INNSPUB

Journal of Biodiversity and Environmental Sciences | JBES
ISSN: 2220-6663 (Print); 2222-3045 (Online)
Website: https://www.innspub.net
E-mail contact: info@innspub.net
Vol. 29, Issue: 5, p. 33-42, 2026

RESEARCH PAPER OPEN ACCESS

Triazole mediated enhancement of antioxidant compounds and carbohydrate metabolizing enzymes in ginger rhizomes

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Key words: Triazole, Hexaconazole, Uniconazole, *Zingiber officinale,* Antioxidant, Carbohydrate metabolism

Received: 19 October, 2026 **Accepted:** 29 October, 2026 **Published:** 06 November, 2026

DOI: https://dx.doi.org/10.12692/jbes/29.5.33-42

ABSTRACT

Triazole fungicides are widely used for disease control in crops, but emerging evidence suggests they can also act as metabolic elicitors that enhance nutraceutical quality in medicinal plants. This study evaluated the effects of hexaconazole and uniconazole, applied individually and in combination, on key biochemical parameters in *Zingiber officinale* (ginger) rhizomes across 20, 40 and 60 days of growth. Total phenol, ascorbic acid and α-tocopherol contents increased progressively with plant age and were significantly elevated by triazole treatments in a dose-dependent manner. The combined application of hexaconazole + uniconazole at 50:50 mg produced the highest total phenol (14.18 ± 0.61 mg GAE/g) and ascorbic acid (6.88 ± 0.13 mg/g) at 60 days, indicating synergistic stimulation of antioxidant biosynthesis. For α-tocopherol, hexaconazole at 50 mg alone was most effective (7.85 ± 0.09 mg/g), surpassing both uniconazole and the combined treatment. Enzymes involved in carbohydrate metabolism starch phosphorylase, acid invertase and sucrose synthase were also up regulated, with hexaconazole generally outperforming uniconazole except for sucrose synthesis, where uniconazole 50 mg yielded the highest activity (5.84 ± 0.13 units). These findings demonstrate that triazole fungicides, beyond their antifungal role, can function as biostimulants that enhance both primary and secondary metabolism in ginger, thereby improving its nutritional and phytochemical quality.

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INTRODUCTION

Ginger (*Zingiber officinale* Roscoe) is a globally valued medicinal and culinary crop, whose rhizomes accumulate a wide range of bioactive phytochemicals and serve as a major reservoir for photosynthesised carbon (Edo *et al.,* 2025). The quality and yield of ginger are strongly influenced by agronomic and environmental treatments that modulate the pathways controlling primary metabolism, particularly those governing carbohydrate synthesis, allocation and utilization (Ghasemzadeh *et al.,* 2014). Key indicators of this metabolic status are total phenolics, ascorbic acid and α-tocopherol compounds. These reflect both antioxidant capacity and the balance between primary and secondary metabolism (Ghasemzadeh *et al.,* 2010). Furthermore, this includes the activities of enzymes associated with starch phosphorylase, acid invertase and sugar complex. All of these regulate the flow of carbon between storage and transport forms.

Increased CO_2, light intensity, salicylic acid and other growth-modifying treatments have been shown to alter the carbohydrate profiles and associated enzymatic activities in ginger.

For example, CO_2 enrichment increases total carbohydrates, sugars, glucose and fructose in leaves and tubers, this occurs in conjunction with enhanced sucrose synthesis and its subsequent hydrolysis via acid invertase. Similarly, variations in photosynthetic intensity affect the synthesis of phenolics and flavonoids, linking the energy available from photosynthesis with the accumulation of secondary metabolites. Exogenous salicylic acid has also been reported to increase the total soluble carbohydrate content in ginger varieties, highlighting the susceptibility of carbon metabolism to hormonal and stress-related signaling (Li *et al.,* 2012).

Although extensive studies have been conducted on the medicinal properties of ginger and its effects on carbohydrate-biochemical enzymes in diabetic models, phenolics, few studies have systematically investigated how different growth treatments reshape the plant's internal carbohydrate metabolism through concurrent changes in total phenol, ascorbic acid, α-tocopherol and key biochemical enzymes. Therefore, this study estimates the accumulation of total phenol, ascorbic acid, α-tocopherol, starch phosphorylase, acid invertase and sugar oxidation in *Z. officinale* subjected to combinations of different growth treatments (Abdulrazaq *et al.,* 2012; Kazeem *et al.,* 2013). This approach aims to elucidate how these methods reshape carbohydrate metabolism and its associated antioxidant defense systems. By integrating these biochemical indicators, this study aims to provide a mechanistic basis for developing agricultural practices that enhance both yield and phytochemical quality in ginger (Hatiskar *et al.,* 2025).

