CIBTech Journal of Biotechnology ISSN: 2319–3859 (Online)
An Open Access, Online International Journal Available at http://www.cibtech.org/cjb.htm
2025 Vol. 14, pp.1-11/Pooja
Research Article

ALTERATION OF ENZYMATIC ANTIOXIDATIVE DEFENSE MECHANISMS IN SUSCEPTIBLE AND RESISTANT TOMATO CULTIVARS INFECTED WITH *MELOIDOGYNE INCOGNITA*

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ABSTRACT
Tomato (*Solanum lycopersicum*) yields are severely threatened by root-knot nematode (*Meloidogyne incognita*) infestations on a global scale. The enzymatic antioxidant responses of two tomato cultivars, one susceptible (Pusa Early Dwarf) and one resistant (Hisar Arun), are examined in this study while they are infected with *M. incognita*. Important enzymatic antioxidant enzymes such as superoxide dismutase (SOD), ascorbate peroxidase (APX), and glutathione reductase (GR) were analysed after 20 days of *M. incognita* inoculation in this experiment. The results showed that the resistant cultivar had significantly higher enzyme activities than the susceptible one, indicating that it has a more effective system for scavenging reactive oxygen species (ROS). The resistant cultivars increased antioxidant capacity was correlated with greatly reduced galling indices, egg mass counts, and nematode reproduction rates. Experiments shed light on possible methods for creating tomato varieties resistant to nematodes through the use of biochemical markers and breeding programs, and they emphasize the importance of enzymatic antioxidant defenses in providing resistance against *M. incognita*.

Keywords: *Tomato, Meloidogyne incognita, Enzymatic antioxidants, SOD, APX, GR*

INTRODUCTION
Tomato (*Lycopersicon esculentum*) is regarded as the second most significant vegetable crop globally, following potato (Wakil *et al.,* 2018). Tomatoes contain significant amounts of carotenoids and phenolic compounds. It is also the source of lycopene, a carotenoid that contributes to its red hue. (Raiola *et al.,* 2014; Sacco *et al.,* 2019). Tomatoes are noted for their high content of Vitamins C and E (Marti and Cebollla 2016; Rao *et al.,* 2020). The production of tomatoes is affected by various abiotic factors. Tomato seedlings exhibit susceptibility to various abiotic stresses, including salinity (Rosca *et al.,* 2023). Moreover, salinity stresses significantly affect the quality and yield of tomato production (Zhang and Dai 2016; Alam *et al.,* 2021; Islam MM *et al.,* 2023). Abiotic stressors act as significant limitations on the growth and development of plants, negatively affecting agricultural productivity and the quality of plant produce (Kiratli *et al.,* 2024). Conversely, biotic stresses refer to the harmful effects induced by various diseases, which encompass bacteria, fungi, oomycetes, nematodes, and herbivores (Bhatla SC, A *et al.,* 2018; Balla A, *et al.,* 2021; Waqar *et al.,* 2023). Plants, as stationary organisms, have evolved complex molecular networks to efficiently respond and adapt to a range of stimuli. The existence of these networks can benefit plant survival by enhancing their resistance to different stimuli; however, this is often associated with a reduction in growth or yield, a phenomenon known as the "growth-immunity tradeoff" (Karasov *et al.,* 2017; Teixeira *et al.,* 2020; Lahlali, *et al.,* 2022). Genetic resistance in plants to incompatible pests is manifested through the activation of an immune system; however, the molecular mechanisms underlying pest recognition and immune expression, despite extensive research, remain inadequately comprehended (Du and Guo 2020; Wani *et al.,* 2022). The immune response elicited by soil-borne parasites, specifically root-knot nematodes (RKNs), in incompatible resistant tomato plants was

examined and contrasted with the compatible response observed in susceptible plants during RKN infestation. In compatible interactions, the invading nematode juveniles were permitted to develop and reproduce fully, whereas this process was hindered in incompatible interactions (Ebd Elgawad 2022; Molinari and Leonetti 2024).

