries can be prevented in plants by traizole application. However, the mechanism of protection from these atmospheric pollutants is not fully understood.

Methods of Application of Triazole Plant Growth Regulators

Triazole plant growth regulators can be applied in various methods to several plants and they include,

Foliar/Spray

Soil – drench/trunk soil line pour method

Trunk injection

Soil injection

Seed treatment

Foliar/Spray Application: The required concentration of triazole plant growth regulator is applied on the canopy of the plant or tree by using high or low volume sprayers. This is considered to be the best method of application as these compounds are relatively immobile in soil and when applied to leaves, they are readily absorbed and translocated within the plants and show immediate results.

Soil Drench: The chemical is mixed with appropriate proportions of water and the soil is drenched with the liquid at the tree or plant basins. At the time of application of the chemical should be kept moist or wet.

Trunk Soil Line Pour Method: The chemical is applied at the point of contact of the trunk and the soil near the tree trunk basins to a particular depth.

Trunk Injection: The chemical is mixed with appropriate proportions of water and then is injected into the trunk at appropriate height by using arbojets.

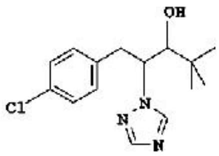
Soil Injection: The chemical is mixed with appropriate proportions of water and then is injected into the soil near tree trunk by using arbojets.

Seed Treatment: A novel seed treatment technology that enables efficient use of triazoles has been developed recently. The triazoles are administered via imbibitions followed by acclimation, and these “programmed” seeds develop seedlings that express a high degree of resistance to a variety of environmental stresses. Depending on the species, seeds were imbibed for a period of 2 to 16 h at room temperature.

Compared to other conventional methods of application like foliar spray or soil drench, seed treatment procedure has several advantages which include simplicity, cost effectiveness reduced chemical concentration, little or no persistence and minimal spread of the chemical in the environment. This procedure also eliminates conventional fungicide seed coating treatment since the triazoles themselves are potent fungicides. The treated seeds may be stored as long as one year without any loss in efficacy.

The two most important triazole plant growth regulators that are proved to be most effective and are widely used on several horticultural crops are uniconazole and paclobutrazol.

Uniconazole (S-3307D, XE-1019, UNZ)

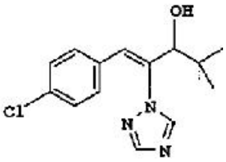


TN: Sumagic, Prunit

CN: (E)-(RS)-1-(4-chlorophenyl)-4, 4-dimethyl-2-(1H-1, 2, 4-triazol-1-yl) pent-1-en-3-ol.

Uniconazole is most widely used in ornamentals (bedding plants, potted plants, woody ornamentals and turf grass management etc.) for growth control and it is proved less effective in fruit crops.

Paclobutrazol (PP333, PBZ)



TN: Cultar, Bonzi

CN: (2RS, 3RS)-1-(4-chloropentyl)-4, 4-dimethyl-2-(1H-1, 2, 4-triazol-1-yl) pentan-3-ol.

Paclobutrazol is very effectively used in several fruit crops as plant growth regulator and is supplied in different formulations like, SL, WP, SC, etc. Cultar contains 25% a.i. of paclobutrazol that is widely used for fruit crops.

Effects of Paclobutrazol Observed in a Wide Range of Fruit Species

Some of the plant responses to paclobutrazol when applied to them by various application methods are listed below as,

1. Reduced vegetative (shoot and internodal) growth and canopy spread
2. Increased radial growth of roots
3. Increased flower bud formation
4. Increased flowering
5. Increased fruit set
6. Improved fruit quality (size, weight, color and storage properties
7. Greater physiological tolerance of plants, flowers and fruits to frost, drought and other environmental stresses
8. Suppression of various fungal diseases (Apple scab, Mango malformation) when used in a repeated foliar spray programme

The effect of paclobutrazol (Cultar) in the retardation of vegetative growth, induction of flowering, enhanced fruit set and improved fruit qualities and also in overcoming the environmental stresses like, drought, high temperatures, chilling (low) temperatures etc. have been reviewed below.

