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Species composition and abundance of weeds in tomato fields with nematicidal potential against *Meloidogyne incognita*

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Abstract. *Adiwena M, Murtilaksono A, Pradana AP, Parameswari AR, Putri D. 2025. Species composition and abundance of weeds in tomato fields with nematicidal potential against* Meloidogyne incognita*. Biodiversitas 26: 5891-5905.* Root-knot nematodes (*Meloidogyne incognita*) cause major crop losses worldwide, yet sustainable management options remain limited. This study assessed weed community structure in tomato fields and tested the nematicidal activity of dominant species. Quadrat sampling (1×1 m) recorded seven species from six families, with moderate diversity (Shannon-Wiener H′: 1.125), low evenness (E: 0.578), and high dominance (Simpson's D: 0.470). *Alternanthera philoxeroides* was ecologically dominant (IVI: 72.0%; RD: 62.5%), while *Eleusine indica* and *Cyperus rotundus* were most frequent (RF: 23.8%). Aqueous root extracts (20% w/v) were tested in vitro, and proportion data were arcsine square-roots transformed and analyzed using one-way ANOVA followed by Tukey's HSD test (α: 0.05). *A. philoxeroides* achieved the strongest egg-hatch inhibition (98.2±0.45% unhatched eggs at 168 h vs. 69.6±3.58% in control), while *Cleome rutidosperma* induced the highest J2 mortality (21.8±6.14%). Gas chromatography-mass spectrometry (GC-MS) revealed 12 constituents in *A. philoxeroides* and 18 in *C. rutidosperma*. Key compounds included methyl palmitate, methyl oleate, and methyl linoleate in *A. philoxeroides*; and lauric acid, methyl palmitate, and 9,12-octadecadien-1-ol in *C. rutidosperma*. These phytochemicals are consistent with the observed suppression of egg hatching and juvenile survival. To our knowledge, this is the first study in Indonesia to explicitly link weed community diversity with in vitro nematicidal activity against *M. incognita* in tomato fields. By integrating ecological survey and bioassay data, this work demonstrates that naturally occurring weeds can serve both as indicators of agroecosystem health and as practical, locally available sources of botanical nematicides. The findings emphasize two major contributions: first, to nematode management through eco-friendly suppression of root-knot nematodes; and second, to biodiversity conservation by recognizing weeds as functional components of sustainable agroecosystems.

Keywords: *Alternanthera philoxeroides*, biodiversity, *Cleome rutidosperma*, GC-MS, phytochemicals

INTRODUCTION

Plant-parasitic nematodes, particularly root-knot nematodes (*Meloidogyne incognita*), pose a significant global threat to crop production, affecting over 2,000 plant species and causing estimated annual yield losses exceeding USD 157 billion (Subedi et al. 2020). The infective second-stage juveniles (J2) invade plant roots, induce gall formation, and disrupt water and nutrient uptake, with yield reductions in certain crops reaching as high as 73% under severe infestations (Rusinque et al. 2021; Tapia-Vázquez et al. 2022). Conventional management of *M. incognita* has predominantly relied on synthetic nematicides (Schleker et al. 2022; Stucky and Dahlin 2022); however, growing concerns regarding their negative impacts on biodiversity, environmental safety, and human health have prompted the search for more sustainable alternatives (Forghani and Hajihassani 2020). Accordingly, the search for alternatives to synthetic nematicides should proceed alongside weed management, because several prevalent weed species are simultaneously hosts of *Meloidogyne* and sources of bioactive compounds.

One promising approach involves the use of bioactive compounds derived from weed species occurring naturally in agricultural fields. Several invasive and common weeds exhibit strong nematicidal activity in laboratory and greenhouse assays (Lopes et al. 2020; Fabiyi 2022). Extracts of *Alternanthera philoxeroides* (alligator weed) at 1% (10 g/L) caused 100% mortality of *Bursaphelenchus xylophilus* within 72 hours (Zhang et al. 2024), while root extracts of *Cyanthillium rutidospermum* (little ironweed, also reported as *Vernonia* sp.) showed an LC_{50} of 55.7 mg/mL against *Meloidogyne* sp. after 12 hours (Abolusoro et al. 2018). Likewise, *Datura stramonium* and *Solanum nigrum* induced juvenile paralysis of *M. incognita* with EC_{50} values of 427 µg/mL and 481 µg/mL, respectively, and reduced root galling when applied as seed meals at only 1.13 mg/g (Hussain et al. 2011).

The nematicidal efficacy of these weed extracts is attributed to the presence of potent allelochemicals, including sesquiterpene lactones, phenolics, and alkaloids, which inhibit nematode egg hatching and cause juvenile mortality (Akhter et al. 2018; Şin and Öztürk 2021). Importantly, these compounds act across multiple nematode

developmental stages and are considered environmentally benign. Incorporating weeds as green manure or biofumigants represents an innovative strategy for suppressing nematode populations while reducing dependency on synthetic chemical inputs. This approach leverages the natural abundance of weeds, transforming them from agricultural liabilities into valuable resources for sustainable nematode management (Fabiyi 2022; Nafea et al. 2023).

The biodiversity of weed communities in tomato agroecosystems plays a critical role in shaping root-knot nematode dynamics and agroecological sustainability. Surveys in tropical regions report considerable weed richness, ranging from 20 to 63 species per field and up to 23 families (Werle et al. 2022; Geremew et al. 2023). However, community structures are often uneven, with certain species dominating. For example, *Portulaca oleracea* contributed nearly 50% of the dominance index in Ethiopian tomato fields, while *Borreria alata*, *Cyperus rotundus*, and *Asystasia intrusa* each represented 10-15% in Indonesian fields (Zaragoza et al. 2002; Cheimona et al. 2016). Such dominance patterns are relevant to nematology, as species like *C. rotundus* and *Eleusine indica* act as efficient hosts of *Meloidogyne* spp., allowing populations to persist even without crop hosts. Weed diversity indices, such as Shannon-Wiener and evenness, serve not only as ecological descriptors but also as indicators of nematode risk under different management regimes (Chapagain et al. 2021). Organic and diversified systems maintain higher weed richness and evenness, promoting soil resilience (Travlos et al. 2018; Mwangi et al. 2024), whereas herbicide-intensive monocultures favor a few resilient weeds that act as long-term nematode reservoirs, reducing diversity and aggravating pest pressure (Sharma et al. 2021).

Weeds influence nematode populations not only as alternative hosts but also through key ecological services (Esposito et al. 2023). Broadleaf species such as *Portulaca*, *Ageratum*, and *Tridax* improve soil organic matter and microclimate, factors that affect nematode egg hatching, juvenile activity, and survival. These species also sustain beneficial microbes and arthropods antagonistic to nematodes (Snyder 2019; Harms and Cronin 2020). Their dual function as reservoirs of nematicidal compounds and contributors to biodiversity-based ecosystem services highlights their value in sustainable pest management. Utilizing locally abundant weeds such as *A. philoxeroides* and *C. rutidospermum* could provide low-cost botanical control options adaptable to regional weed floras, soils, and *Meloidogyne* pressures. Therefore, this study assessed weed community structure in tomato fields and tested the nematicidal activity of dominant species.

MATERIALS AND METHODS

Time and location of study

This research was conducted from June to August 2025 in tomato cultivation fields at Universitas Borneo Tarakan, the Plant Protection Laboratory of Universitas Borneo Tarakan, Indonesia, and the Laboratory of Pest Organism Control Technology, Universitas Jember, Indonesia.

Weed identification and vegetation analysis

Weed species associated with tomato crops were identified through detailed morphological characterization. For each specimen, diagnostic morphological traits were recorded and compared with established taxonomic references to ensure accurate identification. Vegetation analysis was performed using the quadrat sampling method. In each selected plot, 1×1 m quadrats were placed randomly. A total of 10 quadrats were sampled to ensure adequate representation of the weed community. The number of sampling units was considered sufficient because species accumulation curves reached asymptote after approximately eight quadrats during preliminary observations, and a similar sampling intensity (8-12 quadrats) has been shown to be adequate for weed diversity assessments in smallholder tomato fields. Weed community composition and structure were quantified using vegetation indices: absolute density (AD), relative density (RD), absolute frequency (AF), and relative frequency (RF), following the formulas described by Turnip and Arico (2019). AD was calculated as the number of individuals of a species per unit plot area, RD as the percentage of a species' AD relative to the total AD of all species, AF as the proportion of quadrats containing a given species relative to the total number of quadrats, and RF as the percentage of a species' AF relative to the total AF for all species. All data were tabulated and analyzed to determine weed community composition, dominance, and diversity (Satriawan and Fuady 2019).

Vegetation diversity and importance value analysis

Weed community diversity and dominance were further quantified using the Shannon-Wiener diversity index (H′), Pielou's evenness index (E), Simpson's dominance index (D), and the Importance Value Index (IVI). The Shannon-Wiener diversity index (H′) was calculated as:

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

Where, S is the total number of species and p_i is the proportion of individuals belonging to species i relative to the total number of individuals in the sample. Evenness (E) was calculated as:

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

Which, measures the uniformity of individual distribution across all species, ranging from 0 (uneven) to 1 (perfectly even). Simpson's dominance index (D) was calculated as:

$$D = \sum_{i=1}^{S} p_i^2$$

Higher values indicating lower diversity and greater dominance by a few species. The Importance Value Index (IVI) for each species was calculated as:

$$IVI = RD + RF$$

Where, RD and RF are expressed as percentages. IVI provides a composite measure of the relative ecological importance of each species within the community, with higher values indicating greater dominance (Pala et al. 2020).

Source of *Meloidogyne incognita* isolate

The *M. incognita* isolate used in this study was obtained from the culture collection from the Department of Plant Protection, Faculty of Agriculture, Universitas Jember. The culture originated from a single egg mass collected from galled roots of tomato (*Solanum lycopersicum*) and was maintained under controlled conditions on tomato plants to ensure species purity and genetic uniformity. All procedures involving nematodes were conducted in accordance with institutional and national guidelines for the ethical use of invertebrate organisms in research.