Nematodes are ubiquitous and can be found in all conceivable locations worldwide. Nematodes constitute the most numerous metazoans on the planet. The assault by plant-parasitic nematodes is lethal to juvenile plants and frequently correlates with reduced productivity in mature plants. Among all economically significant nematodes, root-knot nematodes (*Meloidogyne spp*.) are among the most critical and destructive. It is recognized for its extensive global distribution. Among the identified *Meloidogyne* species, four major species that induce economic losses are *M. incognita*, *M. javanica, M. arenaria*, and *M. hapla* (Singh and Phulera 2015; Lilley *et al.,* 2024). The plant-parasitic nematodes inflict harm on crops, leading to economic losses for farmers by affecting cultivation and diminishing productivity. The global economic losses attributed to plant-parasitic nematodes are estimated to reach $157 billion, resulting in a 12.3% reduction in yield due to root-knot nematodes. (Phani *et al.,* 2021; Khan, 2023). In brinjal and tomato crops, among various biotic stresses, the plant-parasitic nematode known as root-knot poses a significant challenge. *Meloidogyne incognita* (Kofoid and White) is the predominant species, leading to significant yield and quality reductions, especially in Solanaceae crops (Thakur *et al.,* 2024). The RKN is known to infect crops during both the nursery stage and after transplantation in the field. The RKN attack on brinjal and tomato during the nursery stage can lead to plant mortality after transplanting, resulting in poor plant establishment, subpar harvest quality, and reduced field production (Pradhan, 2022). The RKN prepares the plant for invasion by additional soil-borne pathogens, leading to the emergence of a disease complex (Vashisth *et al.,* 2024).

Superoxide dismutase (SOD) is essential in the primary antioxidative defense mechanism in plants, catalyzing the dismutation of superoxide radicals (O_2^-) into hydrogen peroxide (H_2O_2) and molecular oxygen (O_2) (Saibi and Brini 2018; Ighodaro and Akinloye 2018; Islam *et al.,* 2022). Infection by *M. incognita* in tomato triggers a substantial oxidative burst resulting from nematode-induced cellular damage and stress signaling. Increased levels of reactive oxygen species (ROS), requiring a prompt antioxidative response (Ozougwu JC 2016). The present study revealed a significant up-regulation of SOD activity in both susceptible (Pusa Early Dwarf) and resistant (Hisar Arun) tomato cultivars following nematode inoculation. The resistant cultivar exhibited a more significant and sustained elevation in SOD activity than the susceptible cultivar, especially during the initial phases of infection. This indicates that increased SOD activity correlates with the prompt detection of nematode invasion and a more robust defensive response in resistant plants. The increased SOD activity in resistant cultivars aids in preserving cellular redox homeostasis by reducing oxidative damage, thereby restricting nematode establishment and reproduction. The comparatively diminished and postponed SOD induction in the susceptible cultivar may lead to oxidative damage and promote nematode colonization (Jahanbazian *et al.,* 2024).

Ascorbate peroxide (APX) is a crucial antioxidant enzyme in the ascorbate-glutathione cycle that neutralizes hydrogen peroxide (H_2O_2), a significant reactive oxygen species (ROS) generated during biotic stress, such as nematode infestation (Sakhno *et al.,* 2019; Abdelaal *et al.,* 2022) Following *M. incognita* infection, oxidative stress escalates; resulting in heightened APX activity to eliminate surplus H_2O_2 and avert cellular damage (EI-Beltagi *et al.,* 2011). APX collaborates with SOD and GR to modulate ROS levels. The augmentation of APX activity aids in alleviating oxidative damage in infected root tissues and may inhibit nematode development by fortifying host cell walls and activating resistance pathways (Afifi *et al.,* 2014; Yang *et al.,* 2023). This augmentation constitutes an initial antioxidative defense mechanism activated by nematode infiltration and movement. Resistant cultivars (e.g., Hisar Arun) demonstrate a more pronounced and earlier activation of APX activity compared to susceptible cultivars (e.g., Pusa Early Dwarf).

