PLANT SCIENCE TODAY
ISSN 2348-1900 (online)
Vol 11(sp4): 01–18
https://doi.org/10.14719/pst.5658

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REVIEW ARTICLE

A meta-analysis of root herbivore-induced communication cascades affecting above-ground herbivores, parasitoids, and pollinators via host plants

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ARTICLE HISTORY
Received: 09 October 2024
Accepted: 06 November 2024
Available online
Version 1.0 : 29 December 2024

Check for updates

Additional information

Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

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Indexing: Plant Science Today, published by Horizon e-Publishing Group, is covered by Scopus, Web of Science, BIOSIS Previews, Clarivate Analytics, NAAS, UGC Care, etc
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CITE THIS ARTICLE
Karchikumar AS, Nalini R, Usha RB, Prema P, Kumutha K, Paramasivam M, Suresh K, Saai VB. A meta-analysis of root herbivore-induced communication cascades affecting above-ground herbivores, parasitoids, and pollinators via host plants. Plant Science Today.2024;11(sp4):01-18
https://doi.org/10.14719/pst.5658

Abstract

Several research papers over the past three decades have reported the profound influence of root herbivores on above-ground plant-insect interactions. Root-feeding insects significantly alter plant nutrient levels—carbon, nitrogen(N), phosphorus(P), and amino acids(AA)—triggering the production of defensive compounds like terpenoids, phenolics, gossypol, and DIMBOA in shoots. Jasmonate translocation from roots to shoots impairs shoot herbivore performance, while root herbivory suppresses salicylic acid (SA)-mediated defenses, benefiting phloem feeders. Reduced leaf water content and increased abscisic acid (ABA) levels enhance phloem feeder success. Nematode infestations lower AA and N, but increase foliar nicotine, aiding leaf chewers. Mycorrhizal fungi reduce plant N but raise carbon and P, while earthworms increase phytosterols, hindering aphid fecundity. These systemic changes cascade through trophic levels, even affecting hyperparasitoids. This review highlights root herbivory's intricate, cascading effects, reshaping our understanding of plant defense mechanisms and ecological interactions.

Keywords

above-ground herbivores; defensive compounds; parasitoids; pollinators; root herbivores

Introduction

Though members of the plant kingdom are stationary, they possess various defense mechanisms against their enemies, ranging from large vertebrate animals to small disease-causing microbes. For example, the tomato plant (*Solanum lycopersicum*) responds to herbivory by producing proteinase inhibitors that interfere with insect digestion. Simultaneously, it synthesizes chitinases and glucanases to break down fungal cell walls, providing an effective defense against microbial pathogens (1). Plants have evolved morphological and structural traits, physiological shift mechanisms, and defensive chemical compounds that serve in their direct defense. As an indirect defense mechanism, herbivore-induced volatiles recruit the third trophic level, i.e., their predators or parasitoids, which attack the herbivores. These direct and indirect defenses are well-documented in the above-ground portions of plants and above-ground herbivores. Similar defense mechanisms are also operational in the below-ground parts of plants, namely the roots. Root feeders mainly include insects and nematodes, while other important groups include microbes and decomposers. Plant roots produced diverse secondary compounds that triggered behavioral responses in root-feeding insects (2). These secondary metabolites play a crucial role in plant defense mechanisms by disrupting various biological functions in herbivores, such as feeding, growth, and development (3). Compounds like alkaloids, phenolics, and terpenoids are synthesized in plant roots as a direct response to herbivore attacks (4). For instance, larvae of the African black beetle (*Heteronychus arator*) were deterred by flavonoids such as phaseolin, medicarpin, maackiain, vestitol, coumestrol, genistein, and biochanin (2). Notably, compounds like phaseolin, phaseollinisoflavan, medicarpin, vestitol, maackiain, and 20-methoxyphaseollinisoflavan were found in legume roots at concentrations ranging from 1 to 6 mg/g, contributed significantly to root defense against herbivores (5). Roots also possess an array of plant secondary metabolites, such as alkaloids, glucosinolates(GLS), phenolics, terpenoids, furanocoumarins, and cardenolides (6-8), that confer direct defense against root herbivores. Plant roots generally hold higher concentrations of GLS (7, 9). Lignified roots of perennial plants act as a physical barrier to root herbivores. Roots exhibit impressive plasticity, directing root growth towards favorable niches (10). They also possess the physiological ability to divert root growth and escape from rhizospheric organisms (11). Apical root growth can reach two centimeters daily, enabling roots to escape from sessile rhizospheric organisms (12).

Since 2003, it became evident that root herbivory systematically triggers the production of defensive metabolites in the shoot (13, 14). Signals from the roots travel via the xylem to the shoots. Roots and shoots employ different signaling compounds and cascades during systemic signaling. Previous studies regarding the systemic interactions between roots and shoots have shown significant uniformity. Recent studies have demonstrated the negative interactions between above- and below-ground herbivores in crop systems. For instance, *Diabrotica speciosa* larvae (a below-ground herbivore) and *Rhopalosiphum maidis* (an above-ground aphid) were shown to have detrimental effects on corn fields. Initially, more adult aphids were observed on corn seedlings infested with *D. speciosa* larvae. However, over seven days, *D. speciosa* larvae reduced aphid growth by altering plant defenses and increasing the concentration of the secondary metabolite 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA (15).

Similarly, interactions between *Rhopalosiphum maidis* and *Holotrichia diomphalia* grubs, revealed reciprocal effects: below-ground grubs inhibited aphid growth. In contrast, above-ground aphids limited grub populations, which indicated a complex dynamic between these herbivores (16).

In another study, examining six leaf-chewing herbivore species on cabbage (*Brassica oleracea*) had minimal effects on the performance of the root-feeding specialist *Delia radicum* larvae. However, adult females strongly preferred laying eggs on plants already infested by leaf-chewing herbivores (17).

The impact of below-ground herbivory by striped cucumber beetle larvae on above-ground conspecific adult cucumber beetles and squash bugs (*Anasa tristis*) in squash (*Cucurbita*) showed that the plants damaged by below-ground larvae increased resistance to above-ground herbivores. This enhanced resistance was likely due to alterations in leaf protein content, the protein-to-carbohydrate ratio, and the release of the volatile compound (E)-β-ocimene in the above-ground plant parts (18).

Root herbivores induce more systemic responses in the leaves than *vice versa* (7, 9, 13). Root feeders induce interactions through plants on above-ground herbivores (19). Subsequently, the interactions initiated by root herbivore feeding (20-23) (Fig. 1). Root feeders could significantly influence plant interactions with above-ground herbivores, with these interactions being positive, negative, or neutral (19). Two main hypotheses explained the interactions between root-feeding and foliar herbivores. The “stress response hypothesis” proposed that root herbivores induced plant stress, reduced their ability to absorb water and nutrients uptake, and led to an accumulation of soluble N and carbohydrates in above-ground tissues, which could benefit foliar herbivores (19). Conversely, the “defense induction hypothesis” suggested that root herbivory activated plant defenses, accumulating secondary compounds in above-ground tissues, potentially detrimental to foliar feeders (6, 24).

Subterranean organisms such as nematodes, arbuscular mycorrhizal fungi (AMF), and decomposers also affect the degree of parasitism of foliar herbivory (13, 25-28). Root herbivore-induced systemic changes in above-ground defense levels affected herbivores and their natural enemies (13). Plants hosting root herbivores show reduced attraction for parasitoids (29, 30). The parasitoids avoid these plants (29), following the preference-performance hypothesis (31). Previous studies have reported the influence of root feeders on shoot herbivores and their parasitoids (25, 26, 32). Below-ground herbivores exhibit positive effects on above-ground beneficial insects associated with plants. In wild mustard (*Sinapis arvensis*), root feeding by click beetle larvae attracts more pollinators (33).

This paper reviews and presents the influence of root herbivores (insects, nematodes, soil fungi, decomposers) on above-ground herbivores, parasitoids, and pollinators. Furthermore, we systematically tabulated the plant responses in terms of nutritional levels, metabolic changes, signaling pathways triggered, and their influence on above-ground herbivores for easy understanding. We also conducted meta-analysis through Rstudio-Meta package for which we did iterative keyword searches in Connected Papers and PubMed (1989-2024) to retrieve studies pertaining to the influence of root herbivores on above-ground herbivores, parasitoids, and pollinators. This meta-analysis played a crucial role in deepening our understanding of the impacts of root-feeding insects by synthesizing data from multiple studies. It not only identified trends and knowledge gaps but also enhanced statistical power, which provided a solid foundation for drawing general conclusions.