Preparation of weed root extracts

Roots and leaves of the selected weed species were cut into ±1 cm segments and oven-dried at 52°C until a constant dry weight was achieved. The dried material was ground separately using a laboratory blender to obtain a fine powder. For extraction, 100 mL of distilled water was added to the powdered sample, and the mixture was shaken at 80 rpm for 72 h at ambient temperature using an orbital shaker. The resulting extract was centrifuged at 10,000 rpm until complete separation of solids from the liquid phase was achieved. The supernatant was collected as the 100% (w/v) stock aqueous extract, stored at 4°C, and later diluted with sterile distilled water to a 20% (w/v) working solution for bioassays (Siyar et al. 2019).

Efficacy assay for egg hatch inhibition and juvenile mortality

Eggs and second-stage juveniles (J2) of *M. incognita* were extracted, examined under a stereomicroscope, and counted using hand counter. All bioassays were conducted in 6-well multi-well plates (Biologix) and arranged as a completely randomized design (CRD). For the egg hatch inhibition assay, 100 freshly extracted eggs were placed in each well containing 2 mL of the 20% (w/v) weed extract suspension. Sterile distilled water served as the control. Each treatment was replicated six times. The number of unhatched eggs and dead larvae was recorded daily for seven consecutive days, and egg hatch inhibition (%) was calculated relative to the control.

For the juvenile-mortality assay, experiments were arranged in a completely randomized design (CRD). A total of 100 freshly extracted J2 were transferred into each well containing 2 mL of the 20% (w/v) weed-extract suspension, while sterile distilled water served as the control. Each treatment was replicated six times. Juveniles were considered dead if they failed to respond to probing with a fine needle and displayed no movement within 30 seconds under the stereomicroscope. Mortality was recorded daily for seven consecutive days and expressed as a percentage relative to the control.

Percentage data were arcsine square-roots transformed prior to statistical analysis. Data were analyzed using analysis of variance (ANOVA), and mean separation was performed using Tukey's Honest Significant Difference (HSD) test at a 95% confidence level (Pradana et al. 2025). All analyses were conducted using the DSAASTAT Excel macro (version 1.101; Andrea Onofri, University of Perugia, Italy).

Detection of bioactive compounds

The most effective weed root extract, as determined from the in vitro assays, was analyzed using Gas Chromatography-Mass Spectrometry (GC-MS). The extract was filtered through a 0.14 µm syringe membrane filter before analysis. A 1 µL aliquot of the filtrate was injected into the GC-MS system in split mode. Helium was used as the carrier gas at 64.1 kPa. The injector and MS detector temperatures were set at 250°C and 280°C, respectively.

Separation was performed on a Restek Rtx®-50 column (30 m length × 0.25 mm internal diameter × 0.5 µm film thickness). The oven temperature was programmed to hold at 80°C for 2 minutes, then increase at 10°C/min to a final temperature of 280°C. The mass spectrometer was operated in electron ionization (EI) mode at 70 eV, with a scan range of m/z 40-550. Mass spectra were matched against the Wiley9.LIB database for compound identification (Asyiah et al. 2025; Pradana et al. 2025).

RESULTS AND DISCUSSION

Weed species composition in tomato fields

Weed species associated with tomato crops in the study area were identified through field surveys and morphological characterization. Photographs of representative weed species are presented in Figure 1, while the complete list of species identified is provided in Table 1. A total of seven weed species were recorded, representing seven botanical families. These species displayed diverse morphological types, including broadleaf weeds, grasses, and sedges, reflecting the heterogeneous weed flora typically found in tropical vegetable production systems.

Among the recorded species, broadleaf weeds (*Marsilea crenata*, *Alternanthera philoxeroides*, *Phyllanthus niruri*, *Cleome rutidosperma*, and *Amaranthus spinosus*) were the most represented group, accounting for five out of the seven identified species. The remaining species comprised one grass (*E. indica*) and one sedge (*C. rotundus*). The predominance of broadleaf weeds suggests that the field conditions, including tillage, irrigation, and nutrient management, may favor their establishment and persistence over monocotyledonous weeds (Boutagayout et al. 2025).

Table 1. Weed species identified in tomato fields during the study

Species	Family	Group
Marsilea crenata	Fabaceae	Broadleaf
Eleusine indica	Poaceae	Grass
Cyperus rotundus	Cyperacea	Sedge
Alternanthera philoxeroides	Amaranthaceae	Broadleaf
Phyllanthus niruri	Phyllanthaceae	Broadleaf
Cleome rutidosperma	Cleomaceae	Broadleaf
Amaranthus spinosus	Amaranthaceae	Broadleaf

Figure 1. Weed species identified in tomato fields. A. *Marsilea crenata*, B. *Eleusine indica*, C. *Cyperus rotundus*, D. *Alternanthera philoxeroides*, E. *Phyllanthus niruri*, F. *Cleome rutidosperma*, G. *Amaranthus spinosus*

Several of the dominant broadleaf species identified, particularly *A. philoxeroides* and *C. rutidosperma*, have been reported to possess nematicidal properties (Claudius-Cole et al. 2018; Zhang et al. 2020), making them potential candidates for further evaluation in nematode management strategies. The occurrence of these species in tomato fields indicates their potential dual role: as competitors to the crop and as sources of bioactive compounds with pest-suppressive capabilities. Such findings align with reports that certain weed species, despite being traditionally targeted for removal, can contribute beneficial functions in agroecosystems when managed appropriately.

The presence of grass (*Eleusine indica*) and sedge (*Cyperus rotundus*) species, both known for their competitive vigor and adaptability to various soil conditions, also reflects the resilience of these taxa in disturbed agricultural environments. While these species are less documented for nematicidal activity, their ecological roles, persistence, and interactions with crop and soil biota merit consideration in integrated weed and pest management planning (Deesh et al. 2025).

The vegetation analysis of weed communities in the tomato fields revealed notable variation in both density and frequency among the seven recorded species (Figure 2). *A. philoxeroides* exhibited the highest absolute density, reaching 25 individuals/m², which translated to a relative density of 62.5%. This indicates that *A. philoxeroides* was by far the most dominant species in terms of individual abundance. The second most abundant species was *M. crenata* with an absolute density of 5.4 individuals/m² (13.5% relative density), followed by *P. niruri* with 3 individuals/m² (7.5% relative density). Other species, such as *E. indica*, *C. rutidosperma*, *C. rotundus*, and *A. spinosus*, showed comparatively low absolute densities ranging from 0.4 to 2.8 individuals/m² and relative densities between 1.0% and 7.0%.

In terms of absolute frequency, both *E. indica* and *C. rotundus* recorded the highest values at 1.0, corresponding to a relative frequency of 23.8% each. *P. niruri* and *C. rutidosperma* followed with absolute frequencies of 0.6 (14.3% relative frequency). *A. philoxeroides* was present in fewer quadrats, with an absolute frequency of 0.4 (9.5% relative frequency), despite its high density. *M. crenata* had the lowest absolute frequency (0.2; 4.8% relative frequency), suggesting that while it occurred in fewer sampling units, it tended to grow in dense patches where it was present.

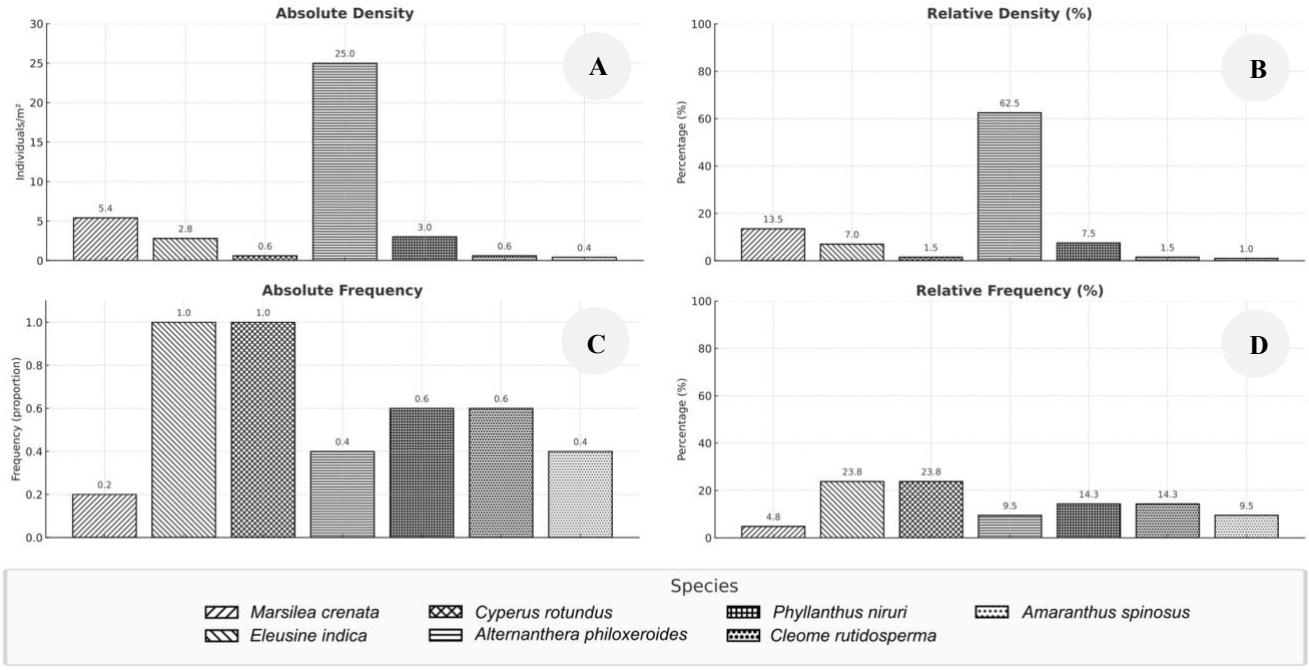


Figure 2. Vegetation analysis of weed species in tomato fields. A. Absolute density (individuals/m²), B. Relative density (%), C. Absolute frequency (proportion), D. Relative frequency (%) for *Marsilea crenata*, *Eleusine indica*, *Cyperus rotundus*, *Alternanthera philoxeroides*, *Phyllanthus niruri*, *Cleome rutidosperma*, and *Amaranthus spinosus*

Overall, the weed community structure was characterized by the dominance of *A. philoxeroides* in terms of abundance, while *E. indica* and *C. rotundus* had the broadest spatial distribution across the sampling area. The combined analysis of density and frequency data indicates a community with low evenness, driven primarily by the numerical dominance of *A. philoxeroides*. However, the relatively balanced frequency distribution among several species points to a potential for ecological interactions and resource sharing among the weed flora, which could influence both crop competition and ecosystem services within the tomato agroecosystem (Ciaccia et al. 2020; Esposito et al. 2023).