Glutathione reductase (GR) is an essential enzyme in the ascorbate–glutathione cycle, which preserves cellular redox equilibrium. It restores reduced glutathione (GSH) from its oxidized variant (GSSG), facilitating the ongoing detoxification of hydrogen peroxide (H_2O_2) by ascorbate peroxidase (APX) (Gill *et al.,* 2013; Couto *et al.,* 2016). Infection by *M. incognita* results in a substantial elevation of GR activity in tomato roots. The increase commences as early as three days post-inoculation and reaches its zenith during the initial formation of galls and the establishment of feeding sites (Talavera and Mizukubo 2001; Yang *et al.,* 2015; Mqsood *et al.,* 2020; Sikandar *et al.,* 2025). GR activity facilitates the regeneration of GSH, which is crucial for mitigating ROS produced as a result of nematode-induced cellular damage. This establishes a protective antioxidant barrier in the infected tissues, particularly in the root tips and developing galls. Resistant cultivars (e.g., Hisar Arun) exhibit elevated and sustained GR activity, facilitating enhanced redox equilibrium and constraining nematode proliferation. Susceptible cultivars (e.g., Pusa Early Dwarf) exhibit diminished or delayed GR activity, leading to inadequate ROS scavenging and increased oxidative stress, which exacerbates gall formation and nematode reproduction.

Plants employ intricate molecular mechanisms to initiate immune responses against pathogens and parasites. The plant immune response is modulated by various phytohormones, such as salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) (Roychowdhury *et al.,* 2025). Adapted pathogens can circumvent plant defenses by directly injecting effector molecules into plant cells. Endoparasitic sedentary nematodes (ESNs), including RKNs of the Meloidogyne genus, synthesize proteins in their esophageal glands and subsequently inject them into root cells through a stylet. An increasing amount of evidence indicates that the majority of these proteins function as effectors that can inhibit plant defense mechanisms during infection (Mantelin *et al.,* 2015; Xie *et al.,* 2016; Lin *et al.,* 2016). ROS are very important for plant defense. Primary and immediate response to pathogens involves the excessive generation of ROS at the infection site, including superoxide anion (O2•−) and hydrogen peroxide (H_2O_2). Reactive oxygen species subsequently elicit defense responses, including the hypersensitive response (Mansoor *et al.,* 2023; Mukherjee *et al.,* 2024). The meticulous regulation of ROS production and removal in plant tissues is essential to prevent irreversible cellular damage resulting from excessive ROS levels (Tyagi *et al.,* 2021). A variety of enzymes collaborates to regulate the plant antioxidant network, maintaining stable levels of ROS within plant cells. For instance, SOD facilitates the conversion of superoxide anions into H_2O_2 while catalase (CAT), the principal antioxidant enzyme in peroxisomes, catalyzes the breakdown of H_2O_2, producing water (H_2O) and oxygen. Guaiacol peroxidase (POD) facilitates the H_2O_2 dependent polymerization of hydroxy cinnamyl alcohol in lignin biosynthesis and the H_2O_2 dependent fortification of cell wall proteins, including. When a pathogen attacks, resistant plants often have lower levels of ROS detoxifying enzymes like peroxidase (POX) and CAT (Del *et al.,* 2006; Xu *et al.,* 2025).

