RESEARCH PAPER

Drought Stress Reshapes Root-Knot Nematode Severity, Plant Growth, and Stress-Responsive Gene Expression in Tomato

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Abstract
Drought stress modulates nematode infection severity, plant growth, and stress-related gene expression in tomato (*Solanum lycopersicum*). Under full irrigation (100% FC), *Meloidogyne incognita* displayed the highest infection parameters, while moderate (50% FC) and severe drought (30% FC) significantly reduced gall formation, egg mass production, and nematode reproduction factor. Vegetative growth traits declined progressively with decreasing soil moisture, exacerbated by nematode infestation. At the molecular level, antioxidant genes (CAT and SOD) were upregulated under moderate drought and nematode stress, but their expression decreased under severe and prolonged drought. In contrast, a drought-responsive gene showed reduced expression with increasing water deficit. These results highlight a complex interaction between water stress and nematode parasitism, where moderate drought can stimulate defense mechanisms and limit nematode development, whereas severe drought suppresses both plant growth and defense gene expression. Effective irrigation management is thus crucial for mitigating nematode impact and maintaining tomato productivity under water-limited conditions.
Keywords: Drought stress; *Meloidogyne incognita*; tomato; nematode severty; antioxidant enzymes; catalase (CAT); superoxide dismutase (SOD); drought-responsive gene expression; combined abiotic and biotic stress

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Introduction

Tomato (*Solanum lycopersicum*) is one of the most economically important vegetable crops worldwide, valued for its high nutritional content, including vitamins, antioxidants, and diverse bioactive compounds that contribute significantly to human health (Abd-Elgawad & Askary, 2015; Dorais et al., 2008). Despite its global importance, tomato production is increasingly challenged by a wide range of biotic and abiotic stresses, which collectively lead to substantial yield losses and deterioration in fruit quality, particularly in arid and semi-arid agroecosystems (Foolad, 2007; FAO, 2021; Ghareeb et al., 2026).

Among the most destructive biotic constraints affecting tomato cultivation are root-knot nematodes (*Meloidogyne* spp.), which are globally distributed and capable of causing severe economic losses (Jones et al., 2013; Ghareeb et al., 2025). Infection by these sedentary endoparasites induces the formation of characteristic root galls that disrupt normal root function, impair water and nutrient uptake, and ultimately suppress plant growth and productivity (Sasser & Freckman, 1987; Perry et al., 2009). *Meloidogyne incognita* is regarded as the most prevalent and aggressive species infecting tomato, particularly under warm climatic conditions that favor rapid nematode development and reproduction (Trudgill & Blok, 2001; Ghareeb et al.,2025).

Nematode infection severity is commonly quantified using several parameters, including galling index, number of egg masses, juvenile (J2) population density in soil, and reproduction factor (Rf) (Taylor & Sasser, 1978). These indicators collectively reflect host susceptibility and nematode parasitic success, as higher nematode severity is generally associated with efficient feeding site establishment and sustained nutrient acquisition from host tissues (Williamson & Gleason, 2003).

Drought stress represents one of the most critical abiotic factors influencing plant performance, as it profoundly alters physiological, biochemical, and molecular processes such as water relations, photosynthetic efficiency, root system architecture, and stress-related signaling pathways (Farooq et al., 2009; Chaves et al., 2009; Ghareeb et al., 2025). Under water-deficit conditions, plants may exhibit altered defense responses, potentially increasing susceptibility to soil-borne pathogens and facilitating nematode penetration, establishment, and reproduction (Atkinson et al., 2013).

Several studies have reported that drought stress can exacerbate root-knot nematode infection by enhancing gall formation, nematode reproduction, and overall

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disease severity, particularly in susceptible tomato cultivars (Hussey & Janssen, 2002)). The interaction between drought stress and nematode infection often results in greater yield reductions than those caused by either stress alone, emphasizing the complexity of plant responses to combined abiotic and biotic stresses (Pandey et al., 2017).

The parasitic success of *Meloidogyne incognita* is largely dependent on the coordinated expression of virulence-related genes encoding effector proteins secreted into host tissues during infection (Haegeman et al., 2012). These effectors include cell wall-degrading enzymes such as endoglucanases and pectate lyases, as well as regulatory proteins that manipulate host cellular metabolism, reprogram gene expression, and suppress plant defense responses (Mitchum et al., 2013).

Environmental stresses, including drought, can significantly influence nematode behavior and pathogenicity by modulating the expression of virulence genes in response to altered host-derived signals and physiological status (Danchin et al., 2016). Quantitative real-time PCR (qRT-PCR) has emerged as a sensitive and reliable tool for quantifying changes in nematode virulence gene expression, enabling direct links to be established between molecular responses and observed disease severity under stress conditions (Livak & Schmittgen, 2001).