MATERIALS AND METHODS

Experimental plant material and treatments

Healthy, uniform rhizomes of *Zingiber officinale* Roscoe were selected and planted under controlled experimental conditions. Plants were maintained with uniform soil, irrigation, nutrient supply, light and temperature conditions throughout the study. Any plants showing mechanical damage, disease symptoms, or poor establishment were excluded. The experiment consisted of seven growth-regulator treatments:

T_0: Control, untreated plants
T_1: Hexaconazole, 25 mg
T_2: Hexaconazole, 50 mg
T_3: Uniconazole, 25 mg
T_4: Uniconazole, 50 mg
T_5: Hexaconazole + Uniconazole, 25:25 mg
T_6: Hexaconazole + Uniconazole, 50:50 mg

The required concentrations of hexaconazole and uniconazole were prepared by using distilled water. The solutions were applied uniformly to the plants by foliar spraying, depending on the experimental design. The control plants received an equal volume of distilled water. Each treatment was maintained in at least three independent replicates and the position of the pots or plots was randomized to minimize environmental variation.

Collection and preparation of samples

Plant samples were collected at the same physiological stage and at the same time of day to reduce variation caused by plant age and diurnal changes in metabolism. Young, fully expanded leaves and/or rhizome tissues were collected separately from each treatment.

Approximately 5–10 g of fresh tissue was collected from each replicate. The samples were washed briefly with distilled water to remove surface particles and were gently blotted dry. A portion of the fresh material was used immediately for ascorbic acid analysis. The remaining samples were rapidly frozen in liquid nitrogen, transferred to labelled sterile bags and stored at −80°C until biochemical and enzyme analyses were performed. For each analysis, the tissue was weighed accurately. All extractions were conducted under cold conditions and the extracts were protected from direct light wherever necessary. Enzyme assays were performed using freshly prepared extracts or appropriately stored frozen extracts.

Estimation of total phenolic content

Total phenolic content was determined using the Folin–Ciocalteu colorimetric method, with minor modifications. Approximately 0.5 g of fresh or freeze-dried *Z. officinale* tissue was homogenized with 5–10 mL of 80% methanol. The homogenate was shaken for 30min and centrifuged at approximately 10,000 rpm for 10 min. The clear supernatant was collected and used for analysis.

For the assay, 0.5 mL of the extract was mixed with 2.5 mL of ten-fold diluted Folin–Ciocalteu reagent. After 5 min, 2.0 mL of 7.5% sodium carbonate solution was added. The mixture was vortexed and incubated at room temperature in the dark for approximately 30 min. The absorbance was measured at 765 nm using a UV–visible spectrophotometer. Folin–Ciocalteu assays are commonly used for ginger phenolic estimation, with gallic acid serving as the calibration standard.

A reagent blank containing extraction solvent instead of plant extract was prepared for background correction. Gallic acid standards were prepared over an appropriate concentration range and a calibration curve was generated (Nithya *et al.,* 2015). The total phenolic content was calculated from the standard curve and expressed as milligrams of gallic acid equivalents per gram of sample:

$$C = c \times V / m$$

Formula components

C: Total phenolic content in mg GAE/g, c: Concentration of gallic acid established from the calibration curve in mg/mL, V: Volume of the extract solution in mL, m: Weight of the plant extract in grams (Ainsworth and Gillespie, 2007).

Estimation of ascorbic acid

Ascorbic acid was estimated using the 2,6-dichlorophenol-indophenol method. Fresh tissue was extracted immediately after collection because ascorbic acid is readily oxidized during prolonged exposure to air, light and high temperature.

Approximately 1 g of fresh tissue was homogenized in chilled 1% phosphate–citrate buffer. The homogenate was centrifuged at 14,000 rpm for 10 min at 4°C. The supernatant was collected and kept on ice until analysis. Phosphate citrate extraction followed by reaction with 2,6-dichlorophenol-indophenol is a commonly reported procedure for plant ascorbic acid estimation.