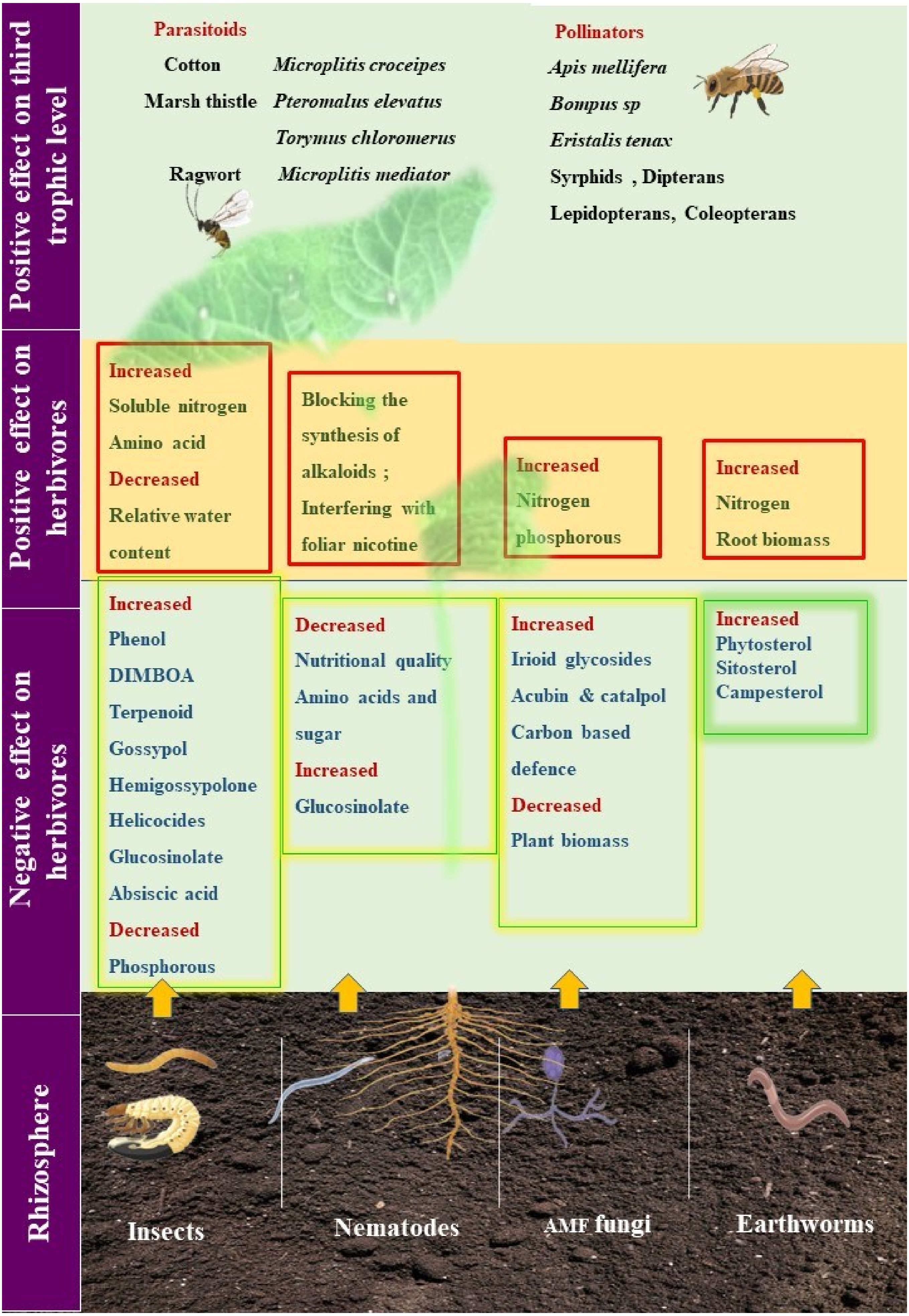

Fig. 1. Illustrative flow chart on the intricate relationships between below- and above-ground herbivores, parasitoids, and pollinators through the host plant.

Additionally, this synthesis would enlighten future research directions, ensuring that subsequent investigations are focused on addressing the most pressing questions in the field. Through this comprehensive approach, the meta-analysis will significantly contribute to both theoretical insights and practical applications. Existing research has not comprehensively analyzed the interactions between root-feeding insects, above-ground herbivores, and plant responses. Notable gaps include a lack of understanding regarding the differential impacts of root herbivory on various herbivore groups (chewing *vs* sucking), an insufficient systematic examination of plant variability in response to root herbivory, and a limited exploration of contextual factors that influenced these ecological dynamics.

For this, 88 relevant papers were selected based on our inclusion criteria, which focused on studies from agricultural and horticultural crops, including weeds. These were further grouped according to the root herbivore type–insects, nematodes, soil fungi, and decomposers. Further sub-categorization was based on the outcomes observed, including synergistic and antagonistic effects on above-ground herbivore performance, leaf chewers or phloem feeders, changes in plant nutritional value, biomass, relative water content (RWC), and defensive compounds. Additionally, papers addressing the impact of root herbivory on parasitoids and pollinators were included. A meta-analysis of these 88 studies was performed using Rstudio with the Meta package (Inverse variance method). The results were graphically represented in a Forest plot, and the significance was discussed.

Root-Feeding Insects: Unveiling Both Synergistic and Antagonistic Effects on Above-Ground Herbivore Performance

The impact of root herbivores extends beyond direct root damage, interacting with above-ground herbivores to shape plant defenses. Root herbivores can substantially alter the dynamics between plants and foliar feeders (19). In response to root herbivore attacks, plants produced secondary metabolites and phytotoxins that deter herbivore assaults (34). In black mustard, damage by cabbage root fly larvae triggers a significant increase in foliar GLS concentrations and N levels, illustrating a stress response (35). Furthermore, alterations in ABA and ethylene (ET) biosynthesis in cabbage (*Brassica oleracea*) were reported in response to herbivory (36).

Belowground herbivory by the turnip root fly (*Delia floralis*), *Brassica oleracea* and *Brassica napus* exhibited contrasting changes in GLS levels. *B. oleracea* showed increased aliphatic GLS, while *B. napus* experienced a decrease in indole GLS (37). Ragwort (*Jacobaea vulgaris*) when subject to below-ground wireworms (*A. lineatus*) herbivory. Significantly reduced the concentration of pyrrolizidine alkaloids (PAs) in the leaves (38).

Potato (*Solanum tuberosum*) plants damaged by tuber moth (*Tecia solanivora*) larvae reduced the performance of aboveground herbivores *Spodoptera exigua* and *Spodoptera frugiperda*. This reduction in performance was attributed to increased levels of foliar phenolics and glycoalkaloids, along with the increased abundance of lipoxygenase 3 (Lox3), a key enzyme involved in plant defense signaling pathways (39).

In general, plants exposed to root herbivores have been documented to exhibit changes in the profile of terpenoids (40), gossypol, hemigossypolone, and heliocides (41), as well as primary metabolites such as carbon, N, P, and AA, and secondary metabolites like phenols (42). Additionally, the levels of 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) in shoots were influenced by root herbivory (43). Root-chewing insects increased foliar secondary plant compounds' levels, which negatively affected leaf chewers, while phloem feeders remained unaffected (13, 14, 44).

Negative effects on shoot herbivores have been observed upon feeding by root herbivores using signaling pathways. Studies showed that root herbivory by *D. v. virgifera* negatively affected shoot herbivores in maize. Specifically, the roots' jasmonic acid (JA) was translocated to the shoots, adversely impacting shoot herbivores' feeding behavior (45).

The transport of jasmonates from roots to shoots negatively impacts the activity of shoot herbivores, as JA from the roots is translocated to the shoots. Root herbivory reduces SA-related defenses in foliage by inducing JA-related defenses. This mechanism also elucidated the increased performance of phloem feeders and reduced performance of insect chewers on plants previously attacked by root-feeding insects (Fig. 2).

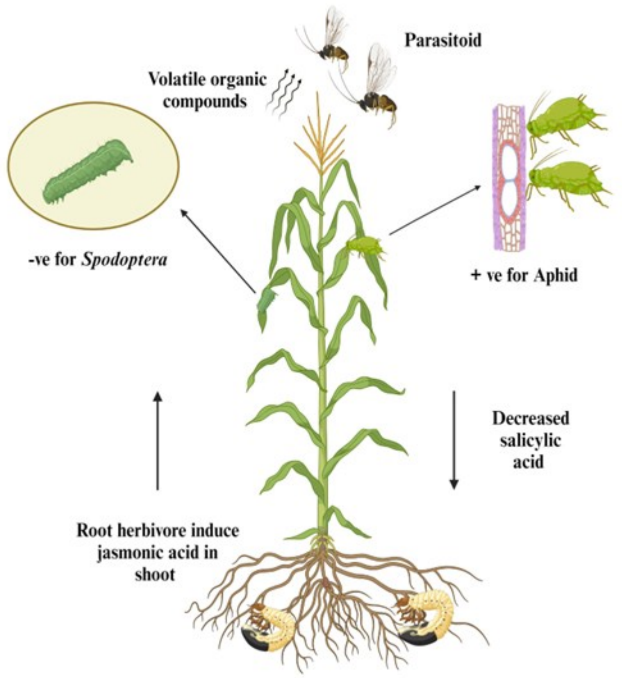

Fig. 2. Impact of root herbivory on the induction of jasmonic acid & salicylic acid with the performance of sucking and chewing insects.

However, in *Zea mays*, neither JA nor SA was found to be induced in the shoots by the rootworm *Diabrotica virgifera* (45). Later, it was found that there was reduced water content and increased ABA levels in the leaves of root-infested maize (46). An overview of the consequences of root-feeding insects on above-ground herbivores, encompassing changes in defensive compounds, resource allocation, hormonal signaling, gene expression, and overall plant physiology, are listed in Table 1 (47-54).