The vegetation analysis of tomato fields revealed marked differences in weed species dominance and diversity (Figure 3). *A. philoxeroides* exhibited the highest Importance Value Index (IVI) at 72.0%, indicating its strong ecological dominance within the community, followed by *E. indica* (30.8%) and *C. rotundus* (25.3%). Species such as *C. rutidosperma* and *A. spinosus* showed notably lower IVI values at 15.8% and 10.5%, respectively. Diversity metrics indicated Shannon-Wiener index (H′) of 1.125, suggesting moderate diversity, with an evenness value (E) of 0.578, reflecting uneven species distribution. Simpson's dominance index (D) was 0.470, confirming that a few species contribute disproportionately to the community composition.

A comparative assessment of relative density (RD) and relative frequency (RF) showed that *A. philoxeroides* combined high density (62.5%) with relatively lower frequency (9.5%), suggesting it forms dense patches rather than being uniformly distributed. Conversely, *E. indica* and *C. rotundus* demonstrated high frequency (23.8% each) despite lower relative densities, indicating broader spatial distribution. The absolute density versus frequency comparison reinforced these patterns, with *A. philoxeroides* standing out for its high density and moderate frequency, while other species displayed a more balanced density-frequency profile.

The marked dominance of *A. philoxeroides* in the present study indicates its strong competitive ability within tomato field weed communities. This dominance can be attributed to its perennial growth habit, rapid vegetative propagation, and tolerance to wide range of environmental conditions, enabling it to form dense patches that exclude other species (Clements and DiTommaso 2022). Such dominance also illustrates a broader ecological principle of weed management, where highly competitive species may serve additional functional roles when their biological traits are harnessed for ecological pest regulation.

Similar patterns have been reported in other tropical cropping systems, where *A. philoxeroides* exhibited both high biomass accumulation and strong competitive suppression of crops and other weeds (Sun et al. 2022). While its competitive nature can negatively affect crop productivity, several studies have demonstrated that *A. philoxeroides* contains bioactive metabolites with nematicidal activity against *Meloidogyne* spp., suggesting that its management could be tailored not only for suppression but also for potential utilization in integrated nematode control strategies (Velasco-Azorsa et al. 2021). This aligns with the emerging paradigm that certain weed species, despite their competitive nature, may serve dual roles as both competitors and beneficial biocontrol resources when managed appropriately (Şin and Öztürk 2021).

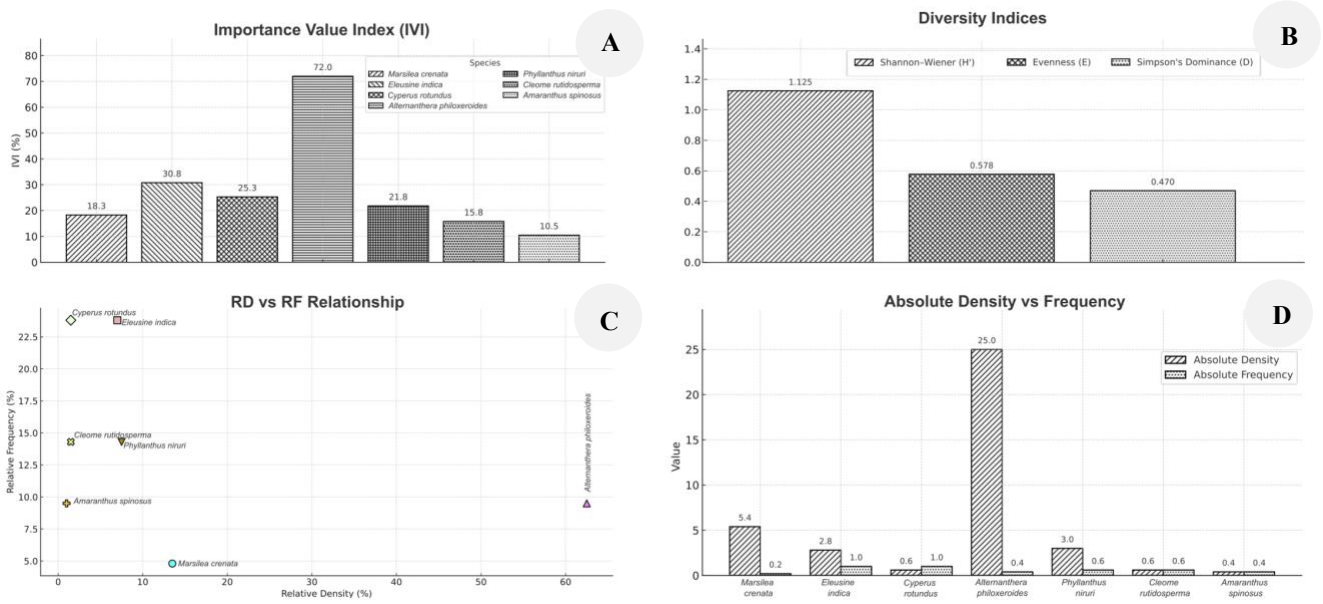


Figure 3. Weed community metrics in tomato fields. A. Importance Value Index (IVI) for each species, B. Diversity indices including Shannon-Wiener index (H′), Pielou′s evenness (E), and Simpson's dominance (D); C. Relationship between relative density (RD) and relative frequency (RF); D. Comparison of absolute density and absolute frequency for each species

The high frequency but relatively lower density of *E. indica* and *C. rotundus* observed in this study reflects their persistence across a wide range of microhabitats in disturbed agroecosystems. This persistence exemplifies how weed species with wide ecological amplitude contribute to system stability, nutrient cycling, and soil biological activity, even as they compete with crops. These patterns are consistent with previous research in tomato, strawberry, and maize fields, where *E. indica* and *C. rotundus* maintained stable populations due to extensive seed banks, efficient vegetative reproduction, and adaptability to diverse soil and moisture conditions (Shiferaw et al. 2018; Sharma et al. 2022). In strawberries, *E. indica* infestation at high densities has been reported to cause yield losses of up to 65% (Buzanini and Boyd 2024), while *C. rotundus* is considered one of the world's most invasive weeds due to its deep rhizome system and rapid regrowth after cultivation (Peerzada 2017; Raj et al. 2018). The ecological resilience of these species makes complete eradication challenging under conventional tillage regimes. Therefore, integrating preventive measures may be necessary to reduce their spread while maintaining certain beneficial ecosystem functions.

The moderate Shannon-Wiener diversity index (H′: 1.125) combined with low evenness (E: 0.578) in the weed community reflects a structure typical of frequently disturbed agroecosystems, where a small number of dominant species contribute disproportionately to total abundance. From an ecological standpoint, such an imbalance reflects a common feature of intensively managed systems, emphasizing the need to maintain functional weed diversity to support beneficial organisms and ecosystem resilience. Comparable findings in other vegetable production systems suggest that such low diversity may reduce habitat heterogeneity for beneficial arthropods and soil microorganisms, potentially limiting biological control services (Gardarin et al. 2018; Beaumelle et al. 2021). However, maintaining a balanced weed flora can enhance ecosystem services, including natural pest suppression, without significantly compromising crop yield when managed in spatially segregated zones. This approach aligns with sustainable pest management frameworks that integrate biodiversity conservation with targeted weed control, reducing reliance on synthetic nematicides and enhancing agroecosystem resilience (Blaix et al. 2018; Barbercheck and Wallace 2021).

Effect of weed extracts on egg hatch inhibition and juvenile mortality of *Meloidogyne incognita*

The inhibition of *M. incognita* egg hatching differed significantly among treatments across the 7-day observation period. At 24 hours, *A. philoxeroides* achieved the highest inhibition (99.8±0.45%), statistically similar to *A. spinosus* (99.8±0.45%) and *C. rutidosperma* (99.6±0.55%), but significantly greater than the control (96.2±2.17%). This early difference was further accentuated at 48 hours, when the control dropped to 92.6±2.88%, while *A. philoxeroides* maintained 99.0±0.0%. Other extracts, such as *E. indica* (98.4±0.55%) and *C. rutidosperma* (98.2±0.84%), also showed high inhibition but remained slightly below the performance of *A. philoxeroides*.

At intermediate time points, weed extracts sustained inhibition above 96%, while the control exhibited a steady decline. By 72 hours, the control was reduced to 89.6±2.61%, significantly different from *A. philoxeroides* (98.4±0.55%), *E. indica* (97.8±0.45%), and *A. spinosus* (97.8±0.45%). At 120 hours, the control had dropped further to 81.2±2.39%, compared with 98.2±0.45% in *A. philoxeroides* and 97.8±0.45% in *E. indica*. These results clearly show that the inhibitory effect of the extracts was stable over time,

whereas the control gradually lost its ability to prevent egg hatching.

By the final observation at 168 hours, the control exhibited a sharp decline to only 69.6±3.58%, in contrast to *A. philoxeroides*, which still maintained 98.2±0.45%. *A. spinosus* (97.8±0.45%), *C. rutidosperma* (97.4±0.89%), and *E. indica* (97.8±0.45%) also remained highly effective, but none consistently outperformed *A. philoxeroides* across all time points. These findings confirm *A. philoxeroides* as the best treatment, combining very high inhibition with remarkable stability across the 7 days. A detailed summary of unhatched egg counts is presented in Figure 4.

The mortality of *M. incognita* juveniles (J2) varied significantly among treatments and across observation times. At 24 hours, mortality was minimal in all treatments, ranging from 0.0±0.0% in the control to 0.6±0.55% in *C. rutidosperma* and *A. spinosus*. These differences were not statistically significant according to Tukey's HSD test ($p>0.05$). By 48 hours, however, variation between treatments became more evident. *C. rutidosperma* reached 1.8±0.84%, which was significantly higher than the control (0.0±0.0%) and *A. spinosus* (0.6±0.55%), while *E. indica* and *P. niruri* both produced intermediate effects at 1.6±0.89%.