Cultar was used to induce flowering in mango cv. Langra during off year. It was applied in both on and off seasons. Effects on flowering, fruiting and fruit qualities were more pronounced in the off year than on year. It was found that soil application of cultar @ 5 g a.i./tree was most effective to induce more number of flowering shoots and improved fruit set and fruit retention during the off year. Highest fruit yield during off year was recorded under soil application of cultar @ 5 g a.i./tree followed by 10 g a.i./tree, the yield being 54.26 and 52.27 Kg/tree respectivel. Soil treatment with cultar also improved all the fruit qualities than foliar treatments and both the controls (Hoda *et al*., 2001).

Burondkar and Gunjate (1993) conducted an experiment in a distinctly alternate bearing mango cultivar, Alphonso for three successive years to control vegetative growth and to induce regular and early cropping with soil drench (5 g and 10 g per tree) and foliar (500,1000 and 2000 ppm) application of paclobutrazol in July-August every year. The pooled data on vegetative growth, flowering and fruit yield revealed that paclobutrazol as soil application @ 5 g and 10 g per tree produced significantly minimum outbreaks of September-October vegetative flushes (5.12 and 5.31%) as compared to untreated control (48.54%). Both of these paclobutrazol treatments gave 3 to 4 weeks early and profuse flowering (82.16 and 85.85%) as compared to control (34.16%) and recorded consistently 2.6 times more annual yields (274.19 and 287.98 fruits per tree) as compared to control (101.98 fruits per tree) without affecting fruit size and quality. Soil drench was more significant, convenient and cost effective.

Smeirat and Qrunfleh (1989) studied the effect of paclobutrazol on vegetative and reproductive growth of 16 year old Lisbon lemon for two seasons. Paclobutrazol sprayed at various concentrations (500, 1000 and 2000 ppm) significantly reduced shoot length and internode length and increased shoot diameter in both the seasons. Paclobutrazol sprayed at 2000 ppm significantly reduced node number also. Initial and final fruit set were significantly increased only in the year of paclobutrazol application.

Application of cultar (paclobutrazol) reduced shoot growth significantly compared to the control, which resulted in profuse flowering, higher sex ratio, increased fruit set and yield of Rose scented litchi. The TSS content of litchi fruits was higher in cultar treated trees. Higher dose of cultar (5 ml/m^2 plant spread) proved better than the lower dose (3 ml/m^2 plant spread) in controlling vegetative flush and increasing flowering and yield. Similarly, cultar application 90 days before bud break was found to be more effective than its application 60 days before bud break. Paclobutrazol thus holds promise in increasing flowering, fruit set, yield and quality of fruits (Ahmad *et al*., 2000).

Trunk Soil Line Pour method (TSLP) of cultar (paclobutrazol) @0.025 to 1.2 g a.i. cm^{-1} Trunk Diameter (TD) at late leaf fall stage over two years controlled vegetative growth, enhanced flowering and fruit quality in 10-11 year old Gola pear trees. Cultar @0.3 g a.i. cm^{-1} trunk diameter lowered the vegetative growth to half to one third with more than 1.35 times increase in yield and considerable improvement in fruit quality. Fruit quality and yield improved further in higher levels of cultar (0.6 and 1.2 g a.i. cm^{-1} trunk diameter) but only at the expense of severe reduction in growth of the fruiting trees (Ratna and Bist, 1997).

Sankhla *et al*. (1989) studied the effect of paclobutrazol on amelioration of drought and high temperature injury in fruits of ber cv. Seb. Soil applied paclobutrazol (@ 8 mg a.i. per tree) inhibited the elongation growth of branches and intensified the green color of the foliage. Fruits from treated plants consistently maintained higher contents of sugars and ascorbic acid than the control fruits. Under stress conditions in the field, fruits from paclobutrazol treated trees exhibited elevated levels activities of scavenger enzymes like catalase, peroxidase and superoxide dismutase and decreased lipid peroxidation. Paclobutrazol also minimized the moisture loss from the fruits and greatly reduced cracking of fruits caused by excessive moisture and thermal stress.

CONCLUSION

The effects of triazoles have also been evaluated on several tropical and temperate fruit plants. Of all the triazole plant growth regulators, paclobutrazol proved to be effective in retarding vegetative growth, enhancing yields and better performance under environmental stresses in a wide range of fruit species. It is more effective in inducing regular and early cropping in alternate bearing cultivars of mango. However, variable effects within a genus/species/cultivar grown in different countries were also apparent. Overall, triazoles appear to have potential beneficial effects on growth and yield of several tropical fruit trees. However, their large scale use in the field may be limited until the problem related to persistency can be fully resolved.

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