Tomato plants are significantly harmed by *Meloidogyne incognita*, resulting in substantial yield and quality losses. The levels of ROS-detoxifying antioxidant enzymes are tightly regulated during pathogen infection, and reactive oxygen species (ROS) play a significant role in plant defenses (Yadav *et al.,* 2023; Abid *et al.,* 2025). The metabolism of ROS was investigated in RKN-resistant and RKN-susceptible tomato cultivars in this investigation. After nematode inoculation, the activities of enzymatic antioxidant (Ascorbate Peroxidase, Superoxide dismutase and Glutathione reductase) were examined in tomato resistant variety (Hisar Arun) and susceptible variety (Pusa Early Dwarf). *M. incognita* infected during the nursery stage and egg masses of *M. incognita* were extracted from the infected brinjal plants. The enzymatic antioxidative enzyme activities of tomato leaves from un-inoculated and inoculated plants were assessed after 20 days of infection. In comparison to susceptible varieties, the activity of antioxidant enzymes increased following infection with root-knot nematode in the resistant varieties of tomato. The activities of all enzymes increased following inoculation, with the exception of the APX enzyme, which showed a decrease.

MATERIALS AND METHODS

Collection of Experimental Plant Material and Egg Mass of M. incognita

Freshly harvested seeds of tomato varieties, Hisar Arun and Pusa Early Dwarf were obtained from Hisar Agriculture University (HAU) and Department of Horticulture IARI, New Delhi respectively. Egg masses of *M. incognita* were obtained from Dr. Zakaullah Khan, Division of Plant Quarantine, National Bureau of Plant Genetic Resources (NBPGR) New Delhi. The egg masses were placed onto tissue paper, which was supported by a wire gauge suspended in water within a petri dish, facilitating the hatching process of the eggs. The second stage juveniles (J2s) were subsequently inoculated onto brinjal plants cultivated in 30 cm diameter earthen pots for further multiplication. Seedlings of tomato genotypes, one week old and sown in pots, were inoculated with freshly hatched larvae of root knot nematode (*M. incognita*) at a concentration of 1 J2s per cc of soil. Samples of leaves were collected at 20 days post-inoculation with root-knot nematode. At the same time, leaf samples were collected from uninoculated plants, transported to the laboratory in an ice box, and analyzed for antioxidant enzymes.The sample underwent homogenization in 5ml of cold (40 C) extraction buffer utilizing a pre-chilled pestle and mortar. The mixture underwent centrifugation at 20,000g for duration of 10 minutes, after which the supernatant was collected and subsequently analyzed for enzyme activity.

Enzymatic Antioxidant

Enzyme extraction prepared to measure the enzymatic antioxidant enzyme activities (*Superoxide Dismutase,* Glutathione reductase and Ascorbate Peroxidase), leaf samples (1g) were taken per treatment and crushed in liquid nitrogen. The sample homogenized in 10 ml of 50 mM potassium phosphate buffer (pH 7.8) was centrifuged at 10,000 g for 20 min at 4 °C. The supernatant collected was used for the determination of enzyme activities.

Superoxide Dismutase (SOD) Activity

The activity of SOD was assessed following the methodology established by Dhinsa *et al.,* 1981. The enzyme SOD was prepared by grinding 1 g of leaf tissues in a pre-chilled mortar and pestle with 10 ml of chilled 0.1 M phosphate buffer at pH 7.5, which included 0.5 mM EDTA. The brie was filtered using cheesecloth, and the filtrate was centrifuged in a refrigerated centrifuge for 15 minutes at 20,000 g. The supernatant served as the enzyme extract. All operations were conducted at 4 degrees Celsius. The enzyme assay involved a 3.0 ml reaction mixture comprising 13 mM methionine, 25 mM nitroblue tetrazolium chloride (NBT), 0.1 mM EDTA, 50 mM phosphate buffer at pH 7.8, 50 mM sodium bicarbonate, and 0.1 ml of enzyme. The reaction commenced with the addition of 2 micromolar riboflavin, followed by exposure of the tubes to 15W fluorescent lamps for a duration of 15 minutes. The reaction was halted by turning off the light and covering the tubes with black cloth. Tubes lacking enzyme exhibited maximal color development. A non-irradiated complete reaction mixture that did not exhibit color functioned as a blank. Absorbance was measured at 560 nm, with one unit of enzyme activity defined as the amount of enzyme that decreased the absorbance reading by 50% relative to the control tubes without enzyme. The enzyme assay was conducted at 27 ± 2 °C. Enzyme activity was estimated using three samples of the material, with three measurements taken from each extract.