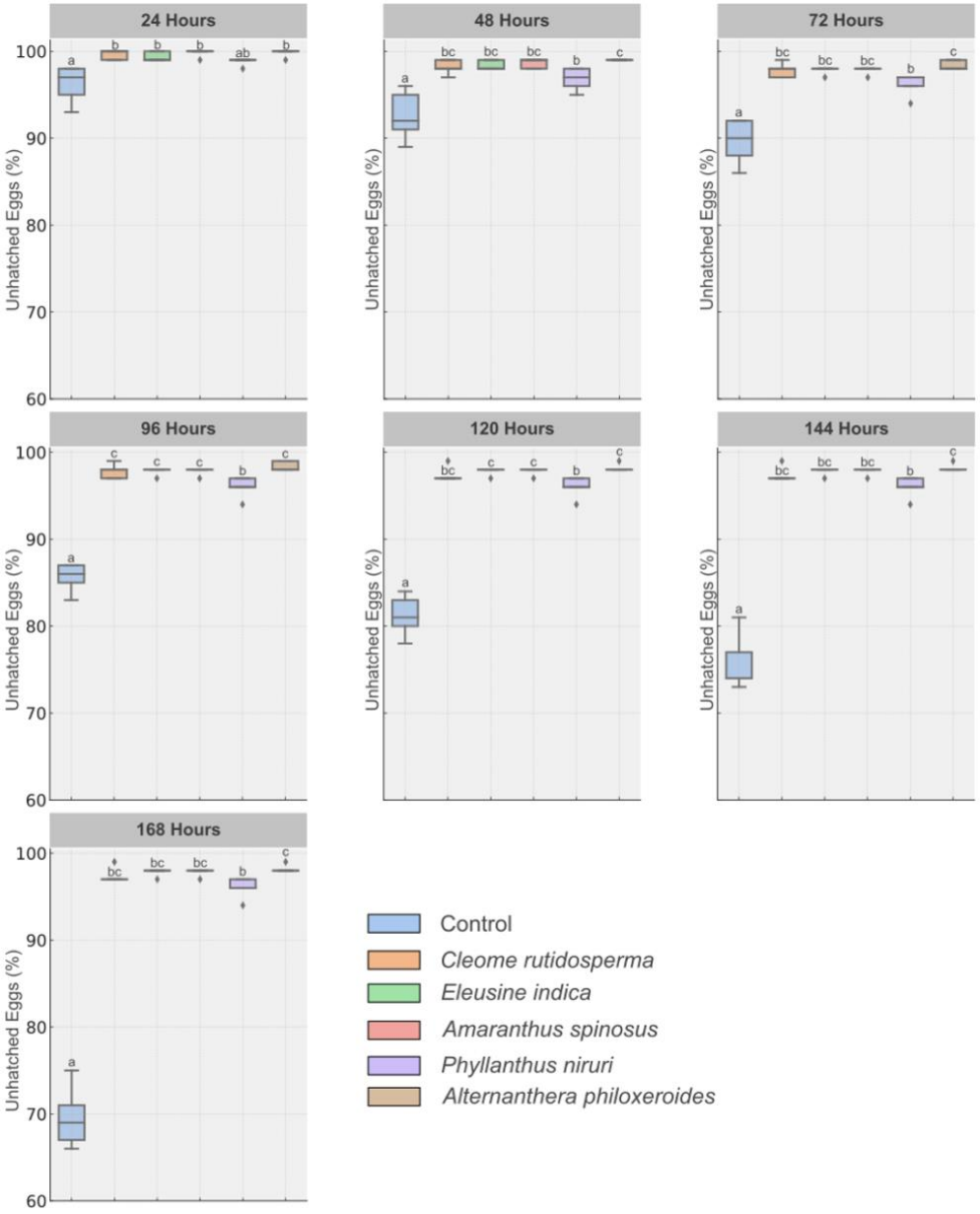


Figure 4. Inhibition of *Meloidogyne incognita* egg hatching following exposure to weed extracts over a 7-day observation period. Different letters above the bars within each time point indicate significant differences among treatments according to Tukey's HSD test at the 95% confidence level

At intermediate time points, a clearer separation in treatment effects emerged. By 96 hours, *C. rutidosperma* showed the strongest effect with 10.2±3.9% mortality, significantly higher than *E. indica* (5.6±2.3%), *A. spinosus* (3.2±1.1%), and *P. niruri* (4.4±0.89%). In contrast, the control remained low at 1.0±0.0%. This pattern persisted at 120 hours, where *C. rutidosperma* increased further to 14.8±4.97%, compared with 7.6±3.21% in *E. indica* and 8.6±2.88% in *P. niruri*. Similarly, *A. spinosus* recorded 5.6±1.52%, while the control stayed unchanged at 1.0±0.0%. These differences highlight the sustained activity of *C. rutidosperma*, which consistently outperformed the other extracts.

By the final observation at 168 hours, *C. rutidosperma* achieved the highest juvenile mortality at 21.8±6.14%, significantly greater than all other treatments. *P. niruri* and *E. indica* followed with 17.4±3.51% and 16.0±3.39%, respectively, while *A. spinosus* showed a more moderate effect at 13.8±3.11%. The control again remained negligible at 1.6±0.55%. Across all time points, the letters indicate that *C. rutidosperma* was consistently in the highest statistical group, while the control remained in the lowest. These results confirm that among the tested weed extracts, *C. rutidosperma* exerted the strongest and most persistent nematicidal activity against J2, suggesting its promising role as a botanical resource for integrated nematode management. A detailed summary of J2 mortality is presented in Figure 5.

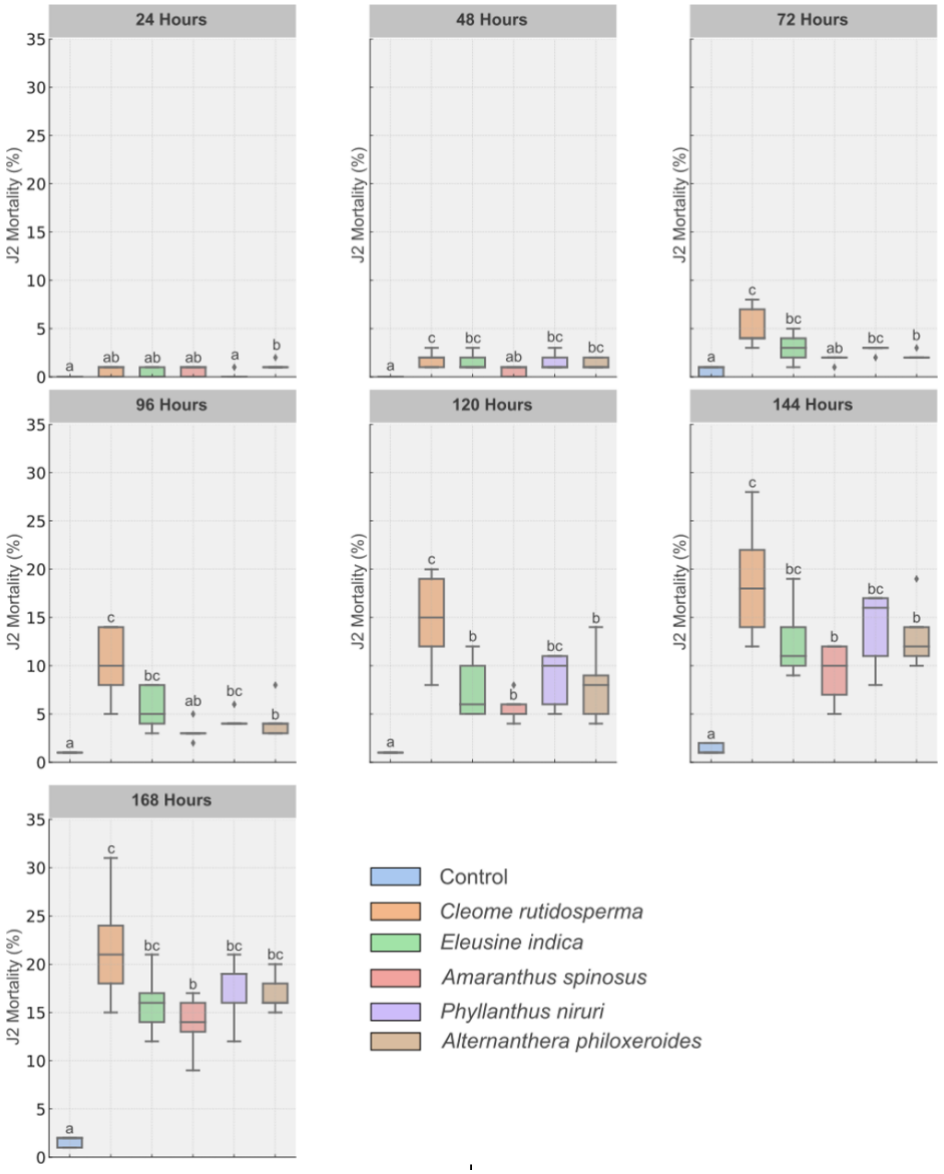


Figure 5. Inhibition of *Meloidogyne incognita* egg hatching following exposure to weed extracts over a 7-day observation period. Note: different letters above the bars within each time point indicate significant differences among treatments according to Tukey's HSD test at the 95% confidence level

The present study demonstrated that aqueous extracts of *A. philoxeroides* and *C. rutidosperma* effectively suppressed egg hatching and increased the mortality of *M. incognita* juveniles. The sustained inhibition of egg hatch, which remained close to 98% after 168 hours in *A. philoxeroides*, indicates a strong and persistent nematicidal effect. These findings are consistent with earlier reports where extracts of *Alternanthera* spp. showed broad nematotoxic activity, including 100% mortality of *Bursaphelenchus xylophilus* at 10 g L^{-1} concentrations within 72 hours (Jiang and Chen 2022). The effectiveness of *C. rutidosperma* in increasing J2 mortality aligns with reports from other *Cleome* species, such as *C. viscosa*, which significantly reduced hatchability and caused rapid juvenile death in *M. incognita* (Claudius-Cole et al. 2018). These results confirm that both weeds possess bioactive phytochemicals capable of disrupting multiple developmental stages of root-knot nematodes.

