



An overview of arbuscular mycorrhizal fungi–nematode interactions

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Received 13 October 2004; accepted 11 April 2005

KEYWORDS

Migratory
endoparasitic;
Sedentary
endoparasitic;
Ectoparasitic;
Resistance;
Tolerance;
Plant-mediated
interactions

Summary

Plant parasitic nematodes and arbuscular mycorrhizal fungi (AMF) share plant roots as a resource for food and space. The interest in AMF–nematode interactions lies in the possibility of enhanced resistance or tolerance of AMF-infected plants to nematodes, and the potential value of this for control of crop pests. Data collated from previous studies revealed a great diversity of AMF–nematode responses and we seek to generalise from these by evaluating and discussing interactions involving three groups of nematodes distinguished by their mode of parasitism: (i) ectoparasites; (ii) sedentary endoparasites; and (iii) migratory endoparasites. Based on proximity in tissue, we expected that the interactions between endoparasites and AMF would be stronger, i.e. more reciprocal effects of endoparasitic nematodes on AMF, than those between ectoparasites and AMF. Contrary to this hypothesis, we found that, relative to AMF-free plants, AMF-infected plants were damaged more by ectoparasites than by endoparasites. Of the sedentary endoparasites, numbers of root-knot nematodes were reduced more by mycorrhizal infection than were those of cyst nematodes. The reduction in nematode damage by AMF was not different for root-knot or cyst nematode infested plants. Migratory endoparasitic nematodes were the only group whose numbers were greater on AMF-infected plants. However, the experiments involving migratory nematodes were characterised by relatively high levels of AMF infection and little nematode damage compared to the other feeding types. The outcomes of the AMF–nematode interactions are determined by many factors during the interactions between organisms and their physical, physiological and temporal environments. Assessing effects by recording plant sizes and total nematode or AMF populations at the end of experiments gives very little information on the mechanisms of the interactions. It is time to stop doing studies of black boxes and time to start observing processes, directly by using microscopy and indirectly by application of molecular genetics.

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Zusammenfassung

Pflanzenparasitierende Nematoden und arbuskuläre Mykorrhiza Pilze (AMF) nutzen Wurzeln als Nahrungsquellen und Besiedlungsraum. Das Interesse an Interaktionen zwischen AMF und Nematoden liegt in einer möglichen Erhöhung der Resistenz oder Toleranz von AMF-infizierten Pflanzen gegenüber Nematodeninfektionen und dem sich daraus ergebenden potentiellen Nutzen zur Kontrolle von Schädlingen in Kulturpflanzen. Daten aus vorhergehenden Studien haben eine grosse Variation an Interaktionen zwischen AMF und Nematoden gezeigt und es ist unser Vorhaben diese Resultate zu generalisieren indem wir die Interaktionen, unterteilt in drei Gruppen von Nematoden je nach Art der Parasitierung (i) Ektoparasiten, (ii) sedentäre Endoparasiten und (iii) wandernde Endoparasiten, auswerten und diskutieren. Ausgehend von der Nähe zum Gewebe sind wir davon ausgegangen, daß die Interaktionen zwischen Endoparasiten und AMF stärker sind, das heißt mehr gegenseitige Effekte zwischen Endoparasiten und AMF bestehen als zwischen Ektoparasiten und AMF. Im Gegensatz zu dieser Hypothese haben wir gefunden, daß AMF-infizierte Pflanzen, relativ zu AMF-freien Pflanzen, mehr durch Ektoparasiten als durch Endoparasiten geschädigt wurden. Von den sedentären Endoparasiten wurde die Anzahl an Wurzelgallen-Nematoden durch Mykorrhiza Infektion stärker reduziert als die Anzahl an Zystennematoden. Die Reduktion von Nematodenschaden durch AMF an Wurzelgallen-Nematoden und Zystennematoden war nicht unterschiedlich. Wandernde endoparasitische Nematoden bildeten die einzige Gruppe, für welche die Anzahl Nematoden in AMF-infizierten Pflanzen erhöht war. Allerdings waren die Experimente, welche mit wandernden Nematoden durchgeführt wurden durch relativ hohe Infektionsraten mit AMF und geringem Nematodenschaden, verglichen mit den anderen Nematodentypen, gekennzeichnet. Die resultierenden Interaktionen zwischen AMF und Nematoden werden durch vielerlei Faktoren so als die physische, physiologische und zeitliche Umgebung bestimmt. Die Erhebung von Pflanzengröße und Populationsgröße von Nematoden oder AMF gegen Ende eines Experimentes sagt wenig aus über die Mechanismen von Interaktionen. Es ist daher an der Zeit die Studien von black box-Systemen zu unterlassen und stattdessen mit der Beobachtung von Prozessen, direkt anhand von Mikroskopie oder indirekt anhand von molekularer Genetik, fortzufahren.