Glutathione Reductase (GR) activity

The activity of GR was assessed following the methodology established by Smith *et al., 1988*. The reaction was conducted in a 3 ml mixture comprising potassium phosphate buffer (100 mM; pH 7.5), 5,5-dithiobis-2-nitrobenzoic acid (DTNB; 0.5 mM), NADPH (66 µM), oxidized glutathione (GSSG; 0.66 mM), and enzyme extract (0.1 ml). The reaction commenced with the addition of 0.66 mM GSSG, and the increase in absorbance at 412 nm was recorded over 2 minutes at 10-second intervals. GR activity was quantified as µmol GSSG reduced per mg of protein per minute. The protein quantification was conducted following Bradford's (1976) methodology, utilizing Bovine Serum Albumin (BSA) as the standard.

Ascorbate Peroxidase (APX) activity

The activity of APX was assayed as given Nakano Y and Asada K (1981) with some modification. For the extract preparation 200mg, leaf extract in 5ml of 100mM PPB (pH7.0) and rotate at 8000*g for 10 minutes. The assay will be conducted on total of 3ml reaction mixture by adding 2.7 ml of 100 mM PPB (pH 7.0), 0.1 ml L-ascorbate and 0.15 ml H2O2. 100 µl of extract will be added to 0.6 ml of phosphate buffer for the assay. 100 µl of methylglyoxal and 0.1 ml of MgCl2 will be added to the same. The addition of 0.1 ml of GSH solution will start the reaction, which will take place at 25 ºC. At 240 nm, an increase in absorbance caused by the formation of S-D lactoylglutathione will be seen (Spectramax Plus, Molecular Devices, USA) every 15 seconds for three minutes. A change in absorbance of 0.1 will be regarded as one unit. Mg/protein/min units will be used to express the enzyme activity.

Bradford Assay for Protein Estimation

Bradford assay for protein estimation performed by the method Bradford (1976). Weigh 0.1g leaf tissue homogenize sample using a mortar and pestle in 0.5ml of phosphate buffer (pH7.5). Transfer leaf extract into centrifuge tube and make the volume 5ml with phosphate buffer. As a reference, distilled water used as blank. Prepared Bradford stock reagent in the lab by dissolving Coomassie Brilliant Blue G-250 dye in a suitable solvent (such as 95% methanol) and distilled water used to dilute the stock solution to the working solution. 0.1 ml of leaf extracts and incubates at room temperature for the 5-10 minutes. After incubation, at 595nm measure the absorbance on spectrophotometer of each sample and the BSA standards at the appropriate wavelength.

STATISTICAL ANALYSIS

Statistical analyses were performed with statistical software's GraphPad Prism (version 7.04) and XLSTAT (version 2023.3.1). All measurements were performed in triplicates. Two-way analysis of variance (ANOVA) with Tukey's correction was performed with Graph Pad Prism and the difference was considered significant at p-value ≤0.05.

RESULTS AND DISCUSSION

Protein content in resistant and susceptible genotypes of tomato infected with root-knot nematode

The protein content showed varying trends in response to *M. incognita* inoculations in both Hisar Arun and Pusa Early Dwarf varieties. In the Hisar arun variety, the protein content in the control plants decreased with *M. incognita* inoculation from 4.39 ± 0.21 to 3.21 ± 0.44. Under *M. incognita* inoculation, the protein content was lower than the control in Pusa Early Dwarf, decreasing from 3.68 ± 0.43 to 2.29 ± 0.13.