A standard ascorbic acid solution was prepared in the same extraction medium. Suitable aliquots of the sample extract were mixed with freshly prepared 2,6-dichlorophenol-indophenol solution. The absorbance was measured rapidly at approximately 518 nm.

Alternatively, the extract may be titrated with standardized dye until a faint pink colour persists for approximately 15 s. The dye was standardized against a known concentration of ascorbic acid before sample analysis (Xie and Gong, 2024).

The ascorbic acid concentration was calculated from the standard curve and expressed as milligrams per gram fresh weight:

$$\text{Ascorbic acid}(mg/100\text{g}) = \frac{\text{Titre value (V)} \times \text{Dye factor(DF)} \times \text{Total volume made up (V)}}{\text{Aliquot of sample taken } (V_1) \times \text{Weight Volume of sample (W)}} \times 100$$

Definition of variables

Titre value (V): Volume of dye (DCPIP) consumed during the titration of the sample extract (in mL)., Dye factor (DF): Amount of standard ascorbic acid equivalent to 1 mL of the dye solution (mg/mL), found by standardizing the dye., Total volume (V_2): Total volume to which the sample extract was diluted., Aliquot (V_1): Volume of the diluted sample extract taken for each titration, Weight (W): Weight of the actual food sample taken initially for extraction (g).

Estimation of α-tocopherol

α-Tocopherol was estimated from the petroleum ether extract using a colorimetric method based on the reduction of ferric ions to ferrous ions and subsequent formation of a coloured complex.

Approximately 1 g of fresh or freeze-dried tissue was homogenized with chilled acetone. The homogenate was filtered or centrifuged and the solvent fraction was transferred to a separating funnel. The extract was partitioned against petroleum ether. The petroleum ether layer was collected, washed with distilled water to remove polar impurities and dried over anhydrous sodium sulfate. The solvent was evaporated under reduced light or a gentle stream of nitrogen and the residue was redissolved in a known volume of ethanol.

An aliquot of the extract was mixed with an appropriate ferric chloride solution and α,α′-dipyridyl reagent. The mixture was incubated in the dark for colour development and absorbance was measured at approximately 520 nm. A reagent blank was prepared without plant extract. A standard curve was prepared using known concentrations of α-tocopherol and the results were expressed as milligrams of α-tocopherol per gram of fresh or dry tissue (Cayuela and García, 2017).

All glassware and extracts were protected from strong light because tocopherols are light-sensitive. The exact solvent system, reagent concentrations, incubation time and detection wavelength should be kept identical for the standards and samples.

$$Concentration\ of\ Tocopherol = \left(\frac{A_{sample}}{A_{standard}}\right) \times\ Concentration\ of\ standard$$

Preparation of enzyme extract

Enzyme extracts for starch phosphorylase, acid invertase and sucrose synthase analyses were prepared at 0–4°C. Approximately 1 g of frozen plant tissue was ground thoroughly in liquid nitrogen and homogenized with 5–10 mL of chilled extraction buffer.

A suitable extraction buffer consisted of 100 mM sodium phosphate or sodium succinate buffer, pH 5.8–6.5, containing 1 mM EDTA, 5 mM magnesium chloride, 10% glycerol, 5 mM β-mercaptoethanol and 1 mM phenylmethylsulfonyl fluoride. The addition of β-mercaptoethanol and a protease inhibitor helped to protect enzymes from oxidation and proteolysis.

The homogenate was centrifuged at 15,000 rpm for 20 min at 4°C. The supernatant was carefully collected without disturbing the pellet and used as the crude enzyme extract. A cold-buffer wash or desalting step may be included when interfering sugars, phenolics, or salts are high. Protein concentration in each enzyme extract was determined using the Bradford method and enzyme activities were expressed both per gram fresh weight and per milligram soluble protein.

Assay of starch phosphorylase

Starch phosphorylase activity was determined by measuring the formation of glucose-1-phosphate from starch and inorganic phosphate. Starch phosphorylase assays commonly use a succinate-based extraction buffer containing glycerol, EDTA, β-mercaptoethanol and magnesium ions (Dai *et al.,* 2016).

The reaction mixture contained sodium succinate buffer, pH 5.8, soluble starch, inorganic phosphate, magnesium chloride and a measured volume of enzyme extract. The reaction was initiated by adding the enzyme extract and incubated at a selected temperature, such as 30°C, for a fixed period. A control reaction was prepared by adding the enzyme extract after termination of the reaction.