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Introduction

Plant parasitic nematodes (PPN) and arbuscular mycorrhizal fungi (AMF) share plant roots as resources of food and space. There is interest in AMF-nematode interactions because of the possibility of enhanced resistance or tolerance of AMF-infected plants to nematodes. Some PPN are economically important crop pests. Most effective nematicides do not comply with current environmental demands and will have to be replaced by other means of nematode control with less impact on non-target organisms. Enhancing host resistance and/or tolerance by AMF could be a promising alternative (Harrier & Watson, 2004).

In general, PPN are detrimental to plant growth, while AMF are beneficial. The effects of both organisms occurring in one host on plant growth, on nematode numbers and on mycorrhizal colonisation, have been the subject of numerous studies, which have been reviewed at regular intervals (Hussey & Roncadori, 1982; Ingham, 1988; Smith,

1988; Pinochet, Calvet, Camprubí, & Fernández, 1996; Roncadori, 1997; Borowicz, 2001). The current consensus is that AMF may enhance host tolerance and increase resistance by slowing down nematode development. The net effects vary with the environment, plant genotype, nematode species and fungal isolates. Nematode species can be grouped by the nature of their parasitism and it may be that this affects the nature and outcome of interactions with AMF.

Most research on AMF-nematode interactions has concentrated on specific groups of nematodes, i.e. root-knot (*Meloidogyne* spp.) and root-lesion (*Pratylenchus* spp.) nematodes. These endoparasites include nematodes that are economically important, but nematodes with different feeding strategies are also major pests e.g. *Tylenchorhynchus* spp. on grasses, *Xiphinema* spp. on fruit trees and *Longidorus* spp. on corn (Barker, Pederson, & Windham, 1998).

We hypothesise that interactions between AMF and ectoparasitic nematodes are less strong than

those between AMF and endoparasites. Many ectoparasites feed on superficial cells, not those in the deeper cortical layers, colonised by AMF. Some long styleted ectoparasites feed on cells in deep layers, for example, *Xiphinema* and longidorids at root tips. Even so, root tips are less likely to be infected by AMF, probably due to the delay between encounter and colonisation (Smith, Dickson, & Walker, 1992), so that this group of nematodes may also be unaffected by direct competition with AMF. Ectoparasitic nematodes are more likely to be affected indirectly by AMF-induced changes in plant physiology than directly by competition with the fungus. Among examples of changes in plant physiology after AMF infection, are increased free amino acids in leaves, especially arginine (Giovannetti, Tosi, Torre, & della Zazzera, 1991), higher chitinase activity in roots (Jothi & Sundarababu, 2002a) and an increase in soluble sugars and phenols in roots (Umesh, Krishnappa, & Bagyaraj, 1988).

Most reviews on AMF–nematode interactions focus on root-knot nematodes only or treat sedentary nematodes as a single group. This is probably for practical reasons, as the available data from sedentary cyst nematodes (*Globodera*, *Heterodera* and *Punctodera* spp.) is much less than that from *Meloidogyne*. The similarities between root-knot and cyst nematodes are that both induce changes in plant cells and feed on the modified cells, but they are also distinguished by their invasion strategies and by nature of the feeding cells. The feeding cells induced within the vascular cylinder by root-knot and cyst nematodes may breach the endodermis, spreading into the cortex where there may be direct competition for space with AMF. However, the feeding cells of some cyst nematodes (e.g. *Heterodera avenae*) are confined to cells within the endodermis and thus may not be affected by direct competition with fungal feeding structures. The dependence of root-knot and cyst nematodes on one feeding site at which the females become sedentary could make them more sensitive to changes in plant physiology by AMF than are the more mobile migratory nematodes. In Borowicz (2001), *Heterodera* interacted with AMF differently from root-knot nematodes: whereas *Heterodera* had a greater effect on AMF-infected than AMF-free plants, the root-knot nematodes reduced growth less when plants were mycorrhizal. In our analyses, which include more studies, we seek to verify whether AMF do indeed have different effects on plants infected by root-knot and cyst nematodes.