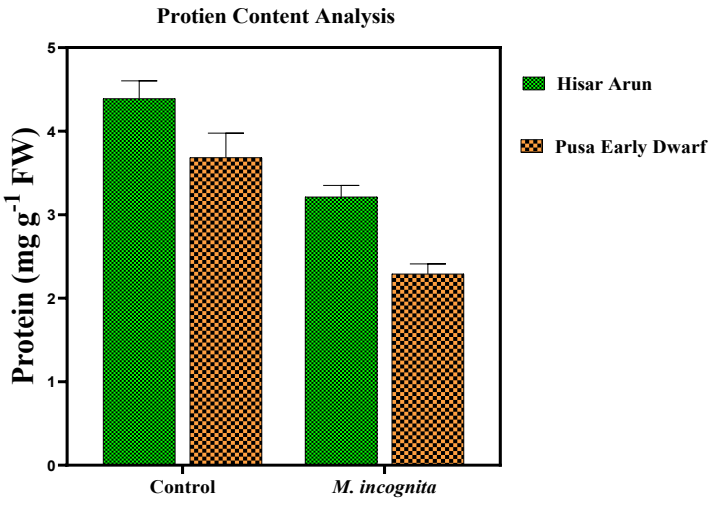

Figure 1: Protein content under un-inoculated (Control) and inoculated with *M .incognita* in resistant (Hisar Arun) and susceptible (Pusa early dwarf) tomato cultivars.

Superoxide dismutase content analysis in resistant and susceptible genotypes of tomato infected with root-knot nematode

SOD activity showed varying trends in response to *M. incognita* inoculations in both Hisar arun and Pusa Early Dwarf varieties. In the Hisar arun variety, the SOD activity in the control plants decresed in un-inoculated check (Control) to *M. incognita* inoculated, from 65.31 ± 0.83 to 62.93 ± .84. However, under *M. incognita* inoculation, the SOD activity was lower than Hisar Arun in Pusa Early Dwarf, decreasing from 62.47 ± 1.11 to 42.61 ± .99.

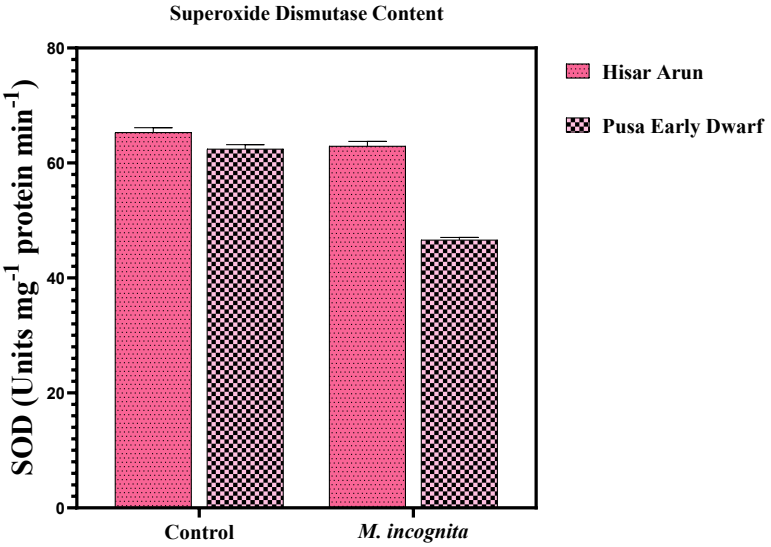

Figure 2: Superoxide dismutase activity under un-inoculated (control) and inoculated with *M. incognita* in resistant (Hisar Arun) and susceptible (Pusa early dwarf) tomato cultivars.