These outcomes are consistent with earlier reports showing the broad nematotoxicity of *Alternanthera* spp., including 100% mortality of *B. xylophilus* at 10 g L^{-1} (Jiang and Chen 2022), and suppression of *Meloidogyne* spp. by *C. viscosa* extracts (Claudius-Cole et al. 2018). However, our results extend current knowledge by demonstrating stable egg-hatch inhibition in aqueous extracts of *A. philoxeroides* and enhanced juvenile mortality in *C. rutidosperma*, highlighting complementary nematocidal modes of action. This dual-stage efficacy underscores their potential for integrated nematode management beyond what has been reported in previous studies.

Microscopic observations provided further evidence of the mechanisms underlying these biological effects. Exposed eggs exhibited lysis of the eggshell and leakage of internal contents, while J2 showed cuticular disruption, vacuolation, and collapse of internal tissues (Figure 6). These lesions are typical of nematode exposure to phenolics, alkaloids, and terpenoids, compounds known to cause membrane destabilization and oxidative damage (Desmedt et al. 2020). Similar cuticular and eggshell deformations have been reported in nematodes treated with plant-derived compounds such as saponins and flavonoids, which act by altering permeability and inhibiting enzymatic processes required for hatching (Castañeda-Ramírez et al. 2020; Sousa et al. 2020). The consistency of our microscopic results with structural damage described in other studies strongly suggests that such phytochemicals mediate the nematicidal activity of the tested weeds.

The combination of hatch inhibition and juvenile mortality has significant implications for nematode management. Egg hatch inhibition is particularly valuable because it prevents the emergence of infective juveniles, reducing initial inoculum pressure in the soil. At the same time, J2 mortality provides a second layer of suppression, eliminating individuals that succeed in emerging. This dual action mirrors reports on other botanical nematicides, such as *Datura stramonium* and *Solanum nigrum*, where egg hatching was suppressed and juvenile survival reduced in parallel (Hussain et al. 2011). While the absolute levels of J2 mortality in our study (up to 22% at 168 h for *C. rutidosperma*) were lower than those reported for some solvent extracts that reached near-complete mortality, the persistence of high egg inhibition even under aqueous extraction conditions suggests that these weeds could serve as practical, low-cost resources in smallholder systems (Sithole et al. 2021; Fabiyi 2022).

From an agroecological perspective, the findings also reinforce the idea that certain weeds, often targeted for eradication, can provide ecosystem services when managed strategically. This approach aligns with holistic weed management principles that emphasize balancing control with conservation of beneficial traits, linking field-scale weed ecology to overall ecosystem health. The occurrence of *A. philoxeroides* and *C. rutidosperma* in tomato fields suggests that they could be harnessed as green manures, soil amendments, or sources of bioactive extracts for integrated nematode management. Their use would reduce reliance on synthetic nematicides, thereby mitigating environmental risks while supporting biodiversity-based pest suppression (Mwamula et al. 2022).

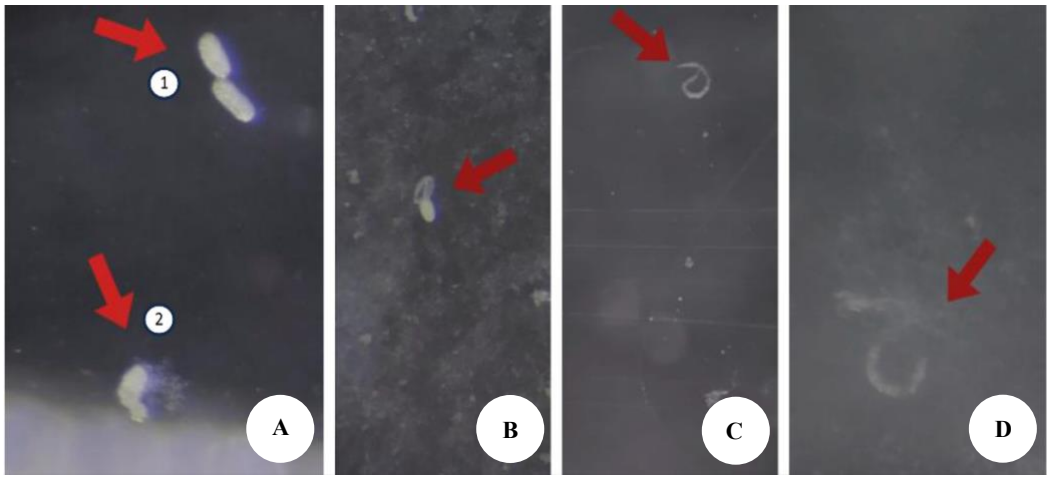


Figure 6. Microscopic observations of *Meloidogyne incognita*. A. Intact egg (1) and lysed egg (2), B. hatched egg, C. normal J2, D. J2 undergoing lysis

However, further work is required to fractionate their active compounds, determine effective dosages under field conditions, and evaluate possible trade-offs with crop competition. Nevertheless, the clear nematicidal effects observed here demonstrate the potential of these species as promising candidates for sustainable nematode management. At the same time, we acknowledge that deploying weeds as management tools must be grounded in rigorous, context-specific field trials and accompanied by careful monitoring of non-target biota and weed proliferation to avoid unintended ecological consequences. To balance benefits with ecological safeguards, practical measures include using off-field extracts or pre-flowering biomass, followed by immediate residue incorporation and routine post-application weed suppression. We also recommend pairing any field use with biodiversity plots (quadrats for plants and simple soil-biota indices) to detect non-target shifts early. These steps retain the nematicidal value while minimizing the risk of weed amplification.

Bioactive metabolites of weed extracts with nematicidal potential

The in vitro bioassays revealed that *A. philoxeroides* extract was the most effective in suppressing egg hatching of *M. incognita*, whereas *C. rutidosperma* extract showed the greatest efficacy in inducing J2 mortality. GC-MS analysis further identified 12 distinct compounds in *A. philoxeroides*, represented by 12 characteristic peaks in the chromatogram (Figure 7), with compound identities presented in Table 2. By comparison, the extract of *C. rutidosperma* produced 18 peaks in its chromatogram (Figure 8), corresponding to 18 detected compounds summarized in Table 3.

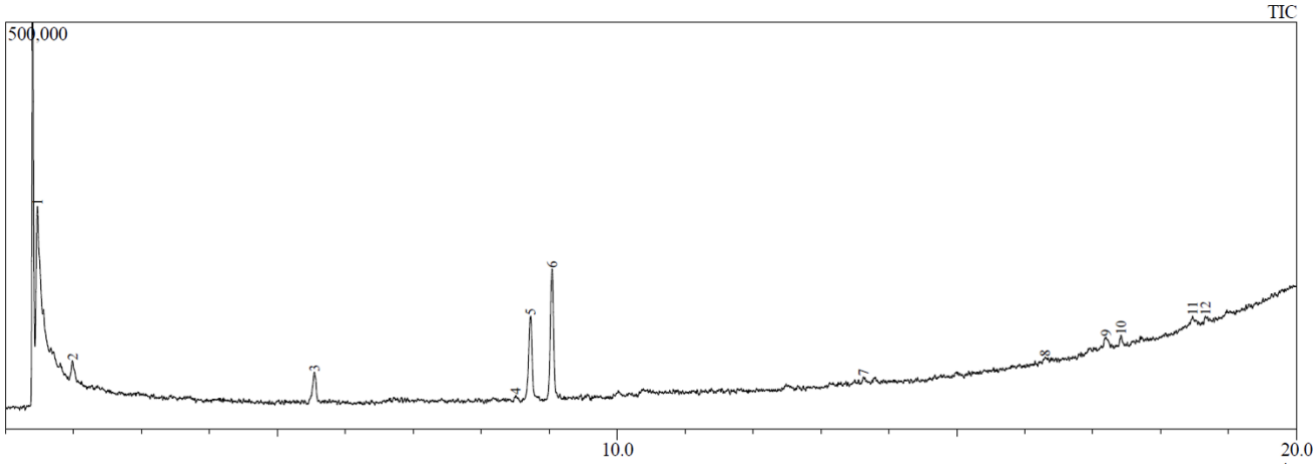


Figure 7. Gas Chromatography-Mass Spectrometry chromatogram of *Alternanthera philoxeroides* extract showing 12 characteristic peaks corresponding to 12 identified phytochemical compounds

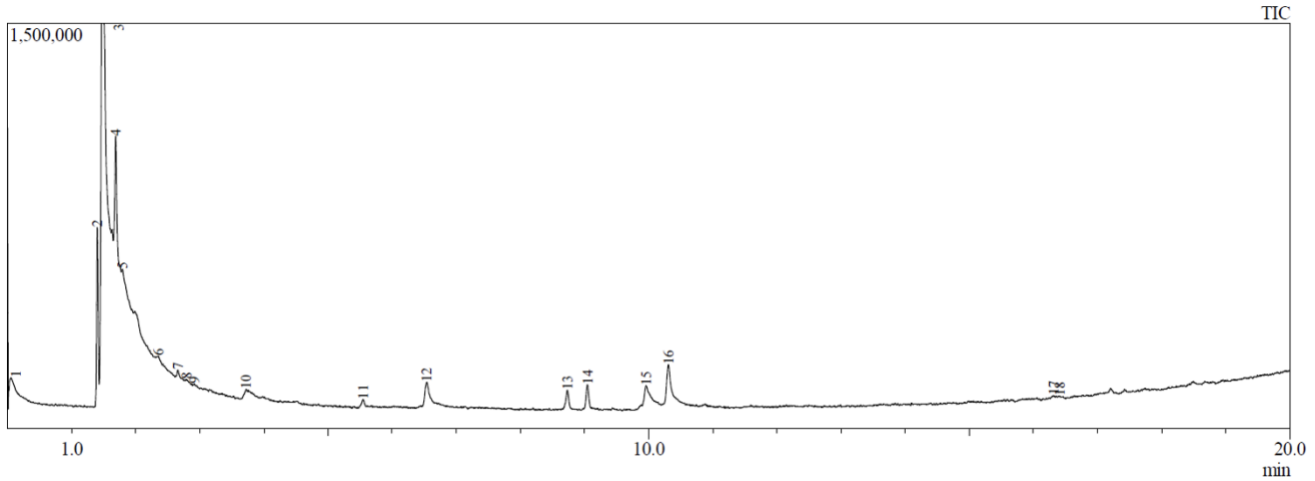
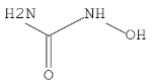
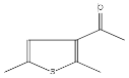
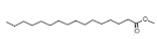
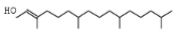
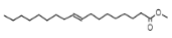
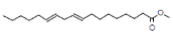
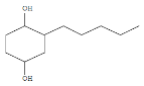
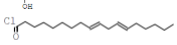
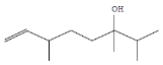
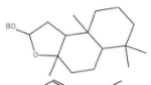
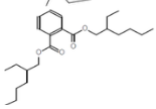
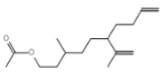