Therefore, the present study aimed to elucidate the impact of drought stress on root-knot nematode severity and the expression of key virulence-related genes of *Meloidogyne incognita* infecting tomato plants. By integrating phenotypic assessments of nematode infection with molecular analysis of virulence gene expression, this work seeks to provide a comprehensive understanding of how water-deficit conditions modulate nematode pathogenicity and plant–nematode interactions under combined abiotic and biotic stress.

Material and Methods

Nematode Inoculum

A pure culture of the root-knot nematode *Meloidogyne incognita* was originally obtained from naturally infected tomato (*Solanum lycopersicum*) roots showing typical galling symptoms. Infected roots were carefully washed under running tap water to remove adhering soil particles, and egg masses attached to the root surface were visually detected.

To establish and maintain a pure nematode population, *M. incognita* was multiplied on susceptible tomato plants grown in sterilized soil under greenhouse conditions. This method is widely used to ensure continuous nematode propagation while minimizing contamination by other plant-parasitic nematodes or soil-borne microorganisms (Hussey and Barker, 1973). Plants were maintained under optimal temperature and moisture conditions suitable for nematode development.

Egg masses were handpicked from heavily galled roots using fine forceps and processed for egg extraction following the sodium hypochlorite (NaOCl) technique as described by Hussey and Barker (1973). Extracted eggs were thoroughly rinsed with sterile distilled water and incubated at room temperature to allow hatching. Freshly hatched second-stage juveniles (J2) were collected within 24–48 h and used as inoculum in all experiments.

Nematode species identification was performed based on morphological characteristics. Adult females were dissected from infected roots, and perineal patterns were prepared according to the method described by Taylor and Netscher (1974). Prepared perineal patterns were examined under a light microscope, and species identification was confirmed based on diagnostic features including the shape of the dorsal arch, striation pattern, and lateral field characteristics, following the taxonomic keys of Eisenback et al. (1981). Based on these criteria, the nematode species was identified as *Meloidogyne incognita*.

The concentration of the nematode inoculum was determined by counting J2 under a stereomicroscope using a counting dish, and the inoculum density was adjusted to obtain a uniform number of juveniles for all treatments. The standardized inoculum was applied to tomato plants at a defined growth stage to ensure consistent infection pressure and reliable comparison among treatments.

Greenhouse experiment

Tomato (*Solanum lycopersicum* cv. Farida) seeds, obtained from Elekhlas Company in Egypt, were surface-sterilized with 1% sodium hypochlorite for 2 minutes and rinsed thoroughly with sterile distilled water. The seeds were sown in plastic pots (15 cm diameter) containing 4 kg of sterilized soil composed of peat, soil, and sand in a 2:1:1 (v/v/v) ratio. The pots were maintained in a greenhouse at the City of Scientific Research, Borg El-Arab, Egypt under controlled conditions of 25±2°C temperature, 60–70% relative humidity, and a 16-hour photoperiod. Seedlings were grown for four weeks to ensure uniform establishment prior to nematode inoculation. The experiment was arranged in a completely randomized design (CRD) with four treatments, each with 10 replicates, and three plants per replicate. The experiment was repeated twice to ensure reproducibility.

The nematode *Meloidogyne incognita* used for inoculation was obtained as a pure culture, maintained on susceptible tomato plants under greenhouse conditions. Egg masses were extracted from infected roots using 0.5% sodium hypochlorite according to the method of Hussey and Barker (1973) and hatched under controlled laboratory conditions to obtain freshly hatched second-stage juveniles (J2). Each seedling was inoculated with 2000 J2 around the root zone by creating small holes in the soil near the base of the plant and gently applying the nematode suspension.

The soil was immediately covered, and plants were maintained under the designated irrigation treatments to allow nematode establishment and infection. Treatments involved four soil moisture levels (Field Capacity, FC) as follows:

Table 1. Soil moisture levels and irrigation volumes for tomato plants

Treatment	Description	Soil Moisture (% FC)
T1 – Control	Well-watered	100%
T2 – Mild Drought	Light water stress	75%
T3 – Moderate Drought	Moderate water stress	50%
T4 – Severe Drought	Severe water stress	30%

The amount of water required to maintain the desired soil moisture levels in each pot was calculated based on the weight of the soil and its field capacity (FC). Each pot contained 4 kg of sterilized soil, and the field capacity of the soil mixture (peat: soil: sand, 2:1:1, v/v/v) was estimated at 0.35 mL water per gram of dry soil. The water volume for 100% FC was calculated using the formula:

Water (mL) = Soil weight (g) ×Field Capacity (mL/g)

Thus, for 4 kg soil: 4000 g × 0.35 mL/g = 1400 mL (1.4 L). Water volumes for drought treatments were adjusted proportionally: 75% FC = 1.05 L, 50% FC = 0.7 L, and 30% FC = 0.42 L per pot. Soil moisture was monitored daily using the weight method, and the required water was added to maintain the target FC. This approach follows standard protocols for pot experiments under controlled drought stress conditions (Hillel, 2003; Kramer & Boyer, 1995; Porcel et al., 2010). All plants received 100% FC water during the first week after transplanting to allow seedling establishment before initiating the drought treatments. The daily watering schedule is summarized in the following table