The reaction was stopped by heating. The amount of glucose-1-phosphate formed was determined using a suitable colorimetric phosphate or reducing-sugar procedure. Absorbance was recorded at the wavelength recommended for the selected assay. Starch phosphorylase activity was calculated using a glucose-1-phosphate standard curve and expressed as micromoles of product formed per minute per gram fresh weight or per milligram protein.

$$(gulcose)_n + P_i = (gulcose)_{n-1} + gulcose - 1 - phposphate$$

$(gulcose)_n$: A starch or α-1,4-D-glucan chain with n glucose units, P_i: Inorganic orthophosphate, $(gulcose)_{n-1}$: The shortened starch chain after removing one terminal glucose unit and Glucose-1-phosphate: α-D-glucopyranosyl phosphate released from the non-reducing end of the chain.

Assay of acid invertase

Acid invertase activity was measured by estimating the reducing sugars released from sucrose under acidic conditions. The enzyme extract was prepared as described above, but the reaction pH was adjusted to 4.5, which is suitable for acid invertase activity.

The reaction mixture contained sodium acetate or citrate buffer, pH 4.5, sucrose as the substrate and an aliquot of enzyme extract. The mixture was incubated at approximately 37°C for 60 min. The reaction was terminated by adding 3,5-dinitrosalicylic acid reagent and heating the tubes in a boiling-water bath for approximately 5 min. After cooling, the volume was adjusted with distilled water and absorbance was measured at 540 nm.

The reducing sugars released during the reaction were calculated using a glucose or fructose standard curve. DNS is frequently used to determine reducing sugars generated by invertase activity. The activity was expressed as micromoles of reducing sugar released per minute per gram fresh weight or per milligram soluble protein (Guo *et al.,* 2020).

$$\text{Acid Invertase Activity } (U/ml) = \frac{B \times D}{T \times V}$$

(B) = Amount of reducing sugar (glucose/fructose equivalents) liberated during the reaction, calculated in micromoles (μmol) from a standard curve. (D) = Dilution factor of the original enzyme extract. (T) = Incubation time of the reaction in minutes. (V) = Volume of the crude/diluted enzyme sample added into the assay mix in milliliters (mL).

Assay of sucrose synthase

Sucrose synthase activity was measured in the sucrose synthesis direction by determining the formation of sucrose from UDP-glucose and fructose. Sucrose synthase assays in the synthesis direction generally contain UDP-glucose and fructose, with the reaction carried out in a buffered medium (Hariyanto *et al.,* 2026).

The reaction mixture contained 100 mM HEPES–NaOH buffer, pH 8.5, UDP-glucose, fructose, potassium chloride, sodium chloride, magnesium chloride and enzyme extract. The reaction was incubated at approximately 37°C for 40 min. The reaction was terminated by heating or by adding DNS reagent, depending on the selected method.

The sucrose formed was quantified using a suitable enzymatic or colorimetric procedure. If the DNS method was used, the reaction products were measured after hydrolysis or conversion to reducing sugars under the validated assay conditions. A sucrose standard curve was used for quantification. The activity was expressed as micromoles of sucrose formed per minute per gram fresh weight or per milligram protein.

Statistical analysis

The experiment was arranged in a completely randomized design with three or more independent biological replicates per treatment. The results were expressed as mean ± standard deviation. Data were tested for normality and homogeneity of variance before analysis.

RESULTS AND DISCUSSION

The total phenol content in *Zingiber officinale* rhizome increased progressively with plant age and was significantly enhanced by triazole fungicide treatments. In untreated control plants, phenol levels rose from 6.16 ± 0.05 mg GAE/g at 20 days to 10.05 ± 0.12 mg GAE/g at 60 days, reflecting natural accumulation of phenolic compounds during ginger development (Fig. 1). All fungicide treatments elevated phenol content above control values at every growth stage, with the combined application of hexaconazole + uniconazole at 50:50 mg producing the highest phenol content (14.18 ± 0.61 mg GAE/g at 60 days) (Ali *et al.,* 2018).