Figure 8. Gas Chromatography-Mass Spectrometry chromatogram of *Cleome rutidosperma* extract showing 18 characteristic peaks corresponding to 18 identified phytochemical compounds

Table 2. Phytochemical compounds identified from *Alternanthera philoxeroides* extract by gas chromatography-mass spectrometry

Peak #	Retention time	11	Compound name	Formula	CAS registry number	Chemical structure
1	1.466	42.17	Urea, hydroxy-	$CH_4N_2O_2$	127-07-1	
2	1.982	7.64	3-acetyl-2,5-dimethylthiophene	$C_8H_{10}OS$	2530-10-1	
3	5.545	5.01	Hexadecanoic acid, methyl ester (CAS)	$C_{17}H_{34}O_2$	112-39-0	
4	8.505	0.92	2-Hexadecen-1-ol, 3,7,11,15-tetramethyl-,	$C_{20}H_{40}O$	150-86-7	
5	8.725	14.25	9-Octadecenoic acid (Z)-, methyl ester (CAS)	$C_{19}H_{36}O_2$	112-62-9	
6	9.042	20.61	9,12-Octadecadienoic acid (Z,Z)-, methyl ester	$C_{19}H_{34}O_2$	112-63-0	
7	13.627	1.19	2-Pentyl-cyclohexane-1,4-diol	$C_{11}H_{22}O_2$	0-00-0	
8	16.298	2.23	9,12-Octadecadienoyl chloride, (Z,Z)-	$C_{18}H_{31}ClO$	7459-33-8	
9	17.200	1.89	7-Octen-3-ol, 2,3,6-trimethyl-	$C_{11}H_{22}O$	118989-21-2	
10	17.419	1.40	3a,6,6,9a-Tetramethyldodecahydronaphtho[2,1-b]furan-2-ol	$C_{16}H_{28}O_2$	52811-62-8	
11	18.470	2.10	1,2-Benzenedicarboxylic acid, bis(2-ethylhexyl) ester	$C_{24}H_{38}O_4$	117-81-7	
12	18.661	0.60	(3RS,6R)-3-Methyl-6-(1′-methylethenyl)dec-9-en-1-yl acetate	$C_{16}H_{28}O_2$	0-00-0	
Total		100.00				

GC-MS analysis of *A. philoxeroides* extract revealed a total of 12 distinct peaks corresponding to different chemical constituents (Table 2). The chromatogram was dominated by hydroxy-urea, which accounted for 42.17% of the total peak area at a retention time of 1.466 minutes. Other compounds present at relatively high proportions included 9-octadecenoic acid (Z)-, methyl ester (14.25%), 3-acetyl-2,5-dimethylthiophene (7.64%), and hexadecanoic acid, methyl ester (5.01%). Several additional components, including 2-hexadecen-1-ol, 3,7,11,15-tetramethyl- (0.92%), and other fatty acid derivatives, were detected at lower percentages, each contributing less than 5% of the total composition. Collectively, the chromatographic profile suggested a mixture dominated by one major constituent alongside a number of medium and minor compounds.

In contrast, the GC-MS profile of *C. rutidosperma* extract displayed 18 peaks, indicating a more complex chemical composition (Table 3). The most abundant constituent was peracetic acid, which represented 40.59% of the total peak area at a retention time of 1.476 minutes. This was followed by 1,2,3-propanetriol (17.05%) and cyclobutanemethanol (16.99%), both of which contributed substantially to the overall chemical makeup. Additional compounds, such as 2,4(1H,3H)-pyrimidinedione, 5-nitro- (3.73%) and methane, chloromethoxy- (4.02%), were also detected, together with several other minor constituents present at less than 5%. Compared to *A. philoxeroides*, the extract of *C. rutidosperma* was characterized by three dominant compounds in addition to a suite of minor constituents, highlighting differences in both diversity and abundance of phytochemicals between the two weed species.

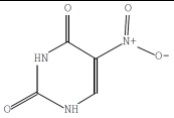
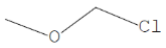
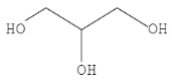
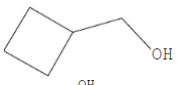
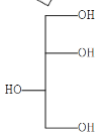
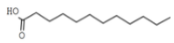
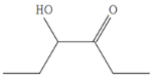
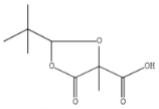
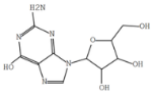
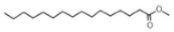
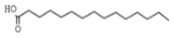
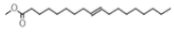
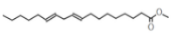
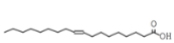
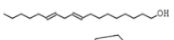
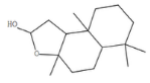
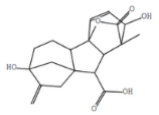
The GC-MS analysis of weed root extracts revealed several phytochemical constituents that can plausibly account for the nematicidal activity observed in vitro. In *A. philoxeroides*, three compounds of particular interest were hexadecanoic acid, methyl ester (methyl palmitate), 9-octadecenoic acid (Z)-, methyl ester (methyl oleate), and 1,2-benzenedicarboxylic acid, bis (2-ethylhexoxycarbonyl) (a phthalic acid derivative). In *C. rutidosperma*, notable compounds included dodecanoic acid (lauric acid), hexadecanoic acid, methyl ester, and 9-octadecenoic acid (Z)-, methyl ester. These fatty acid derivatives and aromatic esters are well documented for their antimicrobial and nematicidal activities, suggesting they play a key role in suppressing egg hatching and inducing juvenile mortality (Fabiyi 2022; Pradana et al. 2025).

Fatty acid methyl esters such as methyl palmitate ($C_{17}H_{34}O_2$; MW 270.5 g mol^{-1}) and methyl oleate ($C_{19}H_{36}O_2$; MW 296.5 g mol^{-1}) are frequently reported in plant extracts with nematotoxic properties (Lu et al. 2020; Pradana et al. 2025). Methyl palmitate has been shown to significantly reduce root galling and egg mass production of *M. incognita*, while also acting as a repellent to infective J2 and suppressing egg hatching (Machado et al. 2015; El-

Sherbiny 2024). Similarly, methyl oleate exerts nematicidal activity by disrupting proteins and enzymes, particularly those associated with the mitochondrial respiratory chain, leading to metabolic dysfunction (Lu et al. 2020; Ahmad et al. 2025). The presence of both compounds in the extracts examined here is consistent with the high inhibition of egg hatching observed in the bioassays, especially in *A. philoxeroides*.

In *C. rutidosperma*, the detection of dodecanoic acid (lauric acid; $C_{12}H_{24}O_2$; MW 200.32 g mol^{-1}) provides an additional mechanistic explanation for the elevated J2 mortality recorded. Lauric acid is known to disrupt lipid bilayers, compromise membrane integrity, and interfere with cellular metabolism (Dong et al. 2014; Lu et al. 2020). Bansal and Bajaj (2003) further demonstrated its strong effect on nematode embryogenesis, where lauric acid inhibited cell division within eggs, caused larval shrinkage, and damaged the eggshell, while also reducing the survival of J2. The identification of this compound supports the enhanced juvenile mortality observed in the *C. rutidosperma* treatment compared to other weed extracts.

Table 3. Phytochemical compounds identified from *Cleome rutidosperma* extract by gas chromatography-mass spectrometry

Peak #	Retention time	Area percentage (%)	Compound name	Formula	CAS registry number	Chemical structure
1	0.053	3.73	2,4(1H,3H)-Pyrimidinedione, 5-nitro-	$C_4H_3N_3O_4$	611-08-5	
2	1.400	4.02	Methane, chloromethoxy-	C_2H_5ClO	107-30-2	
3	1.476	40.59	Peracetic Acid	$C_2H_4O_3$	0-00-0	-
4	1.690	17.05	1,2,3-Propanetriol	$C_3H_8O_3$	56-81-5	
5	1.793	16.99	Cyclobutanemethanol	$C_5H_{10}O$	4415-82-1	
6	2.353	3.18	Butane-1,2,3,4-tetraol	$C_4H_{10}O_4$	0-00-0	
7	2.655	2.27	Dodecanoic acid	$C_{12}H_{24}O_2$	143-07-7	
8	2.795	1.28	Propionoin	$C_6H_{12}O_2$	4984-85-4	
9	2.919	0.58	2-t-Butyl-4-methyl-5-oxo-[1,3]dioxolane-4-carboxylic acid	$C_9H_{14}O_5$	0-00-0	
10	3.722	0.41	Guanosine	$C_{10}H_{13}N_5O_5$	118-00-3	
11	5.548	0.35	Hexadecanoic acid, methyl ester	$C_{17}H_{34}O_2$	112-39-0	
12	6.539	1.68	Pentadecanoic acid	$C_{15}H_{30}O_2$	1002-84-2	
13	8.731	0.82	9-Octadecenoic acid, methyl ester, (E)-	$C_{19}H_{36}O_2$	1937-62-8	
14	9.048	0.97	9,12-Octadecadienoic acid (Z,Z)-, methyl ester	$C_{19}H_{34}O_2$	112-63-0	
15	9.962	2.30	Octadec-9-Enoic Acid	$C_{18}H_{34}O_2$	0-00-0	
16	10.309	3.46	9,12-Octadecadien-1-ol	$C_{18}H_{34}O$	1577-52-2	
17	16.314	0.17	3a,6,6,9a-Tetramethyldodecahydronaphtho[2,1-b]furan-2-ol	$C_{16}H_{28}O_2$	52811-62-8	
18	16.415	0.16	Gibberellin A3	$C_{19}H_{22}O_6$	77-06-5	
Total		100.00				

The phthalic acid derivative 1,2-benzenedicarboxylic acid, bis(2-ethylhexoxycarbonyl) ($C_{16}H_{22}O_4$; MW 278.34 g mol^{-1}) was abundant in *A. philoxeroides*. Such compounds have previously been reported in bioactive plant extracts with strong nematicidal potential (Ntalli and Caboni 2012; Sholkamy et al. 2020; Catani et al. 2023). Its high representation in the chromatogram suggests it may be an important contributor to the potent suppression of egg hatching by *A. philoxeroides*. Taken together, these results demonstrate that both weed species harbor diverse phytochemicals with complementary modes of action, providing strong biochemical foundation for their observed nematicidal efficacy in vitro.