Table 2. Daily irrigation schedule for tomato plants under different soil moisture treatments

Days	T1 – 100% FC	T2 – 75% FC	T3 – 50% FC	T4 – 30% FC	Notes
0 (Planting)	1.4 L	1.4 L	1.4 L	1.4 L	Establishment watering
1	1.4 L	1.05 L	0.7 L	0.42 L	Start of drought treatments
2	1.4 L	1.05 L	0.7 L	0.42 L	Weight checked daily
3	1.4 L	1.05 L	0.7 L	0.42 L	Adjust water based on weight
45	1.4 L	1.05 L	0.7 L	0.42 L	End of experiment, sampling for measurements

After 45 days post-inoculation, plants were carefully uprooted, and root samples were collected for RNA extraction and gene expression analysis, while the rest of the plant was used to record leaf area, shoot and root dry weight. Root systems were stained with 0.1% Phloxine B to assess nematode severity, including the number of galls, number of egg masses, and reproduction factor (RF = final nematode population/initial inoculum).

RNA Isolation and cDNA Synthesis

Total RNA was isolated from tomato (*Solanum lycopersicum*) root tissues collected at 7, 15, and 30 days after nematode inoculation using the TRIzol reagent protocol with minor modifications. Root samples were immediately frozen in liquid nitrogen and ground into a fine powder using a pre-cooled mortar and pestle. Approximately 1 g of powdered tissue was homogenized in 1 mL of TRIzol reagent and incubated at −20 °C for 15 min.

Chloroform (0.2 mL per 1 mL TRIzol) was added, and samples were vigorously mixed, incubated at room temperature for 5 min, and centrifuged at 12,000 rpm for 15 min at 4 °C. The aqueous phase was transferred to a new tube, and RNA was precipitated with isopropanol (0.5 mL per 1 mL TRIzol), followed by centrifugation at 12,000 rpm for 20 min at 4 °C. The RNA pellet was washed with 75% ice-cold ethanol, air-dried, and dissolved in RNase-free water. RNA quality and integrity were verified by electrophoresis on a 1% agarose gel, and RNA concentration and purity were determined spectrophotometrically by measuring absorbance at 260 and 280 nm. Purified RNA samples were stored at −80 °C until further analysis (Hodson et al., 2022).

First-strand cDNA synthesis was performed using M-MLV reverse transcriptase according to the manufacturer's instructions. Briefly, 3 µL of total RNA was reverse transcribed in a reaction mixture containing 5× RT buffer, dNTPs, random hexamer primers, and reverse transcriptase enzyme. The reaction was incubated at 37 °C for 60 min, followed by enzyme inactivation at 70 °C for 10 min. The synthesized cDNA was stored at 4 °C and subsequently used for quantitative real-time PCR analysis, (Sambrook et al.,2006).

Quantitative Real-Time PCR Analysis of Stress-Responsive Genes

Expression levels of three stress-responsive genes catalase (CAT), superoxide dismutase (SOD), and dehydration-responsive element-binding protein (DREB)—in tomato roots at 7, 15, and 30 days after nematode inoculation were quantified using quantitative real-time PCR (qRT-PCR). Total RNA was extracted from root tissues using TRIzol reagent (Invitrogen, USA) and reverse-transcribed into cDNA. β-actin was used as the reference gene.

qRT-PCR reactions (25 µL) contained 2 µL cDNA, 1 µL each of forward and reverse primers (25 pM/µL), 12.5 µL SYBR Green master mix, and 6.5 µL RNase-free water. Reactions were performed on a Rotor-Gene 6000 system (Qiagen, USA) using the following cycling program: initial denaturation at 95°C for 10 min, followed by 40 cycles of 95°C for 15 s, 60°C for 30 s, and 72°C for 30 s with fluorescence acquisition during extension.

Relative expression levels were calculated using the 2^−ΔΔCq method, with β-actin as the internal control. ΔCq = Cq_target − Cq_reference; ΔΔCq = ΔCq_sample − ΔCq_control. (Livak KJ, Schmittgen , 2001). Experiments were performed in three biological replicates, and results are presented as mean ± SD. Statistical analysis was performed using two-way ANOVA and Tukey's multiple comparison test, with $P \leq 0.05$ considered significant.

Results

Impact of Drought Stress on Nematode Severity in Tomato Roots

Irrigation level significantly affected the severity of *Meloidogyne incognita* infection in tomato plants (Fig. 1). Plants grown under full irrigation (100% FC) exhibited the highest nematode infection parameters, including number of galls, egg masses per plant, and J2 population density in soil. A slight reduction in these parameters was observed at 75% FC; however, nematode activity remained relatively high.