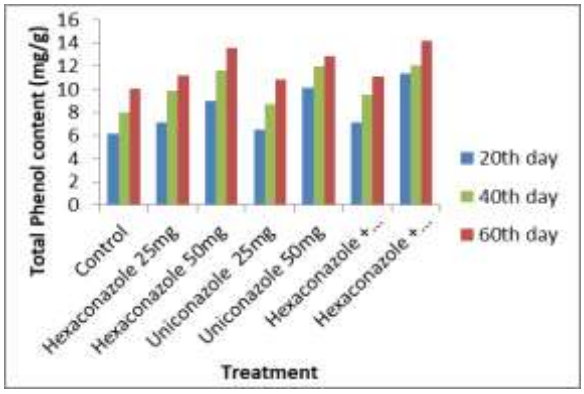


Fig. 1. Estimation of total phenol content of treated and untreated *Zingiber officinale* extract

Among individual treatments, hexaconazole at 50 mg consistently outperformed the 25 mg dose, yielding 13.55 ± 0.06 mg GAE/g at 60 days compared to 11.16 ± 0.56 mg GAE/g.

Uniconazole showed a similar dose dependent response, though its efficacy was lower than hexaconazole at equivalent concentrations. The synergistic effect of combined triazoles was evident, as the 50:50 mg combination exceeded both individual 50 mg treatments. This enhancement of phenolic metabolism aligns with previous reports that triazole compounds can stimulate secondary metabolite biosynthesis in medicinal plants, potentially through modulation of the shikimate phenylpropanoid pathway (Ayustaningwarno *et al.,* 2024).

Ascorbic acid accumulation followed a pattern parallel to total phenols, increasing with plant maturity and responding positively to triazole applications. Control plants exhibited a gradual rise from 0.80 ± 0.12 mg/g at 20 days to 2.89 ± 0.22 mg/g at 60 days (Fig. 2). Hexaconazole at 50 mg induced the most pronounced increase among single treatments, reaching 6.31 ± 0.12 mg/g at 60 days more than double the control value (Sangwan *et al.,* 2014).

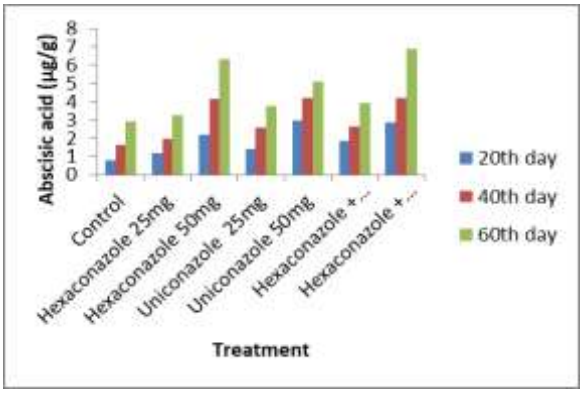


Fig. 2. Estimation of ascorbic acid of treated and untreated *Zingiber officinale* extract

The combined hexaconazole + uniconazole treatment at 50:50 mg produced the highest ascorbic acid content (6.88 ± 0.13 mg/g at 60 days), surpassing even the best individual treatment. This suggests that the two triazoles may act through complementary mechanisms to enhance antioxidant vitamin biosynthesis. Lower doses (25 mg) of both fungicides showed modest improvements over control but were substantially less effective than their 50 mg counterparts. The progressive increase across growth stages indicates that triazole induced ascorbic acid synthesis is sustained throughout ginger development rather than being a transient stress response (Sarker, 2021).

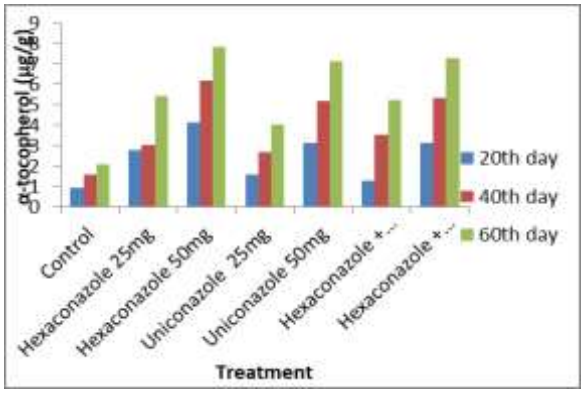


Fig. 3. Estimation of α-tocopherol of treated and untreated *Zingiber officinale* extract