In conclusion, tomato fields in the study area support a moderately diverse weed flora in which *A. philoxeroides* is ecologically dominant and, critically, provides the strongest inhibition of *M. incognita* egg hatching, while *C. rutidosperma* yields the greatest juvenile (J2) mortality under in vitro exposure to 20% aqueous extracts. GC-MS profiling of both species revealed rich suites of phytochemicals, lending clear chemical basis for the observed nematicidal activities. These findings position locally abundant weeds as dual-purpose resources: components of field biodiversity and practical sources of botanicals to suppress root-knot nematodes. This study provides the first evidence from Indonesia linking field weed composition to nematicidal activity against *M. incognita*, demonstrating an integrative approach that connects agroecological diversity with biological pest suppression. Selectively leveraging *A. philoxeroides* and *C. rutidosperma* as green inputs could reduce dependence on synthetic nematicides and support biodiversity-based, sustainable pest management. Priority next steps include field validation across seasons and soils, bioassay-guided fractionation to identify active constituents and optimize dose and delivery, assessment of crop safety and non-target effects, and integration with cultural practices to balance weed competition with ecosystem services. Because weed floras and nematode pressures vary markedly among regions, these validation steps will need to be repeated and adapted under diverse agroecological conditions to generate robust, locally tailored recommendations.

A key limitation of this study is its reliance on in vitro bioassays, which may not fully capture the complexity of soil environments, interactions with rhizosphere microbiota, or persistence of bioactive metabolites under field conditions. Therefore, future work should prioritize multi-season field trials, dose-response optimization, and assessment of crop safety to validate the practical applicability of these weeds as botanical nematicides. Future work will include participatory on-farm trials, cost-benefit assessment, and the co-development of concise extension materials to support adoption across diverse production systems. In this context, effective implementation will require farmer-focused training and extension support that communicates simple, low-cost application protocols and foster collaborative learning among local stakeholders. In practical terms, these findings suggest that farmers could incorporate *A. philoxeroides* and *C. rutidosperma* into integrated nematode management programs through several approaches, including their use as green manure, incorporation of chopped biomass for biofumigation, or preparation of simple aqueous extracts for soil drenching. Such applications would allow smallholders to recycle locally available weeds into low-cost, environmentally friendly biocontrol inputs.

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REFERENCES

Abolusoro S, Izuogu N, Abolusoro P, Ige S, Adebiyi O. 2018. Toxic effects of bitter leaf powder (*Vernonia amygdalina* Del.) on root-knot nematode (*Meloidogyne incognita*) affecting tomato (*Lycopersicon esculentum*). Acad J Agric Sci 7 (6): 121-124. DOI: 10.15413/ajar.2019.0700.

Ahmad A, Yawar-Iqbal E, Siddiqui PJA, Sattar MA, Faizi S. 2025. Nematicidal potential of *Ceriops tagal* extracts and authentic compounds against cyst nematode *Heterodera zeae*. J Agric Food Chem 73 (28): 17550-17564. DOI: 10.1021/acs.jafc.4c12064.

Akhter G, Zafar A, Khan W, Jamshed M. 2018. In vitro nemato-toxic potential of some leaf extracts on juvenile mortality of *Meloidogyne incognita* race-3. Arch Phytopathol Plant Prot 51 (7-8): 399-407. DOI: 10.1080/03235408.2018.1490238.

Asyiah IN, Mudakir I, Budiman A, Pradana AP. 2025. Media optimization for nematode-trapping fungus *Orbilia jesu-laurae* and its effect in managing *Meloidogyne incognita*. Cogent Food Agric 11 (1): 2442667. DOI: 10.1080/23311932.2024.2442667.

Bansal R, Bajaj A. 2003. Effect of volatile fatty acids on embryogenesis and hatching of *Meloidogyne incognita* eggs. Nematol Mediterran 31: 135-140.

Barbercheck ME, Wallace J. 2021. Weed-insect interactions in annual cropping systems. Ann Entomol Soc Am 114 (2): 276-291. DOI: 10.1093/aesa/saab002.

Beaumelle L, Auriol A, Grasset M, Pavy A, Thiéry D, Rusch A. 2021. Benefits of increased cover crop diversity for predators and biological pest control depend on the landscape context. Ecol Solut Evid 2 (3): e12086. DOI: 10.1002/2688-8319.12086.

Blaix C, Moonen AC, Dostatny D, Izquierdo J, Le Corff J, Morrison J, Von Redwitz C, Schumacher M, Westerman P. 2018. Quantification of regulating ecosystem services provided by weeds in annual cropping systems using a systematic map approach. Weed Res 58 (3): 151-164. DOI: 10.1111/wre.12303.

Boutagayout A, Bouiamrine EH, Synowiec A, Oihabi KE, Romero P, Rhioui W, Nassiri L, Belmalha S. 2025. Agroecological practices for sustainable weed management in Mediterranean farming landscapes. Environ Dev Sustain 27 (4): 8209-8263. DOI: 10.1007/s10668-023-04286-7.

Buzanini AC, Boyd NS. 2024. Effects of goosegrass (*Eleusine indica*) competition on strawberry growth and yield. Weed Sci 72 (6): 748-753. DOI: 10.1017/wsc.2024.68.

Castañeda-Ramírez G, Torres-Acosta J, Mendoza-de-Gives P, Tun-Garrido J, Rosado-Aguilar J, Chan-Pérez J, Hernández-Bolio G, Ventura-Cordero J, Acosta-Viana KY, Jímenez-Coello M. 2020. Effects of different extracts of three *Annona* species on egg-hatching