A marked decline in nematode severity was recorded under moderate drought stress (50% FC), as indicated by a significant decrease in gall formation, egg mass production, and J2 counts compared with well-watered treatments (Fig. 1). The lowest nematode infection parameters were observed under severe water stress (30% FC), where all measured indices were drastically reduced. The reproduction factor (Rf) of M. incognita followed a similar trend, showing the highest values under 100% and 75% FC, a pronounced reduction at 50% FC, and the lowest value under 30% FC (Fig. 2).

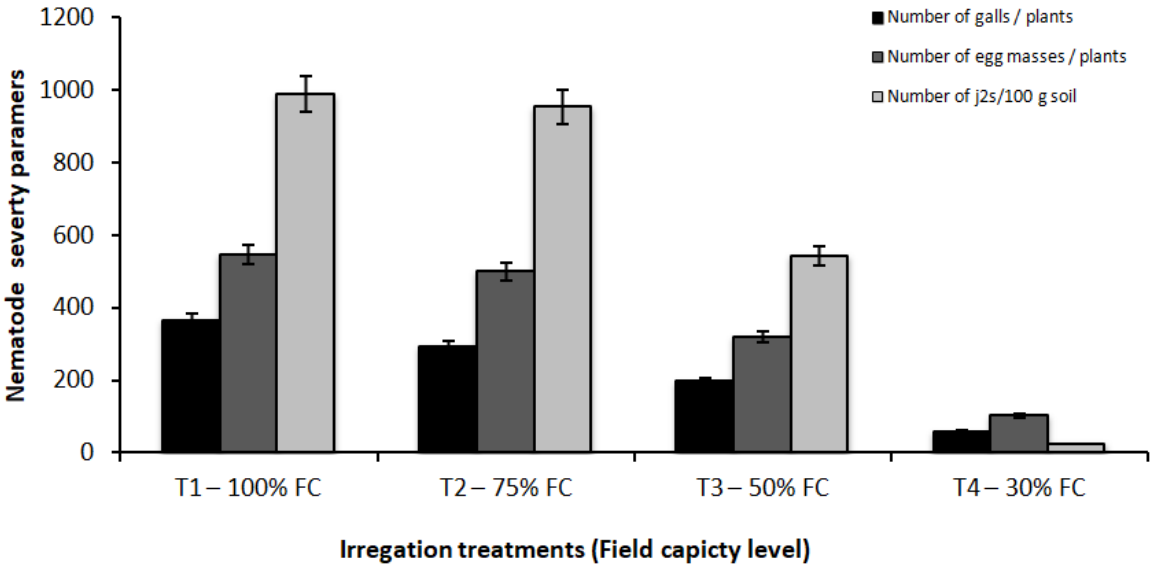

Figure 1. Effect of drought stress on nematode severity parameters of *Meloidogyne incognita* infecting tomato plants under different irrigation levels. Bars represent mean ± SE. Different letters indicate significant differences at $P \leq 0.05$

The impact of water stress on the reproduction of root-knot nematodes was evaluated by exposing tomato plants to different levels of field capacity (FC). The reproduction factor (Rf = Pf / Pi) was calculated for each treatment to determine nematode population development under varying soil moisture conditions (Figure 2).

As shown in Figure 2, the highest nematode reproduction was recorded under full irrigation (T1 – 100% FC), with an Rf of 19.76, indicating optimal

conditions for nematode multiplication. Slight water deficit at 75% FC (T2) resulted in a minor reduction in reproduction factor (Rf = 19.06), suggesting that mild water stress slightly affects nematode development. A more pronounced reduction was observed at 50% FC (T3), where Rf decreased to 10.86, reflecting the sensitivity of nematodes to moderate water stress. Severe water deficit (T4 – 30% FC) drastically reduced nematode reproduction, with an Rf of only 0.5, indicating that extreme drought conditions strongly suppress nematode multiplication.

These results demonstrate a clear negative correlation between water stress intensity and nematode reproduction, highlighting that soil moisture is a critical factor regulating nematode population dynamics. The data are also illustrated in Figure 1, showing the sharp decline in nematode reproduction under severe drought conditions