Table 1. Metabolic alterations in plants upon insect root herbivory and their impacts on the performance of above-ground herbivores

S.No.	Crop	Root herbivore	Influence on above-ground herbivore positive (+) or negative (-)	Metabolic alteration in plants	References
1.	*Shepherd's purse, Capsella bursa-pastoris*	Chafer, *Phyllopertha horticola*	Aphid, *Aphis fabae* (+)	Increased soluble N and amino acid.	(47)
2.	Sowthistle, *Sonchus oleraceus*	Chafer, *Phyllopertha horticola*	Leaf miner, *Chromatomyia syngenesiae* (+)	Increased soluble N. Decreased relative water content	(48)
3.	Rice, *Oryza sativa*	Rice water weevil, *Lissorhoptrus oryzophilus*	Fall armyworm, *Spodoptera frugiperda* (-)	Lower percentage of N. Increased phenolic concentrations.	(49)
4.	Cotton, *Gossypium herbaceum*	Wireworm, *Agriotes lineatus*	Beet armyworm, *Spodoptera exigua* (-)	Reduced root biomass. Increased terpenoid levels in roots as well as in leaves.	(40)
5.	Maize, *Zea mays*	Corn rootworm *Diabrotica virgifera* in the habitat	European corn borer, *Ostrinia nubilalis,* Specialist parasitoid *Macrocentrus grandii* (-)	Plant height and density were reduced in habitats, resulting in more open habitats.	(50)
6.	Maize, *Zea mays*	Corn rootworm, *Diabrotica virgifera*	Tobacco cutworm, *Spodoptera littoralis* and Necrotrophic pathogen, *Setosphaeria turcica.* (-)	DIMBOA (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one) increased in shoots, triggering transcription patterns in the shoot and aiding in ABA induction. Reduced water content. No effect on root biomass.	(43)
7.	Barley, *Hordeum vulgare*	Wireworm, *Agriotes* spp.	Aphid, *Rhopalosiphum padi* (+)	Reduced total plant mass and leaf dry mass by upto 25%. It had little impact on nutritional chemistry. Root herbivory had a synergistic effect, increasing the supply of essential AA to aphids.	(51)
8.	Violet cabbage, *Moricandia moricandioides*	Root feeding herbivore, *Morica hybrida* *Cebrio gypsicola* and Detritivores	Bath white, *Pontia daplidice*(-) Western dappled white, *Euchloe crameri* (-), its parasitoid *Cotesia kazak* and seed predator (-). Diamondback moth, *Plutella xylostella*; Cabbage butterflies, *Pieris rapae* *Pieris brassicae* Aphids (-), Leafhoppers (-)	The negative relationship between seed predators and indol-3-ylmethyl GS, which was induced by root herbivory The negative effect of detritivores on the N content on above-ground tissue led to reduced plant quality, thereby reducing the aphid, planthopper, seed predator, and leaf herbivore abundance. Detritivorous presence affected parasitoid abundance.	(52)
9.	Cabbage, *Brassica nigra*	Root fly, *Delia radicum*	Cabbage butterflies, *Pieris brassicae L.* (-) *Pieris rapae L*(-)	Butterflies preferred plants without root herbivores.	(53)
10.	Maize, *Zea maysvar.delprim*	Corn rootworm, *Diabrotica virgifera*	Tobacco cutworm, *Spodoptera littoralis* (-)	Triggered water loss ABA accumulation.	(46)
11.	Cotton, *Gossypium hirsutum*	Wireworm, *Agriotes lineatus*	*Spodoptera littoralis* (-)	Increased gossypol, hemigossypolone, and heliocides 1–4 in mature cotton leaves.	(41)
12.	Black mustard, *Brassica oleracea L. var. gemmifera cv. Olive*	Root fly, *Delia radicum and Drought*	Aphids, *Brevicoryne brassicae* (-) *Myzus persicae* (-)	Increased foliar GLS concentration. N concentration was decreased under root herbivory and increased under drought.	(35)
13.	Black currant, *Ribes nigrum*	Black vine weevil, *Otiorhynchus sulcatus*	Aphid, *Cryptomyzus galeopsidis* (+) Sawfly, *Nematus olfaciens* (-)	Deficiency of P in the leaves had a negative effect on sawflies development. Rise in foliar essential AA was positively correlated with aphid.	(54)
14.	Cabbage, *Brassica oleracea*	Root fly larvae, *Delia radicum* (elicit a suboptimal defense response in their host plants)	Diamond back moth caterpillars, *Plutella xylostella* Aphid, *Brevicoryne brassicae* (elicit more effective defense)	Strong activation of JA, regulated defense against chewing herbivores both in leaves and root. *D. radicum* caused a change in the expression of ABA and ET biosynthesis.	(36)

The meta-analysis revealed that the root-feeding insects significantly influence above-ground herbivore dynamics by either deterring chewing herbivores or favoring sucking herbivores (Fig. 3). Additionally, root herbivory led to notable changes in plant nutritional quality, reduced RWC, and decreased plant biomass while simultaneously increased the concentration of metabolites that deterred herbivores. In contrast, the outcomes such as increased RWC, the promotion of chewing herbivores, deterrence of sucking herbivores, and an increase in plant biomass were not found to be statistically significant. The overall analysis indicated substantial heterogeneity with Q statistics of 107.56, degrees of freedom of 11, and p-value of <0.0001.

Root-Feeding Nematodes: Unveiling Both Synergistic and Antagonistic Effects on Above-Ground Herbivore Performance

Plant parasitic nematodes were abundant on Earth and were crucial in ecosystems (55). The below-ground population of plant parasitic nematodes, numbering more than one million per square meter in many cases, significantly impacted crop growth and yield. Their presence on various plant species inhibited the flow of nutrients and water, limiting primary productivity (56). Nematode infestation negatively affected crop yields by damaging roots and reducing root surface area, which is critical for nutrient uptake. In legume-sorghum rotations, for example, nematodes adversely affected N dynamics in the soil, further complicating their role in nutrient availability (57). Sedentary endoparasitic nematodes such as root-knot nematode (*Meloidogyne*) and cyst nematode (*Heterodera* spp.) produced feeding cells that triggered hormonal responses in the host plant. In contrast, endoparasitic nematodes like *Pratylenchus* and *Tylenchorhynchus*, which could not create feeding cells, had less impact on host plants (58).

Root-feeding nematodes can increase or decrease defensive compounds in above-ground plant parts. In a study with *Brassica nigra* plants exposed to the root feeders, *Pratylenchus penetrans* and *Delia radicum* to assess their impact on the shoot-feeding specialist *Pieris rapae*, larvae grew more slowly. They produced fewer pupae on root-infested plants, especially those infested with *P. penetrans*. Root feeding significantly altered GLS and phenolic levels, with GLS in *P. penetrans*-infested plants, compared to control or *D. radicum*-infested plants (59). Their interactions with above-ground leaf-chewing insects have been reported to have positive effects (7), negative effects (59), or neutral effects (60). However, interactions of root-feeding nematodes and above-ground sucking insects like aphids consistently showed negative impacts (27, 60, 61). This can be attributed to nematode feeding reducing the rate of AA in the phloem of plants, thereby reducing plant fitness against aphids (27). Gossypol content in cotton increases due to root feeding by *M. incognita* (62). Root herbivory by *M. incognita* improved foliar nicotine expression, positively impacting leaf-chewing

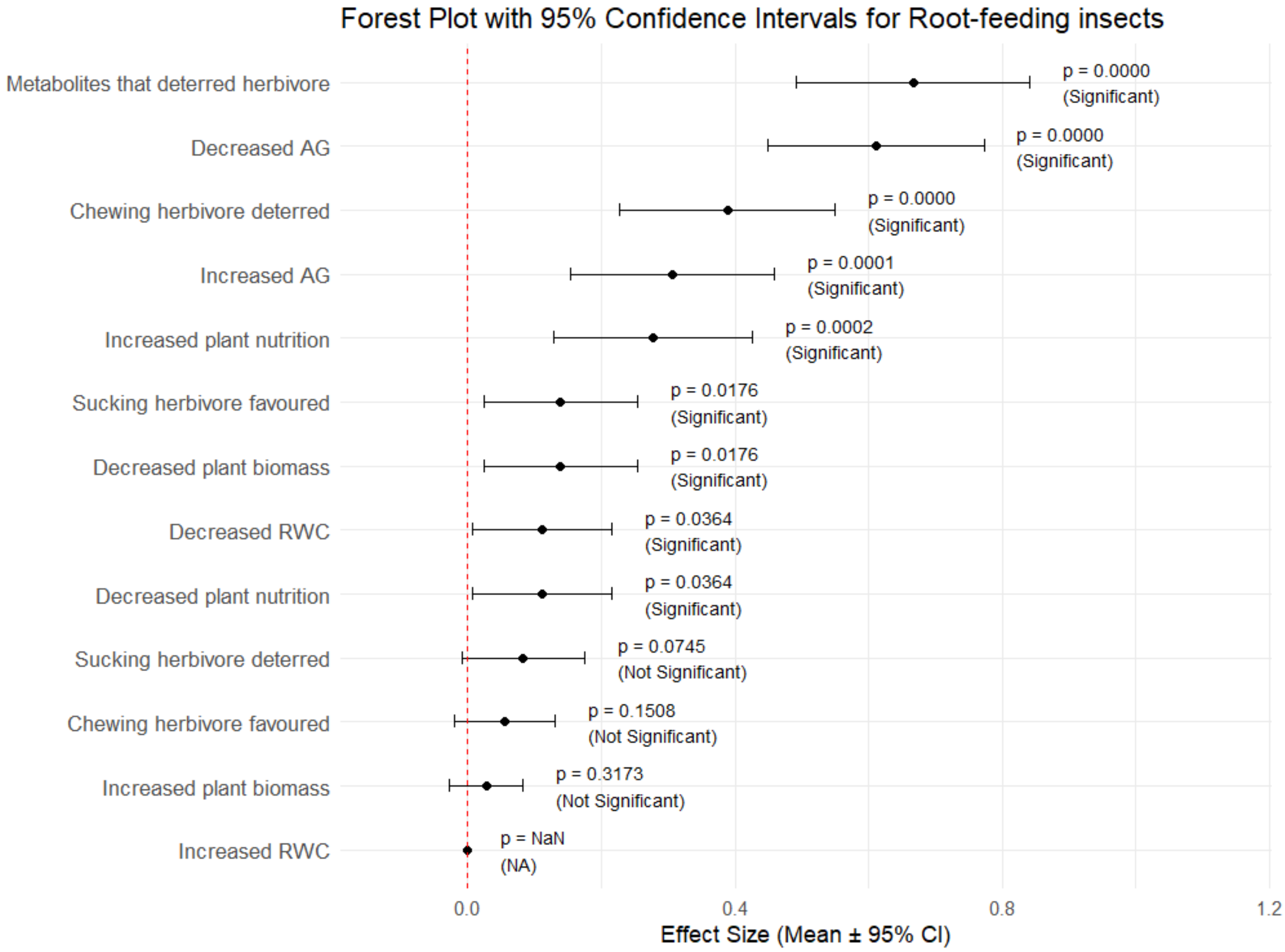

Fig. 3. Root-feeding insects and their significance unveiled through meta-analysis.