Migratory endoparasites, such as root-lesion (*Pratylenchus* spp.) and burrowing (*Radopholus*

spp.) nematodes feed and move within the cortex so may be feeding on cells suitable for AMF colonisation. Adults and eggs of *Pratylenchus vulnus* can be found in the same root tissue as AMF mycelium and vesicles (Pinochet, Calvet, Camprubí, & Fernández, 1995; Lopez, Pinochet, Fernández, Calvet, & Camprubí, 1997). AMF can change root morphology with consequences for penetration and movement of migratory nematodes (Elsen, Declerck, & De Waele, 2003c). Borowicz (2001) suggested that migratory nematodes benefit from AMF while sedentary ones are negatively affected. However, the author warned that the results for the migratory nematodes came from only a few experiments. In an earlier review, specifically on the effect of migratory nematodes in perennial crops, Pinochet et al. (1996) found that migratory nematode reproduction was negatively affected by AMF colonisation in half the reviewed studies but not at all in the other half. We summarise data from studies on migratory nematodes that appeared after 1996 to test whether there is an effect of AMF colonisation on migratory nematode reproduction.

The interaction between stem- and leaf nematodes, which infest aerial parts, and AMF is particularly interesting. Recently, attention has focussed on interactions between aboveground and belowground organisms (van Dam et al., 2003). Mycorrhizal colonisation can increase aphid weight and fecundity (Gange, Bower, & Brown, 1999). In one report on the effect of AMF on stem- and leaf nematodes (Sikora & Dehne, 1979), *Ditylenchus dipsaci* numbers first increased and then decreased on mycorrhizal *Phaseolus vulgaris* compared to non-mycorrhizal controls and *Aphelenchoides ritzemabosi* populations decreased on mycorrhizal compared to non-mycorrhizal tobacco. No information on the effect of nematodes on AMF was given, but it is known that stem nematodes affect root physiology: clover and lucerne plants with inoculated stem and leaf tissue had increased enzyme activities associated with phytoalexin production in roots (Cook, Tiller, Mizen, & Edwards, 1995; Edwards, Mizen, & Cook, 1995). As there are no studies on interactions between AMF and aerial nematodes known to us other than that of Sikora & Dehne (1979), we excluded these interactions from our results due to lack of available data.

Here, we will evaluate and discuss the interactions between the following three nematode groups and AMF: (i) ectoparasites; (ii) sedentary endoparasites; and (iii) migratory endoparasites. Within the sedentary endoparasites, a comparison between root-knot and cyst nematodes will be made.

Material and methods

Data was collected from papers searched for in databases (Commonwealth Agricultural Bureau (CAB) Abstracts; Web of Knowledge) and published reviews (Hussey & Roncadori, 1982; Ingham, 1988; Smith, 1988; Pinochet et al., 1996; Roncadori, 1997; Borowicz, 2001). For *Meloidogyne* spp. and *Pratylenchus* spp. the database searches were limited to papers published after 1996 as the earlier papers have been discussed in other reviews. Not all papers provided data on plant growth, nematode numbers and mycorrhizal colonisation or reproduction. In a number of studies only root fresh weight was given and this was used. In studies with *Meloidogyne*, where root mass is related to extent of gall development, root length was also used to develop an index of root growth responses. If no data on mass were given, size data such as length were used. The biomass or length data were used to calculate nematode damage to the plant, AMF effect on plant biomass and AMF effect on nematode damage. Nematode damage was calculated as the percentage biomass reduction after inoculation with nematodes. AMF effect on plant biomass was calculated as the percentage increase in biomass after AMF inoculation. AMF effect on nematode damage was calculated by subtracting nematode damage on AMF plants from nematode damage on non-AMF plants. A positive value for AMF effect on nematode damage indicates that AMF- and nematode-infected plants grew better than the AMF-free but nematode-infected controls. However, it does not necessarily mean that plants with AMF and nematodes grew as well as the control without AMF without nematodes.

The effect of AMF on nematode numbers is tabulated as 'nematode response'. It was calculated as the percentage reduction in nematode number on AMF plants: the difference between nematode numbers on non-AMF plants and nematode numbers on AMF plants was divided by the nematode numbers on non-AMF plants and multiplied by one hundred. Nematode numbers expressed per root dry weight were excluded, to avoid apparent reductions in nematode number on bigger AMF plants even though total numbers were increased. A positive value for 'nematode response' means fewer nematodes on AMF plants compared to AMF-free plants. For 'AMF response' we looked at effect of nematodes on colonisation, calculated as: (% colonisation in the absence of nematodes-% colonisation in the presence of nematodes). A positive value means more colonisation in the absence of nematodes.