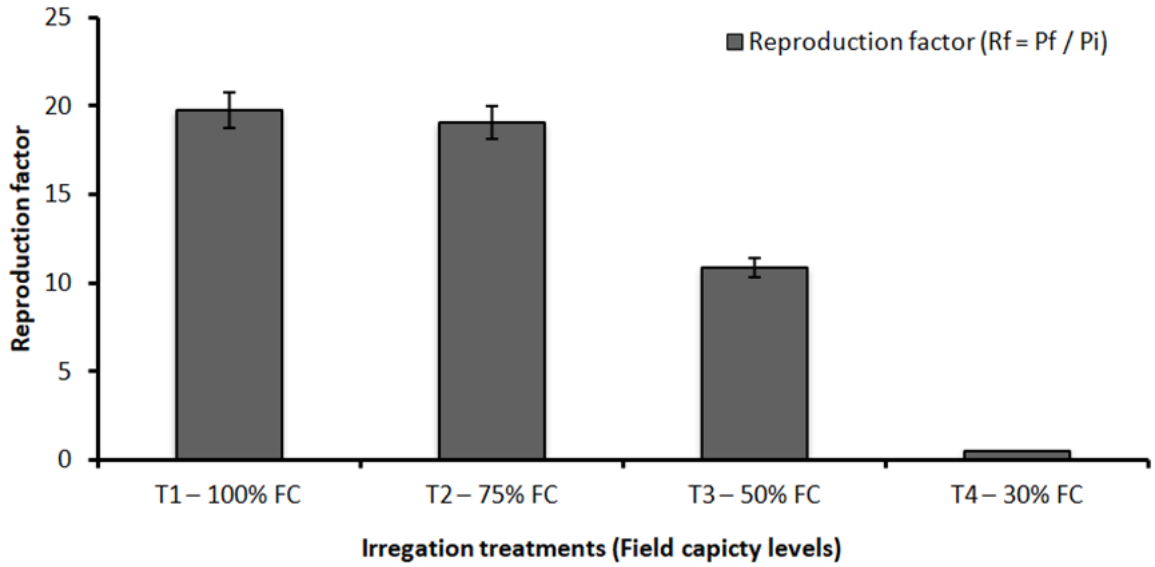

Figure 2. Effect of drought stress on reproduction factor of *Meloidogyne incognita* infecting tomato plants under different irrigation levels. Bars represent mean ± SE. Different letters indicate significant differences at $P \leq 0.05$

Effects of Water Deficit on Tomato Vegetative Growth

The data presented in Fig. (3) illustrate the effect of different irrigation levels (field capacity, FC) and nematode infestation on tomato growth parameters, including root dry weight, shoot dry weight, and leaf area. In general, plant growth was strongly influenced by both water availability and nematode presence. Under well-watered conditions (100% FC), nematode-free plants exhibited the highest values of root and shoot dry weights as well as leaf area. Nematode infestation at the same irrigation level caused a slight reduction in all growth parameters; however, plants maintained relatively high growth performance compared to deficit-irrigated treatments.

Reducing irrigation to 75% FC resulted in a moderate decline in growth traits. This reduction was more pronounced in nematode-infected plants, indicating that water stress amplified the negative impact of nematodes on plant growth. Similar trends were observed at 50% FC, where both root and shoot dry weights, as well as leaf area, showed substantial decreases, particularly in the presence of nematodes. The lowest growth values were recorded under severe water stress (30% FC). Nematode-infected plants at this irrigation level exhibited the most pronounced reductions in all measured parameters, reflecting a strong synergistic effect between drought stress and nematode infection. Overall, the results demonstrate that decreasing irrigation levels progressively reduced plant growth, and nematode infestation further exacerbated these reductions, with the combined stress being most detrimental under low water availability.

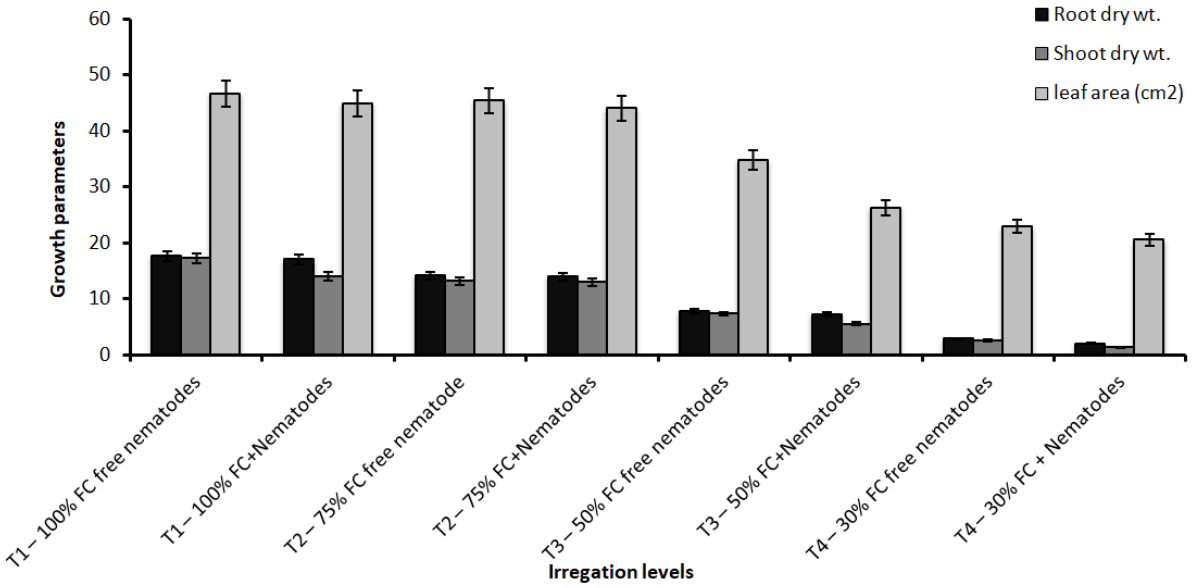

Figure 3.Drought-Mediated Modulation of Antioxidant and Drought-Responsive Gene Expression in Tomato Under *M. incognita* Infestation