Table 2. Metabolic alterations in plants upon nematode root herbivory and their impacts on the performance of above-ground herbivores

S.No.	Crop	Root nematode + Microbes	Influence on above-ground herbivore positive (+) or negative (-)	Metabolic alteration in plants	References
1.	Black mustard, *Brassica nigra*	Endoparasitic nematode *Pratylenchus penetrans* and cabbage root fly, *Delia radicum*	Cabbage white, *Pieris rapae* (-)	Elevated phenolic compounds observed in plants with root herbivory (*D. radicum*). Higher protein content in root infested plants. High GLS content.	(59)
2.	*Common Bent, Agrostis capillaris* and Sweet vernal grass *Anthoxanthum odoratum*	Nematode communities and microorganisms	Aphid, *Rhopalosiphum padi* (-) and parasitoid, *Aphidius colemani* (-)	Soil community had adverse impacts on the N content in the leaves. Nematode decreased the levels of both AA and phenolic compounds. Aphids parasitism rates were greater in microcosms where nematodes were introduced.	(27)
3.	Ribwort, *Plantago lanceolata*	Root-feeding nematode, *Pratylenchus penetrans* and Wireworms, *Agriotes lineatus*	Aphids, *Myzus persicae* (-) and Golden twin-spot moth, *Chrysodeixis chalcites*	Nematodes had no effects on the biomass. Nematode reduced the nutritional quality of the above-ground plant parts. Wireworms reduced the total biomass of plant.	(60)
4.	Tobacco, *Nicotiana tabacum*	Root knot nematode, *Meloidogyne incognita*	Cabbage looper, *Trichoplusia ni* (+) and Aphid, *Manduca sexta* (+)	Enhanced the efficiency of leaf-chewing caterpillars by inhibiting the production of alkaloids. Positive response by both direct and indirect effects on tobacco phenolics and terpenoids. Interference with nicotine synthesis and transport to the shoot.	(14)
5.	Tobacco, *Nicotiana tabacum*	Root knot nematode, *Meloidogyne incognita*	Cabbage looper,*Trichoplusia ni* and Tobacco hornworm, *Manduca sexta* (+)	Leaf chewing insects gained advantages by disrupting the presence of foliar nicotine.	(7)
6.	Tobacco, *Nicotiana tabacum*	Root knot nematode, *Meloidogyne incognita*	Tobacco hornworm, *Manduca sexta* Flea beetle, *Epitrix* sp. Tobacco budworm, *Heliothis virescens* Beet armyworm, *Spodoptera exigua* (+) Aphid*, Myzus persicae* (-)	Chewing insects were not affected by nematode presence. Nematodes reduced the aphid abundance. Root herbivory had positive effect on leaf chewers by interfering with foliar nicotine.	(61)
7.	Soybean, *Glycine max*	Cyst nematode, *Heterodera glycines*	Aphid, *Aphis glycines* (-)	Lower aphid preference for nematode-infected plants. Altered the flavonoids production.	(63)
8.	Beetroot, *Beta vulgaris;* Cabbage, *Brassica oleracea*	Presence of nematodes *Heterodera schachtii* and rare soil microbes Presence of rare soil microbes	Aphid, *Brevicoryne brassicae* (-) on *Brassica oleracea* and *Myzus persicae* (-) on *Beta vulgaris*	Reduced sugar percentage. Enhanced GLS concentration. Reduced AA.	(64)
9.	Chinese tallowtree, *Triadica sebifera*	Root knot nematode, *Meloidogyne incognita;* Flea beetle larvae, *Bikasha collaris* that bore into roots	Flea beetle adults that chew leaves, *Bikasha collaris*	Leaf volatiles induced by *B. collaris* larvae attracted above-ground conspecifics and repelled a heterospecific above-ground herbivore. Root-knot nematode had no effects.	(65)

herbivory (14). Table 2 (63-65) summarizes the influence of root-feeding nematodes on the performance of above-ground herbivores, encompassing changes in plant metabolites.

The meta-analysis revealed that root-feeding nematodes had a significant impact on above-ground herbivore activities by decreasing plant nutrition, deterring sucking herbivores, and increasing the metabolites that deter herbivores. Chewing herbivores were favored, though these effects showed only marginal significance (Fig. 4). In contrast, outcomes such as increased plant nutrition, decreased RWC, deterred chewing herbivores, favored sucking herbivores, and changes in plant biomass (increase or decrease) did not show significant effects. The analysis exhibited moderate heterogeneity, as indicated by a Q statistic of 16.19 with 9 degrees of freedom and a p-value of 0.0631.

Root-Feeding Fungi: Unveiling Both Synergistic and Antagonistic Effects on Above-Ground Herbivore Performance

Arbuscular mycorrhizal fungi are essential soil microorganisms that provide mineral nutrition to plants and induce physiological changes in their hosts (66). Arbuscular mycorrhizal fungi have been observed to modify both inherent and induced defenses within leaf tissues (67). Positive effects of AMF on aphids have been reported (68, 69). In contrast, *Glomus mosseae* and *G. fasciculatum* were found to reduce the growth of the black vine weevil, *Otiorhynchus sulcatus* (70). Arbuscular mycorrhizal fungi also reduced plant N content, negatively impacting larval growth of *Urophora cardui* feeding on *Cirsium arvense* (71). Similarly, mycorrhizal associations reduced plant N content in *Plantago lanceolata* (60) and *Cucumis sativa* (72). Plants with mycorrhizal associations exhibited higher carbon and P concentrations than non-mycorrhizal plants (73).

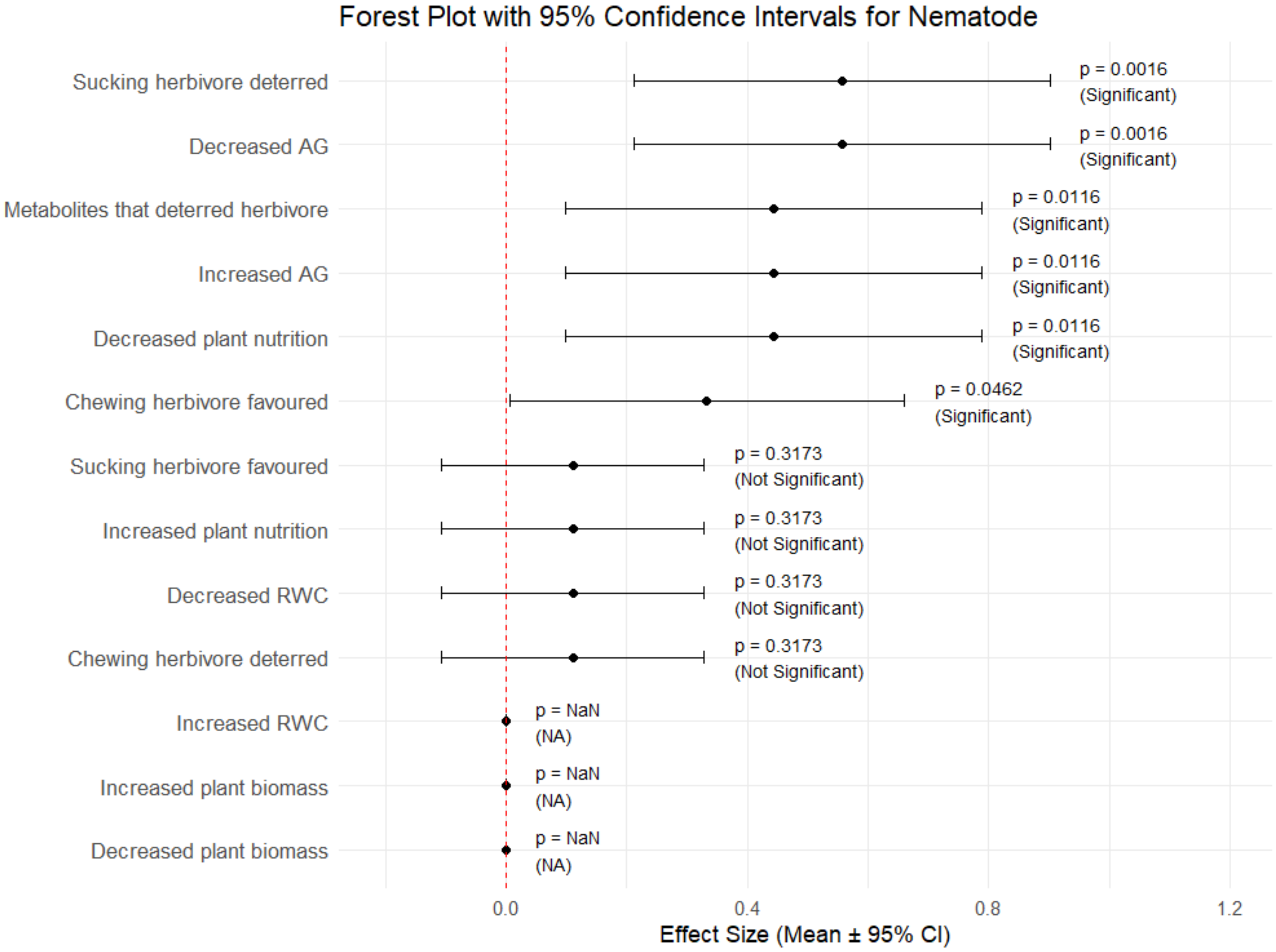

Fig. 4. Below-ground nematode and their significance unveiled through meta-analysis.