For all responses, averages and 95% confidence intervals were calculated. Averages between groups were considered significantly different when the confidence intervals were not overlapping. The AMF effects on nematode damage to shoot and root were compared with the Wilcoxon Matched Pair test. Correlations between AMF effects on nematode damage to shoot and root were tested with Spearman's Rank Correlation. All tests were performed using GenStat 7.1.

Results

In total, data were collected from 65 papers (Tables 1–4). Although there are more papers on experiments with nematodes and AMF, these concerned field observations without mycorrhiza-free or nematode-free control plants.

AMF effect on nematode damage

Overall AMF reduced nematode damage to the shoot by 7% ($n = 227$), but there were differences between nematode groups. AMF reduced endoparasitic nematode damage to the shoot on average by 5% for cyst nematodes and by up to 14% for migratory nematodes (Fig. 1A), with no significant difference between groups of endoparasitic nematodes. AMF did not reduce nematode damage on plants with ectoparasitic nematodes; the average nematode damage to the shoot was actually increased by $1.3\% \pm 3.7$ ($n = 17$, $P = 0.05$, Fig. 1A). The AMF effect on nematode damage to shoots and roots was significantly correlated for all nematode groups (Spearman's Rank Correlation test, $r = 0.43–0.65$, $P < 0.05$), with the effect on nematode shoot damage larger than the effect on nematode damage to the roots. Ectoparasites were the only nematodes whose damage to roots was significantly increased by AMF ($38\% \pm 8$, $n = 16$, $P = 0.05$). AMF can reduce ectoparasitic nematode damage, but timing plays an important role. A number of experiments with the ectoparasite *Tylenchorhynchus* spp. show that nematode damage was only compensated completely when AMF inoculation took place at least 1 week before nematode inoculation (Kassab & Taha, 1990a; Jain, Hasan, Singh, & Pandey, 1998a, b).

Reciprocal effects of nematodes and AMF

Nematode numbers were reduced in the presence of AMF on average by 21% ($n = 271$). Although plants with AMF suffered more damage by

Table 1. Summary of published outcomes of interactions between arbuscular mycorrhizal fungi (AMF) infected plants and ectoparasitic nematodes

Reference	Plant	Nematode	AMF	AMF effect on nematode damage shoot (%)	AMF effect on nematode damage root (%)	Nematode response (%)	AMF response (%)
Hasan and Jain (1987)	<i>Trifolium alexandrinum</i>	<i>Tylenchorhynchus vulgaris</i>	<i>Glomus mosseae</i>	9	Nd	–2	Nd
Kassab and Taha (1990a)	<i>T. alexandrinum</i>	<i>Tylenchorhynchus</i> sp.	<i>Glomus</i> sp.	4–10	–4–1	17–56	13–15
Kassab and Taha (1990b)	<i>Ipomoea batatas</i>	<i>Criconebella</i> spp.	<i>Glomus</i> sp.	Nd	Nd	–73–63	Nd
Jain et al. (1998a)	<i>Medicago sativa</i>	<i>Tylenchorhynchus</i> spp.		Nd	Nd	70–85	Nd
Jain et al. (1998b)	<i>T. alexandrinum</i>	<i>T. vulgaris</i>	<i>Glomus fasciculatum</i>	–9–6	–54–22	7–33	4–23
		<i>T. vulgaris</i>	<i>G. fasciculatum</i>	–11–11	–58–25	–7–50	3–18

AMF effect on nematode damage: nematode damage on non-AMF plants minus nematode damage on AMF plants. Nematode response: differences in numbers on non-AMF and AMF-plants relative to numbers on non-AMF plants; AMF response: difference in % root colonisation of nematode-free and nematode-infected plants; (ranges are given, Nd: no data presented).

ectoparasites than plants without AMF, nematode numbers were reduced by 19% when AMF was present. However, even within the ectoparasite group there could be large differences in response to AMF between nematode species. Most studies with *Tylenchorhynchus* spp. showed severe reductions in nematode numbers on AMF plants (Table 1), but *Criconebella* spp. greatly increased; these responses were also observed whether the two genera were inoculated alone or together (Kassab & Taha, 1990b).