Catalase (CAT) Gene Expression

Catalase (CAT) expression exhibited clear temporal and treatment-dependent variations in response to irrigation level and nematode infestation. At 7 days, transcript levels were generally low across all treatments, with only a slight increase observed in nematode-infected plants, indicating an early but limited antioxidant response. By 15 days, CAT expression increased markedly under moderate water stress (75% and 50% FC), with nematode-infected plants showing higher transcript accumulation than nematode-free plants, suggesting enhanced activation of antioxidant defenses under combined drought and nematode stress. At 30 days, CAT expression remained elevated under moderate irrigation deficit, particularly at 75% FC, whereas a pronounced decline was recorded under severe water stress (30% FC) in both nematode-free and nematode-infected plants, indicating possible suppression of CAT transcription under prolonged and severe stress due to metabolic constraints and cellular damage,(Fig. 4).

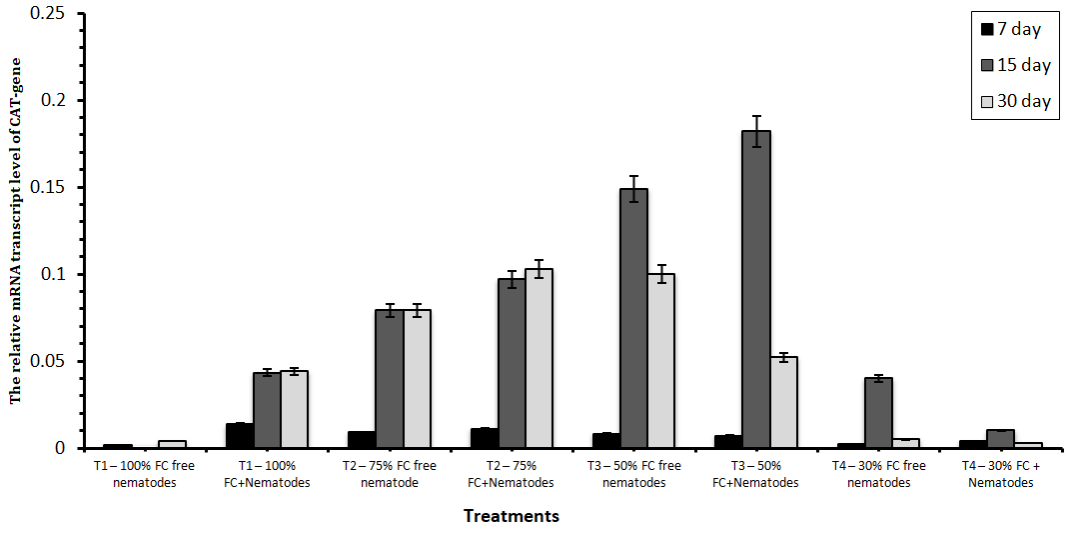

Figure 4**.** Relative expression of the catalase (CAT) gene in tomato plants subjected to different irrigation levels (% of field capacity, FC) and nematode infestation at 7, 15, and 30 days after treatment. Gene expression was quantified using qRT-PCR and calculated by the ΔΔCq method

Superoxide Dismutase (SOD) Gene Expression

Superoxide dismutase (SOD) gene expression was significantly influenced by irrigation level, nematode infestation, and sampling time. At 7 days, SOD expression remained low in well-watered, nematode-free plants, while nematode-infected plants displayed a marked increase, reflecting an early activation of antioxidant defenses. Moderate (75% FC) and high (50% FC) water stress led to a progressive rise in SOD transcript levels in both infected and non-infected plants, with consistently higher expression in nematode-infected treatments. The highest expression levels at this stage were observed under severe water stress (30% FC). By 15 days, SOD expression further increased under all water-deficit treatments, particularly at 50% and 30% FC, with nematode infestation enhancing transcript accumulation across all irrigation regimes. At 30 days, SOD expression remained relatively high under moderate water stress (75% and 50% FC), whereas a pronounced decline was noted under severe water stress (30% FC) in both nematode-free and nematode-infected plants, (Fig. 5).