Oxeye daisy (*Leucanthemum vulgare*) plants colonized by three AMF species and exposed to ovipositing adults of the leaf-mining fly, *Chromatomyia syngenesiae* (26), showed increased plant growth due to various mycorrhizal species combinations. However, none of the combinations increased the damage caused by the fly, and some even reduced it. Mycorrhizal colonization enhanced the levels of various chemicals in roots, many of which were effective against pathogenic fungi and nematodes, and some showed efficacy against insects (74). Table 3 summarizes the effects of

Table 3. Metabolic alterations in plants as influenced by root infecting fungus and their impacts on the performance of above-ground herbivores

S.No	Crop	Root fungus	Influence on above-ground herbivore positive (+) or negative (-)	Metabolic alteration in plants	References
1.	Soybean, *Glycine max*	AMF, *Glomus fasciculatum*	Corn earworm, *Heliothts zea* (-), Fall armyworm, *Spodoptera frugiperda* (-)	Changes in toxins or antifeedants or leaf nutritional quality. The altered C/N ratio led to increased allocation of C-based defenses and reduced larval performance.	(75)
2.	Ribwort plantain,*P. lanceolata*	Natural AMF	Garden tiger moth, *Arctia caja* (-) and Aphid *Myzus persicae* (+)	Poorer food quality in terms of total N and carbohydrates. Higher levels of aucubin and catalpol. Lowered the C/N balance.	(47)
3.	Soybean, *Glycine max*	AMF, *Glomus etunicatum*	Mexican bean beetle, *Epilachna varivestis* (-)	VAM colonization increased resistance to Mexican bean beetle.	(76)
4.	Ribwort plantain, *Plantago lanceolata*	AMF, *Glomus intraradices*	Aphids, *Myzus ascalonicus and Myzus persicae* (+)	AMF changed the N status of the host plant. *M. persicae* showed greater growth in plants characterized by a limited P level.	(69)
5.	Common bird's-foot trefoil, *Lotus corniculatus*	AMF, *Glomus sp*. isolate BEG 21) (*Glomus sp*. isolate Basle Pi) (*Glomus sp*. isolate BEG 19)	Common blue butterfly, *Polyommatus icarus* (+)	Higher carbon and phosphorous concentration.	(73)
6.	Rice, *Oryza sativa*	Arbuscular mycorrhizal fungi, *Glomus intraradices*	Oviposition of rice water weevil, *Lissorhoptrus oryzophilus* (+)	Reduced plant biomass. Elevated levels of N and P in both leaves and roots. Increased N in the root.	(77)
7.	Ribwort, *Plantago lanceolata*	AMF, *Funneliformis mosseae*	Beet armyworm, *Spodoptera exigua* (-)	Reduction in plant biomass. Systemic induction of iridoid glycosides. AMF-induced Catalpol level.	(78)
8.	Rice, *Oryza sativa*	AMF, *Glomus intraradices*	Rice water weevil, *Lissorhoptrus oryzophilus* Fall armyworm *Spodoptera frugiperda*, Sheath blight, *Rhizoctonia solani* (+)	Increased shoot biomass. Improved plant nutrient status. Improved plant hormone signals lead to changes in genes responsible for defense.	(79)

AMF on above-ground herbivores coupled with plant metabolic alterations (75-79).

The meta-analysis revealed that the root-feeding fungi significantly influenced above-ground herbivore activities by enhancing plant nutrition, favoring or deterring chewing herbivores, favoring sucking herbivores, decreasing plant biomass, and elevating metabolite levels that repelled the herbivores (Fig. 5). Conversely, non-significant effects were observed regarding decreased plant nutrition, changes in RWC, the deterrence of sucking herbivores, and increased plant biomass. The analysis showed moderate heterogeneity, with a non-significant Q statistic with 10 degrees of freedom and a p-value of 0.1464.

Rhizosphere Decomposers: Unveiling Both Synergistic and Antagonistic Effects on Above-Ground Herbivore Performance

Earthworms, although not directly harmful to roots, substantially affect the rhizosphere, hence influencing higher trophic levels. They are recognized for promoting nutrient cycling in soil, breaking down organic materials, and enhancing microbial activity (80). Earthworms have been shown to enhance plant biomass (28). Conversely, no associated increase in plant biomass was observed, but an increase in foliar N and soil nitrate levels was detected in *Veronica persica* and *Cardamine hirsuta* (81). Studies indicated that soils inhabited by earthworms reduce plant damage by above-ground herbivores and lower the population of root-feeding nematodes.

Earthworms have been shown to alter the concentrations of defensive compounds, such as phytosterols and iridoid glycosides (82, 83). Aphid populations were affected as these defensive compounds were transported via the phloem (84). Earthworms have been shown to significantly influence plant defensive chemistry by altering the concentration of protective compounds like phytosterols (82). A study revealed that earthworms increased N concentration and phytosterol content in *Plantago lanceolata* shoots, but only when the litter was evenly mixed into the soil. The rise in phytosterols, which coincided with higher N levels, suggested that N availability played a role in the biosynthesis of these protective compounds. Consequently, by influencing N levels, earthworms indirectly affected the phytosterol content in plants, potentially impacting herbivore development and reproduction (82).

Soil invertebrates, specifically protozoa, and earthworms, influenced the performance of the above-ground aphid *Sitobion avenae* on barley. Aphid performance was significantly affected by protozoa, while earthworms had no notable effect (85). In contrast, reproduction rate of aphids (*Myzus persicae*) increased on *Poa annua* and *Trifolium repens* in the presence of earthworms (86). Studies with Brassicaceae, demonstrated the effects of earthworms on N-based secondary metabolites, specifically GLS in leaves (87, 88).

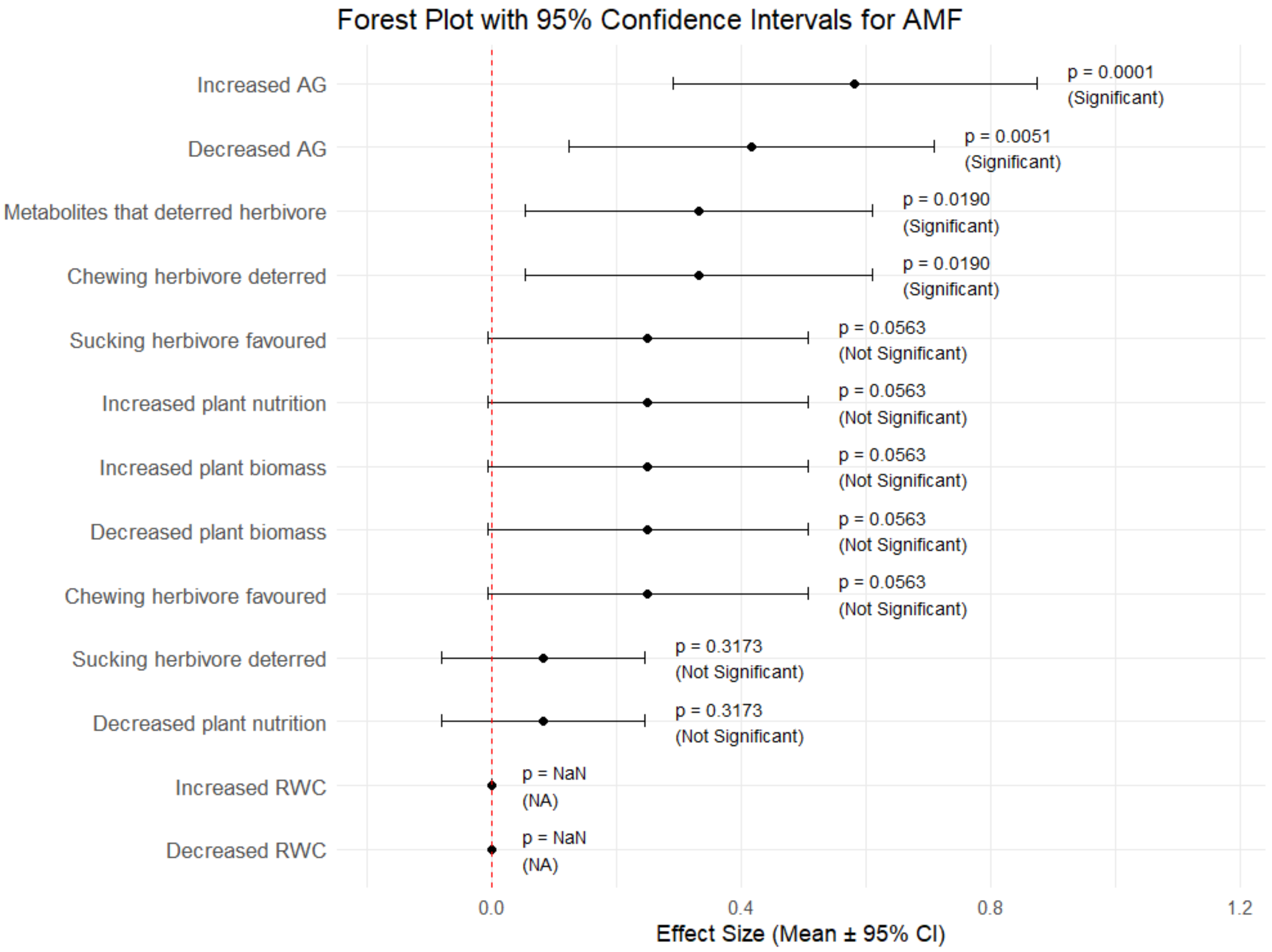

Fig. 5. Below-ground AMF and their significance unveiled through meta-analysis.