Glutathione reductase content analysis in resistant and susceptible genotypes of tomato infected with root-knot nematode

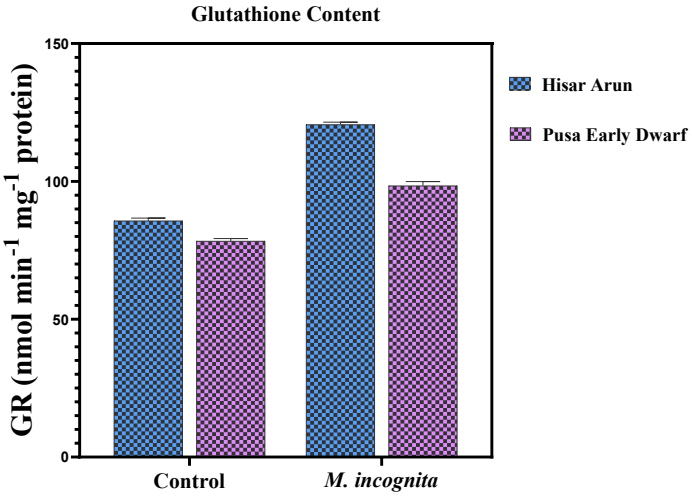

Figure 3: Glutathione reductase activity under un-inoculated (control) and inoculated with *M. incognita* in resistant (Hisar Arun) and susceptible (Pusa early dwarf) tomato cultivars.

The data shows a significant increase in GR content in both tomato varieties in response of *M. incognita* inoculation. At control (Uninoculated), the Hisar arun variety had a increased GR content (85.886 ± 0.557

µmol/g FW) compared to the Pusa Early Dwarf variety (78.91 ± 0.006 µmol/g FW). However, under the M. inognita inoculated , the GR content of Hisar arun (120.465 ± 1.773 µmol/g FW) was significantly higher ($p<0.01$) than Pusa Early Dwarf (98.608 ± 2.279 µmol/g FW).

Ascorbate peroxidase content analysis in resistant and susceptible genotypes of tomato infected with root-knot nematode

The ascorbate peroxidase (APX) activity decreased in both Hisar arun and Pusa Early Dwarf varieties under *M. incognita* inoculation. In the Hisar arun and Pusa Early Dwarf varieties, the APX activity varies from uninoculated (control) to *M. incognita* inoculated from 86.83 ± 1.29 to 63.59 ± 1.15 and 79.83 ± .94 to 51.39 ± 1.09 respectively.