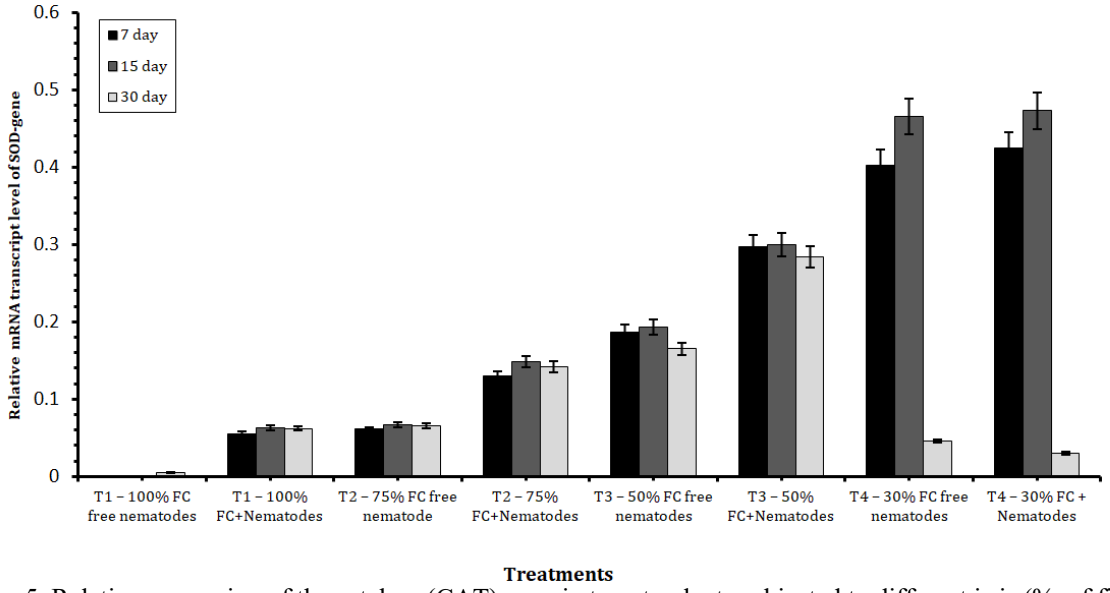

Figure 5**.** Relative expression of the catalase (CAT) gene in tomato plants subjected to different irris (% of field capacity, FC) and nematode infestation at 7, 15, and 30 days after treatment. Gene expression was quantified using qRT-PCR and calculated by the ΔΔCq method

Drought-Responsive Gene Expression

Expression of the drought-responsive gene was significantly affected by irrigation level, nematode infesta ion, and sampling time. Overall, transcript levels decreased progressively with increasing water stress days, (Fig. 6).

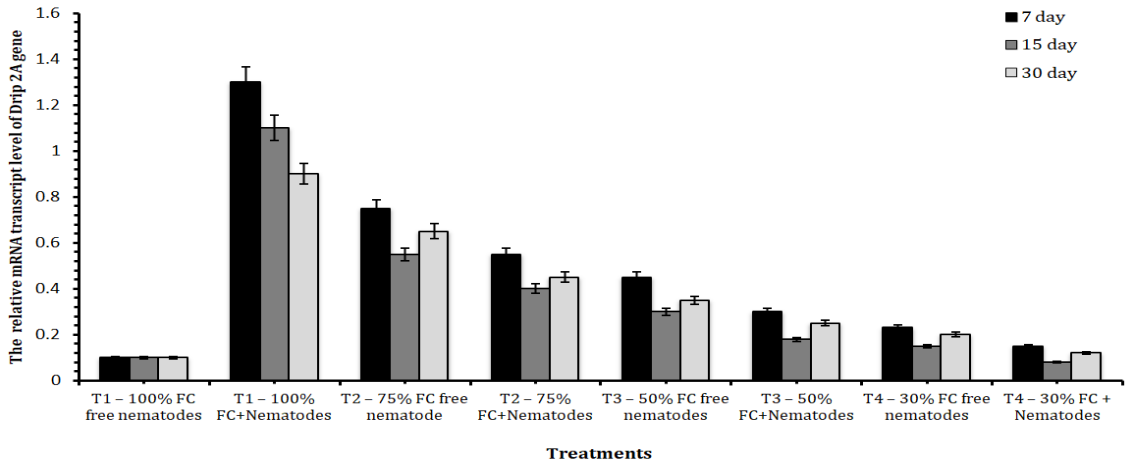

Figure 6**.** Relative expression (fold change) of a drought-responsive gene in plants grown under different irrigation levels (% of field capacity, FC) with and without nematode infestation at 7, 15, and 30 days after treatment. Gene expression was quantified by qRT-PCR and calculated using the ΔΔCq method

Discussion

The present study investigated the integrated effects of water deficit and *Meloidogyne incognita* infestation on

tomato plants, focusing on nematode severity, plant performance, and expression patterns of the drought-responsive gene DREB as well as antioxidant-related genes SOD and CAT. The findings reveal a complex interaction between a biotic (drought) and biotic (root-knot nematode) stresses, reflecting both plant tolerance mechanisms and pathogen susceptibility to soil moisture.

Our results demonstrated that irrigation level significantly influenced root-knot nematode infection severity in tomato roots. Under full irrigation (100% of field capacity, FC), tomato plants exhibited the highest numbers of galls, egg masses, and second-stage juveniles (J2), confirming that *M. incognita* proliferates effectively under optimal soil moisture conditions. This observation is consistent with previous findings indicating that adequate soil moisture enhances nematode mobility, root penetration, and reproductive success (Rohde et al., 2010). A slight reduction in severity at 75% FC suggests that mild water deficit may impose some limitation on nematode activity, yet does not drastically impair the nematode life cycle, which aligns with reports showing moderate soil drying can delay but not prevent nematode development (Williamson & Hussey, 1996).