Besides their effects on primary and secondary metabolites, changes in plant gene expression have also been confirmed. An increase in lipoxygenase (lox) gene expression and a significant decrease in cysteine protease gene expression were observed in rice in the presence of earthworms (89). Additionally, earthworms are known to suppress the number of root-feeding nematodes (90). However, studies reported reduced plant damage by nematodes in the presence of earthworms without affecting root biomass (88), indicating that qualitative changes in the plants played an important role. The metabolic alterations in plants as influenced by rhizosphere decomposers and their impacts on the performance of above-ground herbivores are summarized in Table 4 (91).

The meta-analysis demonstrated that root-feeding decomposers significantly affected above-ground herbivore activities by altering the plant nutrition, increasing the presence of sucking herbivores, and enhancing the production of metabolites that deterred herbivores (Fig. 6). However, their impact on favoring or deterring chewing herbivores, deterring sucking herbivores, and changes in plant biomass was not statistically significant. The analysis revealed moderate to high heterogeneity, with a significant Q statistic of 22.79, with 10 degrees of freedom and a p-value of 0.0116.

Interactions Between Root Herbivores and Parasitoids

Plants employ diverse mechanisms to respond to attacks by herbivores and pathogens, utilizing direct and indirect strategies. Direct defenses included leaf morphological structures such as trichomes, glandular hairs, and surface wax, which deterred herbivores. Additionally, plants synthesized toxic compounds to deter herbivores. For example, GLS, sulfur-containing compounds primarily found in the Brassicaceae family, played a crucial role in the defense mechanism (92). Similarly, tobacco plants with nicotine synthesis in response to herbivory affected the growth of invading organisms (93).

Indirect defense mechanisms involve synthesising and emitting volatile plant chemicals when herbivores attack the plant. Predators and parasitoids were attracted by these herbivore-induced plant volatiles (HIPVs) (94). Over the years, there has been significant attention on HIPVs mediating interactions between plants, herbivores, and their natural enemies (95).

Root-feeding herbivores induce changes in plant biomass and alter the concentrations of primary and secondary metabolites in shoots (31, 40, 47). Previous research on subterranean organisms such as nematodes, AMF, and root-feeding insects has also shown effects on the degree of parasitism of above-ground herbivores (13, 25-28). Root herbivores significantly influence both the herbivore and its parasitoid. The presence of root herbivory prolonged the development time of the leaf herbivore and the parasitoid while also reducing the adult size of both the parasitoid and the hyperparasitoid simultaneously (31). Moreover, these effects could cascade up to the fourth trophic level, influencing the hyperparasitoid (Fig. 7). The influence of root herbivores on the performance of parasitoids is summarized in Table 5 (96, 97).

The meta-analysis revealed that the root-feeding

Table 4. Metabolic alterations in plants as influenced by rhizosphere decomposers and their impacts on the performance of above-ground herbivores.

S.No.	Crop	Rhizosphere decomposers	Influence on above-ground herbivore positive (+) or negative (-)	Metabolic alteration in plants	References
1.	Annual bluegrass, *Poa annua,* and White Clover, *Trifolium repens*	Collembola, *Heteromurus nitidus* and *Onychiurus scotarius* and Earthworms, *Aporrectodea caliginosa,* and *Octolasion tyrtaeum*	Aphids, *Myzus persicae*	Earthworms Impacted plant tissue carbon (C) concentration. Affected aphid reproduction. Collembola Increased plant tissue N concentration. Reduced aphid reproduction on *Trifolium repens.*	(86)
2.	Barley *Triticum aestivum*	Protozoa - Naked amoebae, flagellates, ciliates, and Earthworms, *Aporrectodea caliginosa*	Aphid, *Sitobion avenae*	Protozoa stimulated the development of above-ground herbivores. Protozoa enhanced and increased food quality (N).	(85)
3.	*Hairy Bitter Cress,Cardamine hirsuta*	Earthworms, *Aporrectodea caliginosa*	Aphid, *Myzus persicae* (+)	Increased root biomass and C content. The N content in both shoots and roots increased.	(32)
4.	Hairy Bittercress, *Cardamine hirsuta,* and Persian speedwell, *Veronica persica*	Earthworms, *Aporrectodea caliginosa* *Aporrectodea longa* *Aporrectodea nocturna* *Aporrectodea tuberculata* *Allolobophora chlorotica* *Octolasion lacteum*	Cabbage moth, *Mamestra brassicae* (+)	Soil nitrate and foliar N concentrations were enhanced No effect of earthworms on the biomass of the larvae. Leaf mass consumed by *M. brassicae* was higher.	(81)
5.	Ribwort plantain, *Plantago lanceolata*	Earthworms and litter	Aphid, *Myzus persicae* (-)	Increased the N concentration increased the total phytosterol, sitosterol, and campesterol. Reproduction of *M. persicae* decreased with increasing shoot N concentration.	(82)
6.	Wild mustard, *Sinapis arvensis*	Earthworm, *Octolasion tyrtaeum*, larvae of the click beetle *Agriotes sp.* root herbivory	Cotton leafworm, *Spodoptera litoralis* Aphids, *Brevicoryne brassicae* (+) *Lipaphis erysimi* (+)	Increased N availability to aphids.	(28)
7.	Wheat, *Triticum aestivum*	Earthworms, *Aporrectodea caliginosa* and Collembola, *Protaphorura armata*	Aphid, *Rhophalosiphum padi*	Earthworms strongly increased the N content which reduced aphid reproduction. Collembolans reduced total N concentration but did not affect aphid reproduction.	(91)

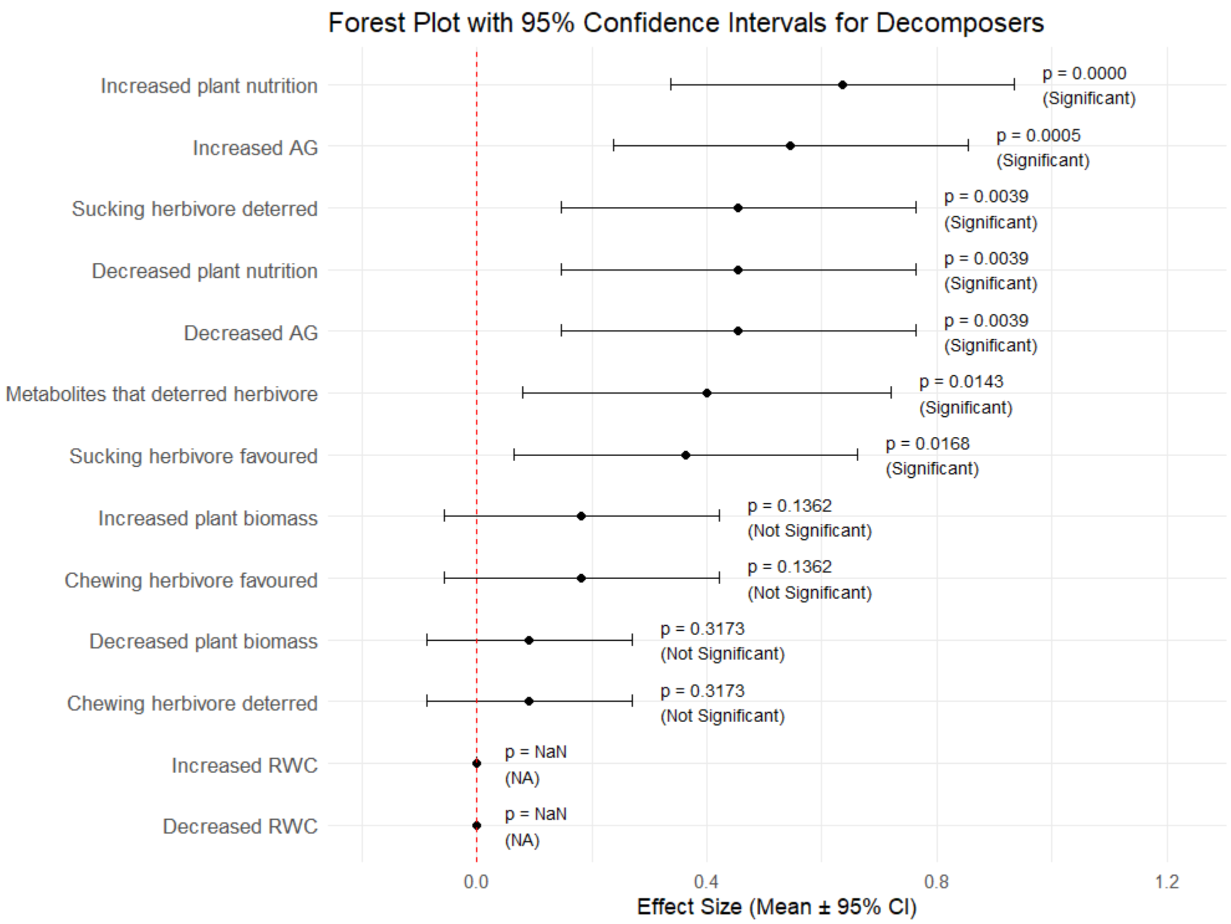

Fig. 6. Below-ground decomposer and their significance unveiled through meta-analysis.