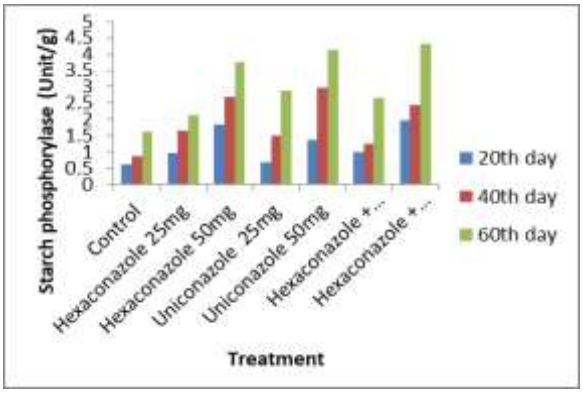


Fig. 4. Analysis of starch phosphorylase of treated and untreated *Zingiber officinale* extract

α-Tocopherol levels in ginger rhizome were markedly elevated by triazole treatments, with hexaconazole demonstrating superior efficacy compared to uniconazole. Control plants accumulated α-tocopherol from 0.96 ± 0.08 mg/g at 20 days to 2.11 ± 0.07 mg/g at 60 days (Fig. 3).

Hexaconazole at 50 mg produced the highest values among all treatments, reaching 7.85 ± 0.09 mg/g at 60 days approximately 3.7 fold higher than the control.

Uniconazole treatments, while effective, yielded lower α-tocopherol content than equivalent hexaconazole doses (7.15 ± 0.96 mg/g for 50 mg uniconazole vs. 7.85 ± 0.09 mg/g for 50 mg hexaconazole at 60 days). Interestingly, the combined 50:50 mg treatment did not exceed hexaconazole 50 mg alone (7.29 ± 0.51 mg/g), suggesting that for α-tocopherol biosynthesis, hexaconazole may be the dominant active component. The substantial enhancement of this lipid soluble antioxidant indicates that triazole fungicides can improve the nutritional quality of ginger by boosting its vitamin E content (Mesomo *et al.,* 2012).

Starch phosphorylase, a key enzyme in starch metabolism, showed increased activity in response to triazole treatments. Control plants exhibited enzyme activity of 0.60 ± 0.20 units at 20 days, rising to 1.62 ± 0.24 units at 60 days (Fig. 4). Hexaconazole at 50 mg induced the highest activity (3.74 ± 0.21 units at 60 days), followed closely by the combined 50:50 mg treatment (4.32 ± 0.07 units) (Tiwari and Kumar, 2012).

The dose-dependent response was clear, with 50 mg treatments consistently outperforming 25 mg applications for both fungicides. Uniconazole at 50 mg yielded 4.12 ± 0.36 units at 60 days, indicating comparable efficacy to hexaconazole for this particular enzyme. Enhanced starch phosphorylase activity suggests improved starch turnover and carbohydrate metabolism, which may contribute to the increased tuber yield and quality reported in triazole treated ginger. The progressive increase across growth stages indicates sustained enzymatic enhancement throughout rhizome development.

Acid invertase, responsible for sucrose hydrolysis into glucose and fructose, was significantly upregulated by triazole applications. Control plants showed activity increasing from 0.39 ± 0.45 units at 20 days to 0.96 ± 0.05 units at 60 days. Hexaconazole at 50 mg produced the highest activity (2.61 ± 0.28 units at 60 days), representing a 2.7 fold increase over control (Fig. 5).

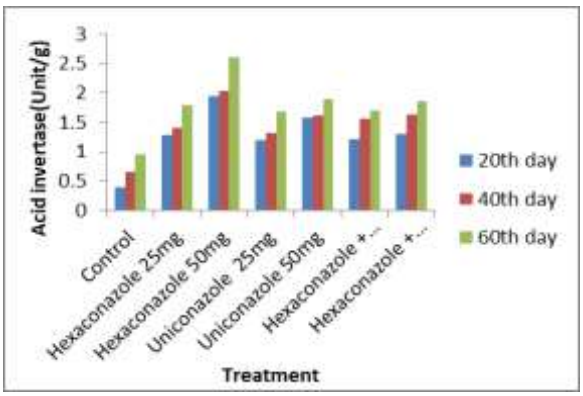


Fig. 5. Analysis of acid invertase of treated and untreated *Zingiber officinale* extract