A marked decline in nematode infection indices under moderate (50% FC) and severe (30% FC) water stress indicates that drought conditions adversely affect nematode development and reproduction. This outcome agrees with studies demonstrating that soil moisture deficits limit nematode invasion and feeding site establishment due to restricted migration and altered root exudation patterns (Gillet et al., 2017; Atkinson & Urwin, 2012). In our study, the reproduction factor (Rf) decreased sharply as irrigation levels declined, with the lowest value recorded at 30% FC, demonstrating a strong negative correlation between water stress intensity and nematode propagation—a trend also reported in similar crop systems exposed to progressive soil drying (Grant et al.,2003).

Water deficit alone significantly reduced tomato growth parameters, including shoot and root dry weight and leaf area. These reductions were further amplified when nematode infestation was combined with water stress. Well-watered, nematode-free plants maintained the highest vegetative performance, while the presence of nematodes under drought conditions exacerbated growth inhibition. This synergistic adverse effect aligns with the well-established understanding that both drought and root-knot nematodes independently compromise root architecture and plant water relations, leading to reduced nutrient acquisition and assimilate allocation (Farooq et al., 2009; Atkinson & Urwin, 2012). Under combined stress, the impaired root system becomes less capable of water uptake, further intensifying growth suppression, consistent with the concept of stress additive effects reported by Pandey et al. (2015).

The expression profiles of stress-related genes revealed distinct regulatory patterns in response to irrigation levels and nematode infestation. The drought-responsive gene DREB exhibited a progressive decline in fold change expression with increasing water stress severity and over time, irrespective of nematode presence. Under well-watered conditions, nematode infection initially induced upregulation, likely reflecting a general stress perception and activation of defense signaling pathways (Nakashima & Yamaguchi-Shinozaki, 2013). However, as drought severity increased, DREB expression decreased significantly, suggesting that severe and prolonged water deficit may suppress or saturate upstream signaling cascades responsible for the transcriptional activation of drought-responsive genes. This pattern is consistent with findings in tomato and other crop species subjected to severe drought, where stress signaling pathways become inhibited under extreme dehydration (Shinozaki & Yamaguchi-Shinozaki, 2007; Huang et al., 2012).

In contrast to DREB, the antioxidant-related genes superoxide dismutase (SOD) and catalase (CAT) were strongly induced under moderate water stress (75% and 50% FC), particularly when nematode infection was present. This upregulation reflects enhanced reactive oxygen species (ROS) production triggered by both drought-induced oxidative stress and nematode parasitism. Antioxidant defenses serve to detoxify ROS and mitigate cellular damage, a response widely documented as a primary defense mechanism under combined abiotic and biotic stresses (Apel & Hirt, 2004; Gill & Tuteja, 2010). The elevated fold change values of both SOD and CAT suggest an active adjustment of the antioxidative system to maintain cellular redox homeostasis in stressed plants.

Interestingly, under severe stress (30% FC), both SOD and CAT expression levels declined despite significant oxidative pressure. This suggests that prolonged and intense drought may exceed the plant's capacity to sustain increased antioxidant gene transcription, possibly due to metabolic and cellular dysfunction. Similar suppression of antioxidant gene expression under extreme stress has been observed in other studies where the collapse of redox balance coincided with declines in SOD and CAT transcription (Mittler, 2002; Hasanuzzaman et al., 2013).

The contrasting expression patterns between DREB and antioxidant genes in this study underscore the complexity of stress regulation in plants. While DREB functions primarily in early stress signaling and osmotic adjustment, SOD and CAT operate downstream in mitigating ROS accumulation. A coordinated yet differential regulation of these pathways is essential for stress adaptation. The observed upregulation of antioxidant genes under moderate stress likely provides a protective buffer that supports plant survival and reduces damage caused by ROS, whereas severe stress may override transcriptional control mechanisms, leading to overall gene suppression. (Hodson et al., 2022) The modulation of gene expression by nematode infection

highlights the intricate crosstalk between abiotic and biotic stress signaling networks, where nematode presence can amplify antioxidant responses under moderate water stress but fail to compensate under extreme drought conditions. Refaiy et al., 2025

Conclusion

Our study demonstrates that soil moisture is a critical determinant of nematode severity, plant growth, and stress gene responses in tomato. Full irrigation promotes nematode infection and reproduction, while moderate drought significantly reduces nematode success and activates antioxidant defenses. Severe and prolonged drought, however, suppresses growth and stress gene expression, indicating detrimental effects on plant resilience. These findings emphasize the importance of optimizing irrigation strategies to balance plant stress responses and pathogen pressure. The interaction between drought and nematode infection is complex and distinct from single stress responses, suggesting targeted breeding and management strategies are needed to enhance tomato tolerance to combined stresses in future climate scenarios.

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