herbivores had both significant positive and negative effects

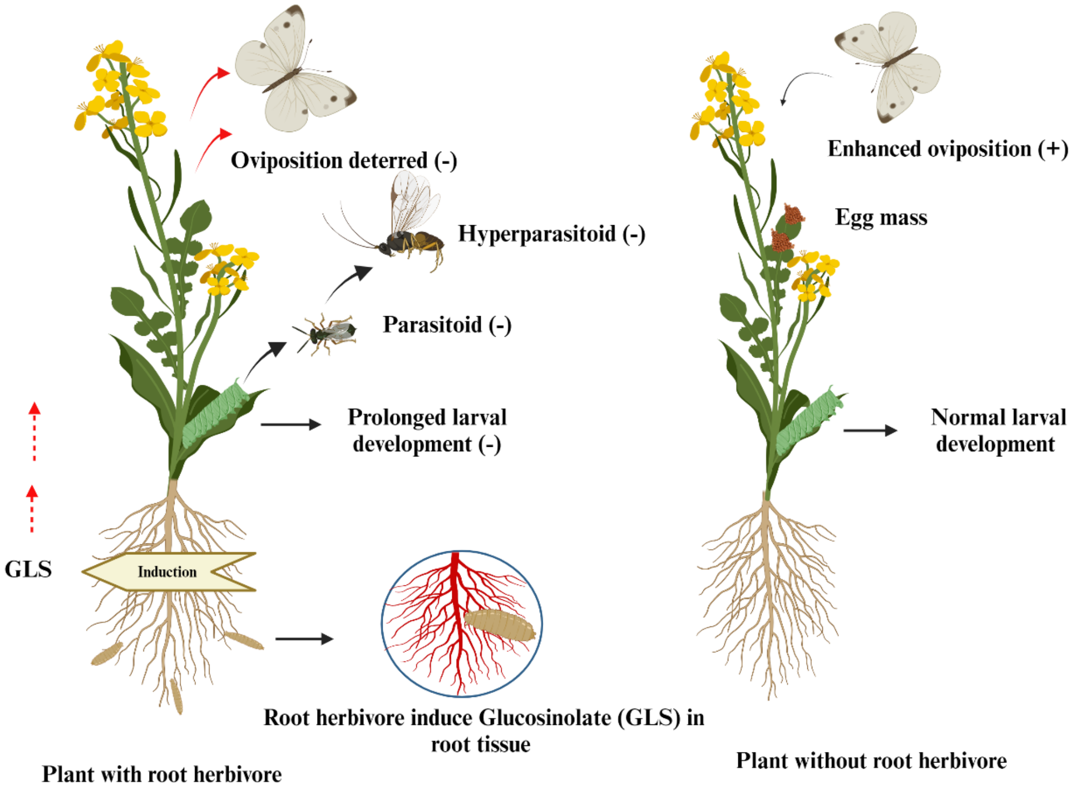

Fig. 7. Root herbivory communication cascade up to the fourth trophic level.

Table 5. Influence of root herbivores on the performance of parasitoids

S.No.	Crop	Root herbivore	Above-ground herbivore with parasitoid positive	Rationale	References
1.	Maize, *Zea mays*	Corn rootworm, *Diabrotica virgifera virgifera,* and entomopathogenic nematode, *Heterorhabditis*	Tobacco cutworm, *Spodoptera littoralis* parasitic wasp *Cotesiamarginiventris* (-)	Double infestation negatively affected the attractiveness of the parasitoid and the nematode. Attractant (E)-b-caryophyllene decreased when both Spodoptera larvae and D. virgifera attacked maize plants.	(29)
2.	Cotton, *Gossypium spp.*	Root-feeding nematode, *Meloidogyne incognita*	Corn earworm, *Heliocoverpa zea* parasitic wasp *Microplitis croceipes*(+)	Increased gossypol levels the cotton roots following *M. incognita*. *M. croceipes* preferred plants affected by earworms compared to those only damaged by *M. incognita*.	(62)
3.	Black mustard, *Brassica nigra*	Cabbage root fly, *Delia radicum*	Cabbage butterfly, *Pieris brassicae* and parasitoid *Cotesia glomerata (-)*	Parasitoid-recognized plants with the presence or absence of root herbivores. The preference performance pattern showed high amounts of dimethyl disulfide and dimethyl trisulfide. Females of *C. glomerata* did not lay eggs in plants	(30)
4.	Black mustard, *Brassica nigra*	Cabbage Root fly, *Delia radicum*	Cabbage butterfly, *Pieris brassicae* (-), Parasitoid *Cotesia glomerata* (-) and Hyperparasitoid, *Lysibia nana* (-)	High root fly population Root biomass reduced. Decreased N concentration. Low root fly population Higher GLS (sinigrin) levels.	(31)
5.	Cabbage, *Brassica oleracea*	Cabbage root fly, *Delia radicum*	Cabbage butterfly, *Pieris brassicae,* and its parasitoid, *Cotesia glomerata*	Parasitoid discovered their hosts three times faster when adjacent plants were infected with root herbivory.	(96)
6.	Cabbage, *Brassica oleracea*	Root fly, *Delia radicum*	Aphids *Myzus persicae*, *Brevicoryne brassicae*, parasitoids *Aphidius colemani* and *Diaeretiella rapae* (-)	Drought stress and root herbivory combined had a negative effect on parasitoid performance. Parasitoids avoided aphid hosts feeding on plants under drought stress and root herbivory.	(35)
7.	Wild cabbage, *Brassica oleracea*	Root fly, *Delia radicum*	Diamondback moth, *Plutella xylostella* and its endoparasitoid wasp, *Cotesia vestalis* (-)	(GLS, sugar and amino acid) stored in the body tissues of *Plutella* strongly affected the parasitoid.	(97)
8.	Ragwort, *Jacobaea vulgaris*	Wireworms, *Agriotes lineatus*	Cabbage moth, *Mamestra brassicae* (-) and its parasitoid *Microplitis mediator* (+)	Adverse effect on the levels of pyrrolizidine alkaloids (PAs) in shoot tissues. Root biomass was not affected. No impact on PA in the roots. As PA decreased in the leaves, *M. brassicae* exhibited slower growth on the plants with root herbivory. Development of parasitoid was rapid in the presence of increased jacobine-type PAs in the foliage.	(38)

on parasitoids (Fig. 8). The analysis showed no heterogeneity among the studies, evidenced by a Q statistic of 1.30 (p-value = 0.7296), indicating consistent results across the included studies. This lack of variability suggests that the observed effects are robust and reliable, reflecting a stable relationship between root-feeding herbivores and parasitoid dynamics.

Interactions Between Root-Herbivores and Pollinators

Few research papers have examined the impact of root herbivores on pollinators and the flower visitation rate by pollinators. These impacts have been reported as positive (28, 33), negative (98), or with no effect (99). Root herbivory has been found to modify floral characteristics, such as increased flower size, flower number per plant, altered flower sex ratios, enhanced floral nectar production, and increased sugar concentration (100).

Root herbivory altered flower sex ratios by reducing female flower production, which caused observed changes in honey bee behavior because female flowers are more rewarding than male flowers (101). Honey bees extend their probing duration on *Cucumis sativus* (Cucurbitaceae) flowers for longer on plants that have suffered root herbivory (102).

Mycorrhizal colonization in plant roots has also been shown to increase flower number and size and pollen and nectar production, thereby enhancing pollinator visitation (100, 103). In contrast, the rate at which honey bees probe flowers significantly decreases on plants inoculated with a single

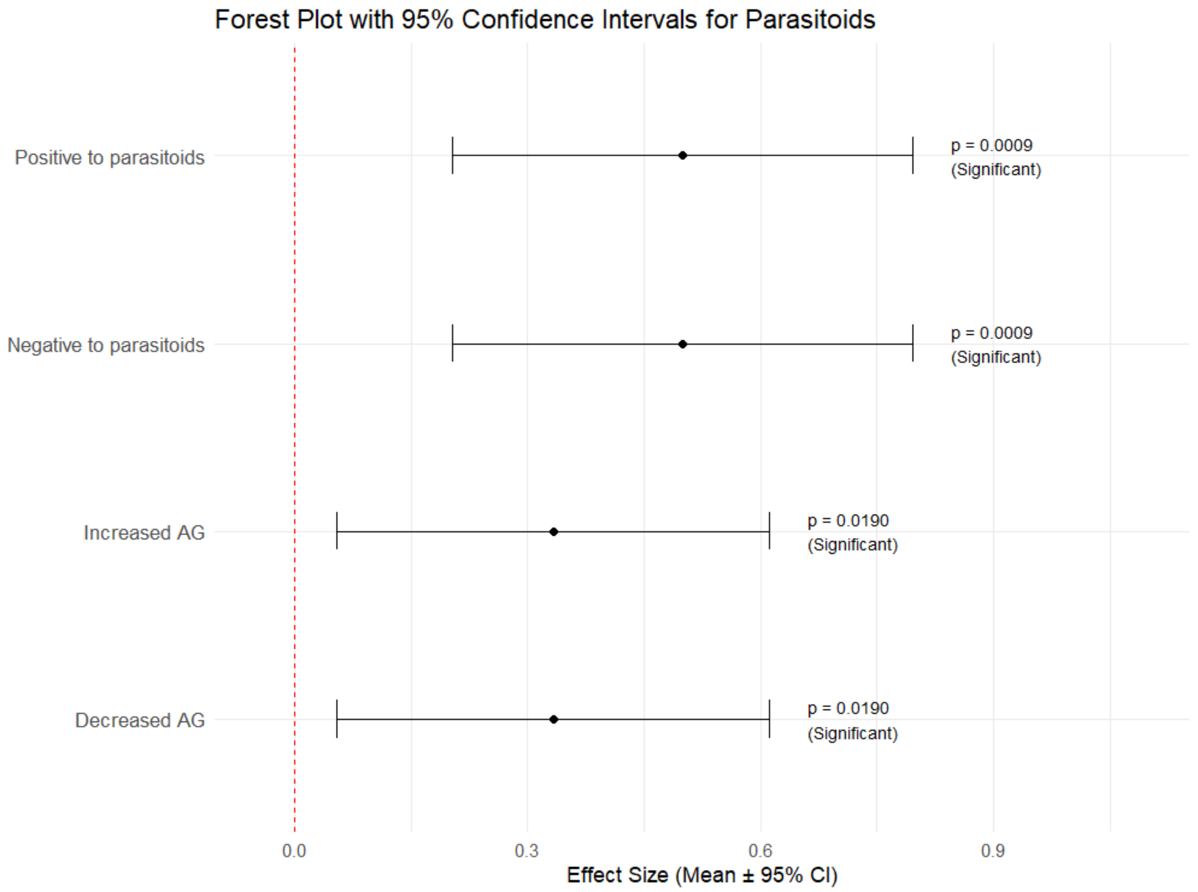

Fig. 8. Impact root feeding herbivory on above-ground parasitoids and their significance unveiled through meta-analysis.