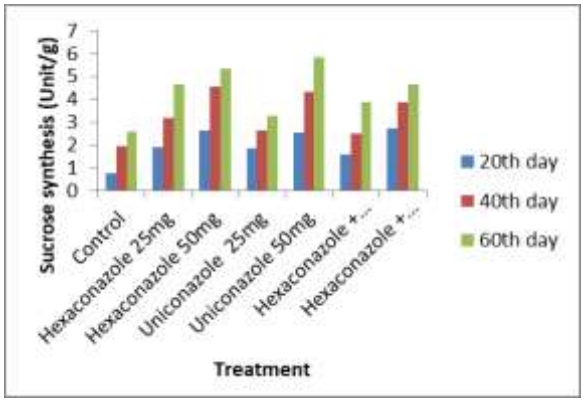


Fig. 6. Analysis of sucrose synthesis of treated and untreated *Zingiber officinale* extract

Uniconazole treatments were less effective than hexaconazole for acid invertase induction, with 50 mg uniconazole yielding 1.89 ± 0.11 units at 60 days. The combined treatments did not show synergistic enhancement beyond hexaconazole 50 mg alone. This selective enhancement of acid invertase by hexaconazole suggests differential regulation of sucrose metabolizing enzymes by different triazole structures. Elevated acid invertase activity may facilitate increased hexose availability for secondary metabolite biosynthesis and energy metabolism in developing rhizomes (Tauzin and Giardina, 2014).

Sucrose synthesis activity increased substantially in triazole treated plants, with hexaconazole 50 mg producing the highest values (5.34 ± 0.22 units at 60 days) compared to control (2.64 ± 0.05 units). Uniconazole 50 mg was remarkably effective for this parameter, yielding 5.84 ± 0.13 units at 60 days the highest among all treatments. These contrasts with other parameters where hexaconazole generally outperformed uniconazole, indicating that uniconazole may have specific stimulatory effects on sucrose synthase or related enzymes (Dangwal and Suri, 2023).

The combined 50:50 mg treatment produced intermediate values (4.67 ± 0.26 units), suggesting that for sucrose synthesis, uniconazole's effect may be partially antagonized by hexaconazole when applied together. The progressive increase across all treatments from 20 to 60 days indicates that triazole induced enhancement of sucrose metabolism is maintained throughout rhizome development (Abdulrazaq *et al.,* 2012). Enhanced sucrose synthesis capacity likely supports increased carbohydrate allocation to developing tubers, contributing to improved yield and quality parameters (Paudel *et al.,* 2025).

The data demonstrate that triazole fungicides, particularly hexaconazole and uniconazole applied at 50 mg, significantly enhance the biochemical quality of *Zingiber officinale* rhizomes. The consistent dose dependent responses across all measured parameters suggest that these compounds act as metabolic elicitors, stimulating both primary carbohydrate metabolism (starch phosphorylase, acid invertase, sucrose synthesis) and secondary antioxidant biosynthesis (phenols, ascorbic acid, α-tocopherol) (Ali *et al.,* 2018).

The superior performance of combined treatments for phenol and ascorbic acid content indicates potential synergistic interactions between hexaconazole and uniconazole for certain biosynthetic pathways. However, for α-tocopherol and sucrose synthesis, individual treatments (hexaconazole 50 mg and uniconazole 50 mg, respectively) outperformed combinations, suggesting pathway specific optimization may be beneficial. These findings support the use of triazole fungicides not only for disease management but also as biostimulants for enhancing the nutraceutical quality of ginger rhizomes (Ayustaningwarno *et al.,* 2024).

CONCLUSION

The present investigation reveals that triazole fungicides, particularly hexaconazole and uniconazole, exert significant biostimulatory effects on the biochemical profile of ginger rhizomes. Across all growth stages, triazole applications consistently enhanced the accumulation of phenolic compounds, ascorbic acid and α-tocopherol, with the most pronounced effects observed at the 50 mg dose. The superior performance of the hexaconazole + uniconazole combination for total phenol and

ascorbic acid suggests synergistic interactions that may amplify flux through the shikimate-phenylpropanoid pathway, a central route for phenolic and antioxidant biosynthesis in plants.

From an agricultural and nutraceutical perspective, these results support the dual use of triazole fungicides not only for managing fungal diseases but also as tools for biofortification of ginger rhizomes. Optimizing triazole type, dose and combination could allow targeted enhancement of specific quality traits, such as antioxidant capacity and vitamin content, thereby increasing the functional food value of ginger. Future studies should explore the molecular mechanisms underlying these effects, including gene expression changes in phenylpropanoid and terpenoid pathways and assess whether similar biostimulatory effects occur in other medicinal and spice crops.

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