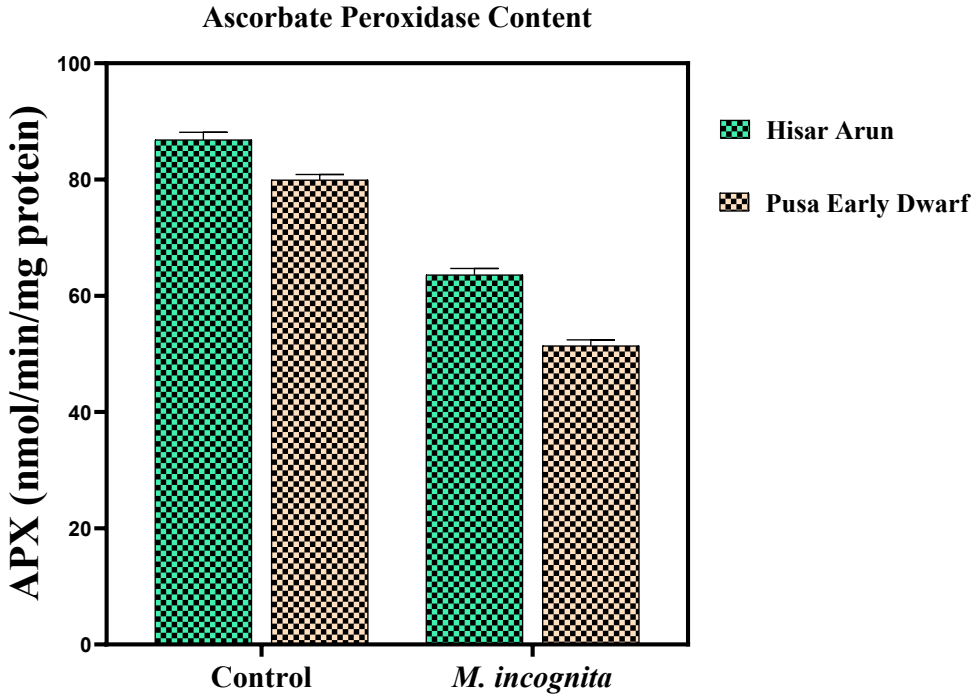

Figure 4: Ascorbate peroxidase activity under un-inoculated (control) and inoculated with *M. incognita* in resistant (Hisar Arun) and susceptible (Pusa early dwarf) tomato cultivars.

DISCUSSION

When plants are attacked by pathogens, they often go through oxidative stress. It is very important to be able to change the way antioxidants work in order to protect cells and keep their normal functions. The higher enzymatic activities in Hisar Arun were strongly linked to lower galling indices, lower egg mass production, and lower nematode reproduction rates. This means that a stronger antioxidant response not only protects plant tissues from oxidative damage, but it also directly stops nematodes from growing and spreading. The present are in line with what other studies have found, which show that resistant plant genotypes often have higher levels of antioxidant enzymes when they are attacked by nematodes or other pathogens. The data support the idea that enzymatic antioxidants are good biochemical markers for screening for resistance and could be used in breeding programs to create tomato varieties that can resist nematodes. In addition, the results show how important it is to focus on oxidative stress pathways in integrated nematode management plans. This study supports the idea that the different regulation of antioxidant defense enzymes is very important for how tomatoes and nematodes interact. It also gives us

important information about the molecular and biochemical basis of crop plant resistance. In light of the fact that susceptible tomato cultivars (Pusa Early Dwarf) and resistant tomato cultivars (Hisar Arun) react differently to infection from *Meloidogyne incognita*, this study sheds light on the topic. The fact that the two genotypes reacted differently highlights how important it is to control oxidative stress when dealing with nematodes in plants. Hisar Arun, a resistant cultivar, showed significantly higher levels of key antioxidant enzymes like superoxide dismutase (SOD), ascorbate peroxidase (APX), and glutathione reductase (GR) after infection than Pusa Early Dwarf, a susceptible cultivar. Enzymes like these are absolutely necessary for the detoxification process because plants produce reactive oxygen species (ROS) as a defense mechanism. An effective antioxidative system that reduces oxidative damage and fortifies plant defense is indicated by the resistant cultivar's enhanced activity of these enzymes. The vulnerable cultivar, on the other hand, showed reduced antioxidant enzyme activities; this could have caused reactive oxygen species (ROS) to build up, which in turn increased cellular damage and made nematode development easier. The results of the phenotypic observations corroborate the biochemical data, which show that Hisar Arun outperformed the susceptible genotype in terms of gall formation, egg mass production, and nematode reproduction rates. This research backs up previous claims that root-knot nematode resistance relies heavily on the antioxidant defense system. By sustaining structural and signaling defense pathways and keeping redox homeostasis in check, the increased antioxidant response in resistant genotypes may mitigate damage caused by nematodes. One possible biochemical marker for screening resistant cultivars is the differential expression of enzymatic antioxidants. This method provides a helpful resource for breeding programs that aim to create tomato varieties that are resistant to nematodes by utilizing marker-assisted selection techniques.

ACKNOWLEDGEMENT
The author thankfully acknowledges to the Chaudhary Ranbir Singh University Jind, Haryana, Dr. Sarvajeet Singh Gill from Maharshi Dayanand University, Rohtak, Haryana and my sincere thanks to Principal Scientist Dr. Zakaullah Khan, Division of Plant Quarantine, National Bureau of Plant Genetic Resources (NBPGR), New Delhi, for providing the *Meloidogyne incognita* culture and offering the necessary facilities to support this research.

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