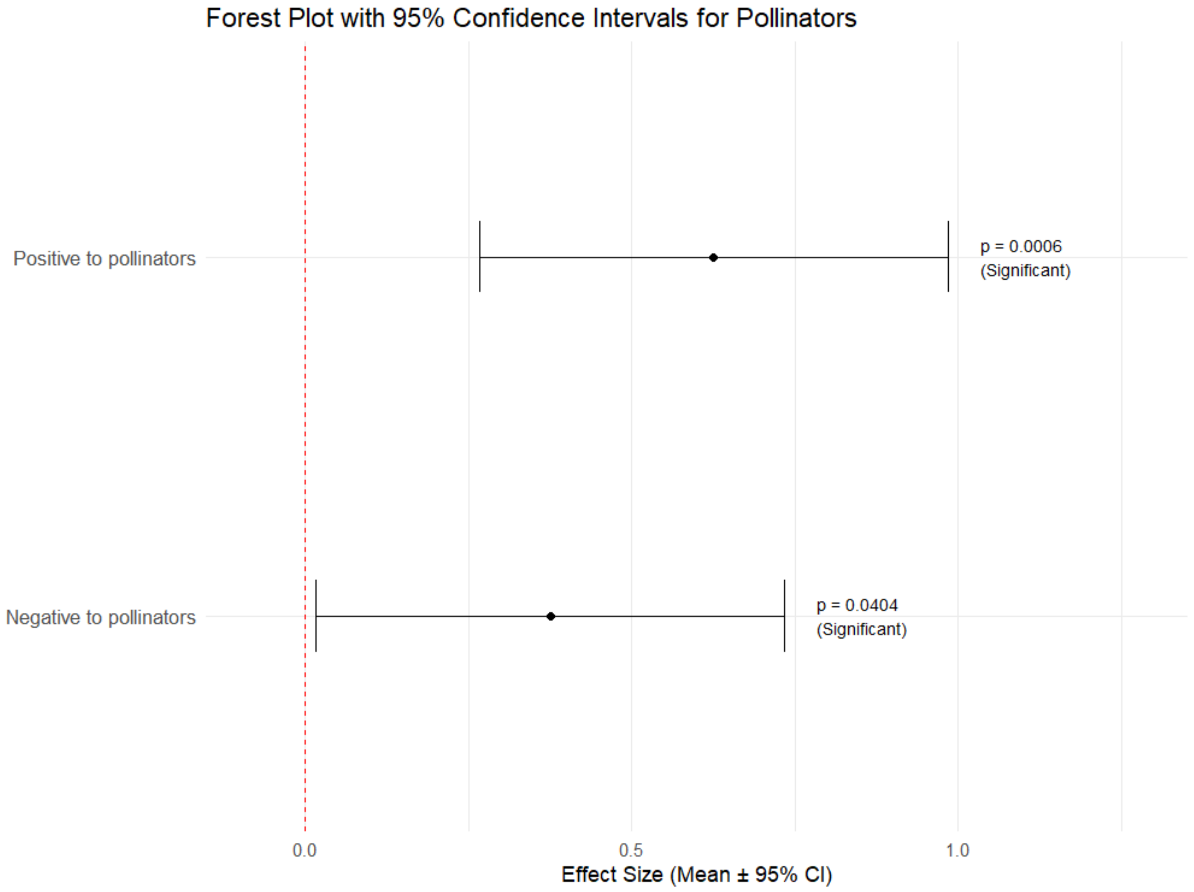

Fig. 9. Impact of root-feeding herbivory on above-ground pollinators and their significance unveiled through meta-analysis.

Table 6. Influence of root herbivores on the performance of pollinators

S. No.	Crop	Root herbivore	Pollinators	Rationale	References
1.	Wild mustard, *Sinapis arvensis*	Wireworm, *Agriotes* spp.	*Apis mellifera*, Syrphid, *Eristalis tenax*, *Bombus* spp., Dipterans (+)	Flower visitor rate is higher in plants with root herbivores due to enhanced nectar production.	(28, 33)
2.	Cornflower, *Centaurea cyanus*		*Apis mellifera*, *Bombus* spp., Dipterans and few Lepidopterans and Coleopterans (+)	Increased floral visitation rates by insects, due to increase in flower number per plant, floral nectar production and sugar concentration.	(100)
	African Marigold, *Tagetes erecta*			Increased floral visitation rates by insects, due to enhanced flower size, floral nectar production, and sugar concentration.	
	French marigold, *Tagetes patula*			Increased floral visitation rates by insects are due to an increase in flower number per plant and increase in flower size, floral nectar production, and sugar concentration.	
3.	Broad bean, *Vicia faba*	*Glomus aggregatum,* *G. clarum,* *G. deserticola,* *G. intraradices, G. monosporus, G. mosseae, Gigaspora margarita and Paraglomus brasilianum*		Plants inoculated with AMF produced significantly fewer extrafloral nectaries.	(106)
4.	Cucumber, *Cucumis sativus*	Arbuscular mycorrhizal fungus, *Glomus clarum, G. custos, Rhizophagus irregularis*	Honey bee (-) Bumble bees Lepidoptera	Bumble bees preferenced to plants inoculated with *R. irregularis*, whereas Lepidopterans to plants inoculated with *G. clarum.* Floral quality. High-reward plant.	(104)
5.	*Houndstongue Cynoglossum officinale*	Root weevil *Mogulones cruciger*	Six species of Bumble bees, one solitary bee (-)*	Larval root herbivory reduced the plant size and had fewer flowers, negatively impacting pollinator visitation.	(105)
6.	Cucumber, *Cucumis sativus*	Striped cucumber beetle, *Acalymma vittatum,* Oomycete pathogen, *Pseudoperonospora cubensis,* and AMF	Honey bee, *Pieris* specifically (-)	Reduced flower production following root damage.	(98)
7.	Cucumber, *Cucumis sativus*	Striped cucumber beetle, *Acalymma vittatum* Adult beetles feed on leaves, stems, and flowers while larvae feed on roots	Honey bees (+) *Bombus spp*. *Apis mellifera* Pierid butterflies Skippers Hoverflies Sweat bees	Root herbivory changed floral scent or nectar composition. Root herbivory altered flower sex ratios by reducing female flower production because female flowers are more rewarding than male flowers.	(102)
8.	Fireweed, *Chamerion angustifolium*	AMF, *Glomus intraradices, Gigaspora gigantea*	Pollinators (bumble bees and honey bees)	Increased pollinator visitation due to larger and more conspicuous inflorescence.	(103)

species of mycorrhizae (104). Root herbivory reduced plant size and resulted in fewer flowers, negatively impacting pollinator visitation (105). The impacts of root herbivory on pollinators are summarized in Table 6 (106).

The meta-analysis indicated that root-feeding herbivores had significant positive and negative effects on pollinators (Fig. 9). The heterogeneity test, with a Q value of 0.93 with one degree of freedom and a p-value of 0.3340 revealed no significant variability among the studies.

Conclusion

This comprehensive review illustrates the intricate relationships between below-ground and above-ground herbivores influenced by the induction or exclusion of plant defense metabolites. Emphasizing the importance of below-ground interactions in shaping above-ground ecosystems and in biodiversity conservation and sustainable agriculture is crucial. Over the past three decades, numerous controlled experiments have been conducted to elucidate these interactions' individual and combined effects on below-ground and above-ground herbivores. In the future, there should be a focus on validating these results under field conditions across diverse ecosystems to enhance ecological relevance and gain insights into the stability and dynamics of these interactions over time. Advanced molecular techniques can be employed to uncover the underlying mechanisms of these interactions. Developing ecological models based on empirical data and validating them under various environmental conditions will enhance predictive accuracy.

Acknowledgments

The authors express their deep gratitude to Tamil Nadu Agricultural University, Coimbatore, for providing an invaluable platform and support that enabled the publication of this article. Special thanks are Department of Agricultural Entomology at the Agricultural Cextended to the ollege and Research Institute, Madurai, for their unwavering assistance and for facilitating the work .

Authors' contributions

KAS: was responsible for data collection, drafting the original manuscript and editing NR: contributed by providing critical insights on specific topics, data collection, drafting the original manuscript, editing and supervision UB provided overall supervision, while PP handled data analysis and supervision KK, PM, SK and SB: were involved in supervision and editing. All authors reviewed and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

AI declaration

We hereby declare that no AI or automated tools were used in the writing, editing, or creating this review article, except for Grammarly, which was used solely for grammar and spelling checks.

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