processes of *Haemonchus contortus*. J Helminthol 94: e77. DOI: 10.1017/S0022149X19000397.
Catani L, Manachini B, Grassi E, Guidi L, Semprucci F. 2023. Essential oils as nematicides in plant protection: A review. Plants 12 (6): 1418. DOI: 10.3390/plants12061418.
Chapagain U, Chapagain BP, Nepal S, Manthey M. 2021. Impact of disturbances on species diversity and regeneration of Nepalese Sal (*Shorea robusta*) forests managed under different management regimes. Earth 2 (4): 826-844. DOI: 10.3390/earth2040049.
Cheimona N, Angeli C, Panagiotou E, Tzanidaki A, Drontza C, Travlos I, Bilalis D. 2016. Effect of different types of fertilization on weed flora in processed tomato crop. Agric Agric Sci Proc 10: 26-31. DOI: 10.1016/j.aaspro.2016.09.005.
Ciaccia C, Armengot-Martinez L, Testani E, Leteo F, Campanelli G, Trinchera A. 2020. Weed functional diversity as affected by agroecological service crops and no-till in a mediterranean organic vegetable system. Plants 9 (6): 689. DOI: 10.3390/plants9060689.
Claudius-Cole A, Okayi H, Wodoyin R. 2018. Potential of *Cleome viscosa* L. for the management of root-knot nematodes (*Meloidogyne incognita*) in okra (*Abelmoschus esculentus* (L.) Moench). Trop Agric 95 (4): 6-13.
Clements DR, DiTommaso A. 2022. Climate change and the persistence of weeds. In: Upadhyaya MK, Clements DR, Shrestha A (eds). Persistence Strategies of Weeds. John Wiley and Sons, United States.
Deesh AD, Ubaub LT, Furlong M, Lomavatu MF. 2025. Weed population dynamics and composition in a tropical island eggplant (*Solanum melongena* L.) agroecosystem: Implications for sustainable weed management. Pac Sci 78 (4): 429-443. DOI: 10.2984/78.4.6.
Desmedt W, Mangelinckx S, Kyndt T, Vanholme B. 2020. A phytochemical perspective on plant defense against nematodes. Front Plant Sci 11: 602079. DOI: 10.3389/fpls.2020.602079.
Dong L, Li X, Huang L, Gao Y, Zhong L, Zheng Y, Zuo Y. 2014. Lauric acid in crown daisy root exudate potently regulates root-knot nematode chemotaxis and disrupts Mi-flp-18 expression to block infection. J Exp Bot 65 (1): 131-141. DOI: 10.1093/jxb/ert356.
El-Sherbiny AA. 2024. Nematicidal performance of *Ipomoea carnea* and *Pluchea dioscoridis* extracts towards *Tylenchulus semipenetrans* and their possible application in nematode management on Washington navel oranges. Egypt J Agronematol 23 (2): 91-109. DOI: 10.21608/ejaj.2024.400577.
Esposito M, Westbrook AS, Maggio A, Cirillo V, DiTommaso A. 2023. Neutral weed communities: The intersection between crop productivity, biodiversity, and weed ecosystem services. Weed Sci 71 (4): 301-311. DOI: 10.1017/wsc.2023.27.
Fabiyi OA. 2022. Evaluation of weeds against root-knot nematode (*Meloidogyne incognita*) in vegetables. Sarhad J Agric 38 (4): 1289-1299. DOI: 10.17582/journal.sja/2022/38.4.1289.1299.
Forghani F, Hajihassani A. 2020. Recent advances in the development of environmentally benign treatments to control root-knot nematodes. Front Plant Sci 11: 1125. DOI: 10.3389/fpls.2020.01125.
Gardarin A, Plantegenest M, Bischoff A, Valantin-Morison M. 2018. Understanding plant-arthropod interactions in multitrophic communities to improve conservation biological control: Useful traits and metrics. J Pest Sci 91 (3): 943-955. DOI: 10.1007/s10340-018-0958-0.
Geremew D, Dechassa N, Bedada S, Bekele G, Hundessa N, Abdisa T, Gella D, Duguma M. 2023. Assessment of weed species composition and diversity in tomato (*Solanum lycopersicum* L.) farms in Ethiopia. F1000 Res 12: 1429. DOI: 10.12688/f1000research.133468.1.
Harms N, Cronin J. 2020. Biological control agent attack timing and population variability, but not density, best explain target weed density across an environmental gradient. Sci Rep 10 (1): 11062. DOI: 10.1038/s41598-020-68108-w.
Hussain MA, Mukhtar T, Kayani MZ. 2011. Efficacy evaluation of *Azadirachta indica*, *Calotropis procera*, *Datura stramonium* and *Tagetes erecta* against root-knot nematodes *Meloidogyne incognita*. Pak J Bot 43 (1): 197-204.
Jiang Y, Chen F. 2022. Nematocidal activity of extracts of *Alternanthera philoxeroides* and *Cayratia japonica* against *Bursaphelenchus xylophilus*. J Nanjing For Univ 46 (4): 45-52. DOI: 10.12302/j.issn.1000-2006.202009032.
Lopes A, Soares M, Chidichima L, Dias-Arieira C. 2020. Weed hosts of *Meloidogyne* spp. and the effect of aqueous weed extracts on egg hatching. Weed Res 60 (2): 142-149. DOI: 10.1111/wre.12399.
Lu Q, Liu T, Wang N, Dou Z, Wang K, Zuo Y. 2020. Nematicidal effect of methyl palmitate and methyl stearate against *Meloidogyne incognita* in bananas. J Agric Food Chem 68 (24): 6502-6510. DOI: 10.1021/acs.jafc.0c00218.
Machado ART, Ferreira SR, da Silva Medeiros F, Fujiwara RT, de Souza Filho JD, Pimenta LPS. 2015. Nematicidal activity of *Annona crassiflora* leaf extract on *Caenorhabditis elegans*. Parasites Vectors 8 (1): 113. DOI: 10.1186/s13071-015-0708-6.
Mwamula AO, Kabir MF, Lee D. 2022. A review of the potency of plant extracts and compounds from key families as an alternative to synthetic nematicides: History, efficacy, and current developments. Plant Pathol J 38 (2): 53. DOI: 10.5423/PPJ.RW.12.2021.0179.
Mwangi O, Mucheru-Muna M, Kinyua M, Bolo P, Kihara J. 2024. Organic farming practices increase weed density and diversity over conventional practices: A meta-analysis. Heliyon 10 (12): e32761. DOI: 10.1016/j.heliyon.2024.e32761.
Nafea ÛA, Mousa E-SM, Mahdy ME, Bakr RA. 2023. Nematicidal potential of some wild weeds on root-knot nematodes infecting tomato plants. Egypt J Crop Prot 18 (2): 24-42. DOI: 10.21608/EJCP.2023.310402.
Ntalli NG, Caboni P. 2012. Botanical nematicides: A review. J Agric Food Chem 60 (40): 9929-9940. DOI: 10.1021/jf303107j.
Pala F, Erman M, Cig F, Dilmen H, Pala F, Erman M, Cig F, Dilmen H. 2020. A study on weed flora and importance value index of weeds in wheat crop. Intl J Sci Technol Res 6 (1): 49-59. DOI: 10.7176/JSTR/6-01-05.
Peerzada AM. 2017. Biology, agricultural impact, and management of *Cyperus rotundus* L.: The world's most tenacious weed. Acta Physiol Plant 39 (12): 270. DOI: 10.1007/s11738-017-2574-7.
Pradana AP, Sholehah S, Andriyani DR, Hoesain M, Astuti W, Hadiani RU, Masnilah R, Adiwena M, Putri D. 2025. Nematicidal activity of *Trichoderma harzianum*-derived secondary metabolites against *Meloidogyne incognita* and metabolomic profiling of selected potent isolates. Asian J Agric 9: 326-338. DOI: 10.13057/asianjagric/g090134.
Raj R, Das T, Kaur R, Singh R, Shekhawat K. 2018. Invasive noxious weed management research in India with special reference to *Cyperus rotundus*, *Eichhornia crassipes,* and *Lantana camara*. Indian J Agric Sci 88 (2): 181-196. DOI: 10.56093/ijas.v88i2.79160.
Rusinque L, Maleita C, Abrantes I, Palomares-Rius JE, Inácio ML. 2021. *Meloidogyne graminicola*, a threat to rice production: Review update on distribution, biology, identification, and management. Biology 10 (11): 1163. DOI: 10.3390/biology10111163.
Satriawan H, Fuady Z. 2019. Analysis of weed vegetation in immature and mature oil palm plantations. Biodiversitas 20 (11): 3292-3298. DOI: 10.13057/biodiv/d201123.
Schleker ASS, Rist M, Matera C, Damijonaitis A, Collienne U, Matsuoka K, Habash SS, Twelker K, Gutbrod O, Saalwächter C. 2022. Mode of action of fluopyram in plant-parasitic nematodes. Sci Rep 12 (1): 11954. DOI: 10.1038/s41598-022-15782-7.
Sharma G, Shrestha S, Kunwar S, Tseng T-M. 2021. Crop diversification for improved weed management: A review. Agriculture 11 (5): 461. DOI: 10.3390/agriculture11050461.
Sharma P, Singh MK, Verma K, Prasad SK. 2022. Soil weed seedbank under different cropping systems of middle Indo-Gangetic plains. Plant Soil Environ 68 (11): 542-551. DOI: 10.17221/162/2022-PSE.
Shiferaw W, Demissew S, Bekele T. 2018. Ecology of soil seed banks: Implications for conservation and restoration of natural vegetation: A review. Intl J Biodivers Conserv 10 (10): 380-393. DOI: 10.5897/IJBC2018.1226.
Sholkamy EN, Muthukrishnan P, Abdel-Raouf N, Nandhini X, Ibraheem IB, Mostafa AA. 2020. Antimicrobial and antinematicidal metabolites from *Streptomyces cuspidosporus* strain SA4 against selected pathogenic bacteria, fungi and nematode. Saudi J Biol Sci 27 (12): 3208-3220. DOI: 10.1016/j.sjbs.2020.08.043.
Şin B, Öztürk L. 2021. Nematicidal weeds in the control of plant parasitic nematodes. J Agric Biotechnol 2: 78-96. DOI: 10.1016/j.fct.2007.09.106.
Sithole N, Kulkarni M, Finnie J, Van Staden J. 2021. Potential nematicidal properties of plant extracts against *Meloidogyne incognita*. S Afr J Bot 139: 409-417. DOI: 10.1016/j.sajb.2021.02.014.
Siyar S, Majeed A, Muhammad Z, Ali H, Inayat N. 2019. Allelopathic effect of aqueous extracts of three weed species on the growth and leaf chlorophyll content of bread wheat. Acta Ecol Sin 39 (1): 63-68. DOI: 10.1016/j.chnaes.2018.05.007.
Snyder WE. 2019. Give predators a complement: Conserving natural enemy biodiversity to improve biocontrol. Biol Control 135: 73-82. DOI: 10.1016/j.biocontrol.2019.04.017.
Sousa AJ, Souza PF, Gifoni JM, Dias LP, Freitas CD, Oliveira JT, Sousa DO, Vasconcelos IM. 2020. Scanning electron microscopy reveals deleterious effects of *Moringa oleifera* seed exuded proteins on root-

knot nematode *Meloidogyne incognita* eggs. Intl J Biol Macromol 154: 1237-1244. DOI: 10.1016/j.ijbiomac.2019.10.278.

Stucky T, Dahlin P. 2022. Fluopyram: Optimal application time point and planting hole treatment to control *Meloidogyne incognita*. Agronomy 12 (7): 1576. DOI: 10.3390/agronomy12071576.

Subedi S, Thapa B, Shrestha J. 2020. Root-knot nematode (*Meloidogyne incognita*) and its management: A review. J Agric Nat Resour 3 (2): 21-31. DOI: 10.3126/janr.v3i2.32298.

Sun J, Javed Q, Du Y, Azeem A, Abbas A, Iqbal B, He Y, Xiang Y, Du D. 2022. Invasive *Alternanthera philoxeroides* has performance advantages over natives under flooding with high amount of nitrogen. Aquat Ecol 56 (3): 891-903. DOI: 10.1007/s10452-022-09951-z.

Tapia-Vázquez I, Montoya-Martínez AC, Santos-Villalobos S, Ek-Ramos MJ, Montesinos-Matías R, Martínez-Anaya C. 2022. Root-knot nematodes (*Meloidogyne* spp.) a threat to agriculture in Mexico: Biology, current control strategies, and perspectives. World J Microbiol Biotechnol 38 (2): 26. DOI: 10.1007/s11274-021-03211-2.

Travlos IS, Cheimona N, Roussis I, Bilalis DJ. 2018. Weed-species abundance and diversity indices in relation to tillage systems and fertilization. Front Environ Sci 6: 11. DOI: 10.3389/fenvs.2018.00011.

Velasco-Azorsa R, Cruz-Santiago H, del Prado-Vera I, Ramirez-Mares MV, Gutiérrez-Ortiz MdR, Santos-Sánchez NF, Salas-Coronado R, Villanueva-Cañongo C, Lira-de León KI, Hernández-Carlos B. 2021. Chemical characterization of plant extracts and evaluation of their nematicidal and phytotoxic potential. Molecules 26 (8): 2216. DOI: 10.3390/molecules26082216.

Werle IS, Castro E, Pucci C, Chakraborty SB, Broderick S, Tseng TM. 2022. Identification of weed-suppressive tomato cultivars for weed management. Plants 11 (3): 411. DOI: 10.3390/plants11030411.

Zaragoza C, Tei F, Montemurro P, Baumann D, Dobrzanski A, Giovinazzo R, Kleifeld Y, Rocha F, Rzozi S, Sanseovic T. 2002. Weeds and weed management in processing tomato. Acta Hortic 613: 111-121. DOI: 10.17660/ActaHortic.2003.613.13.

Zhang Q, Si G, Chen L, Hu L, Cui G, Wang M, Zhao D. 2024. Current status and prospects of pine wilt disease management with phytochemicals: A review. Plants 13 (15): 2129. DOI: 10.3390/plants13152129.

Zhang Z, Liu J, Wang L-C, Wang Y, Deng L-L. 2020. Impact of the invasive plant *Alternanthera philoxeroides* (Mart.) Griseb on soil meso-and microfaunal community. Appl Ecol Environ Res 18 (2): 3073-3085. DOI: 10.15666/aeer/1802_30733085.