The observed reductions in cyst nematode numbers could be due either to reduced penetration of roots by juveniles (Jain & Sethi, 1988) or to a pathogenic effect of *Glomus* spp. on cysts (Franc & Dropkin, 1985; Singh, Sharma, & Sharma, 1996). Root-knot nematode numbers were most reduced by AMF, on average by 33% although this average may be distorted as it includes some estimates based on root gall counts. Lower gall indices can be recorded and yet there may be more nematodes in the roots (Koshy, Sosamma, & Samuel, 2003; Diedhiou, Hallmann, Oerke, & Dehne, 2003). Taking into account only reports that presented actual numbers of nematodes in the roots ($n = 37$), root-knot numbers were reduced by only 22%, which is not significantly different from the cyst nematodes.

Migratory endoparasitic nematodes were the only group with increased numbers in the presence of AMF ($9\% \pm 27$, $n = 34$, $P = 0.05$), but with large variation between experiments (Fig. 1B). Reduction of nematodes by AMF was not correlated with reduction in AMF colonisation in the presence of nematodes. AMF colonisation was reduced by all nematode groups, on average by 9%. Root-knot nematodes had the least effect on AMF colonisation with only 6.6% reduction (Fig. 1B).

Differences between nematode groups

Most experiments were performed with nematode population densities that reduced plant biomass in the absence of AMF, on average by 28%. Migratory nematodes did the least damage and cyst nematodes the most, although there were no significant differences between nematode feeding groups (Fig. 1C). However, the effect that AMF had on plant biomass varied greatly between groups. Plants in the experiments with migratory nematodes increased up to 119% in biomass after inoculation with AMF, while plants in experiments with cyst nematodes increased only 8% after inoculation with AMF.

Table 2. Summary of published outcomes of interactions between arbuscular mycorrhizal fungi (AMF) infected plants and cyst nematodes

Reference	Plant	Nematode	AMF	AMF effect on nematode damage shoot (%)	AMF effect on nematode damage root (%)	Nematode response (%)	AMF response (%)
Jain and Sethi (1987)	<i>Vigna unguiculata</i>	<i>Heterodera cajani</i>	<i>Glomus epigaeus</i>	–11–33	–29–31	–19–29	1–17
			<i>Glomus fasciculatum</i>	–3–40	–13–1	–7–20	–1–19
Jain and Sethi (1988)	<i>V. unguiculata</i>	<i>H. cajani</i>	<i>G. epigaeus</i>	–2–43	1–40	–28–4	8–21
			<i>G. fasciculatum</i>	–0–51	–11–25	–5–20	4–35
Tylka et al. (1991)	<i>Glycine max</i>	<i>Heterodera glycines</i>	<i>Glomus+Gigaspora</i>	–17–34	–27–11	–142–38	Nd
Price et al. (1995)	<i>G. max</i>	<i>H. glycines</i>	<i>Glomus intraradices</i>	–11	–8	Nd	10
Siddiqui and Mahmood (1995a)	<i>Cajanus cajan</i>	<i>H. cajani</i>	<i>Gigaspora margarita</i>	–3–8	Nd	22–43	6–11
Siddiqui and Mahmood (1995b)	<i>C. cajan</i>	<i>H. cajani</i>	<i>G. fasciculatum</i>	–3–10	Nd	37–57	3–13
Siddiqui and Mahmood (1996)	<i>C. cajan</i>	<i>H. cajani</i>	<i>Glomus mosseae</i>	–3–9	Nd	15–50	4–9
Siddiqui et al. (1998)	<i>C. cajan</i>	<i>H. cajani</i>	<i>G. mosseae</i>	–3–8	Nd	18–42	5–11
Ryan et al. (2000)	<i>Solanum tuberosum</i>	<i>Globodera pallida</i>	'Vaminoc'	Nd	Nd	Nd	3
		<i>Globodera rostochiensis</i>		Nd	Nd	Nd	2.3
Todd et al. (2001)	<i>G. max</i>	<i>H. glycines</i>	<i>G. mosseae</i>	–19–3	–17–10	Nd	27–28
Ryan et al. (2003)	<i>S. tuberosum</i>	<i>G. pallida</i>	'Vaminoc'	–13	18	6	Nd
		<i>G. rostochiensis</i>		–3	30	–87	Nd

AMF effect on nematode damage: nematode damage on non-AMF plants minus nematode damage on AMF plants. Nematode response: differences in numbers on non-AMF and AMF-plants relative to numbers on non-AMF plants; AMF response: difference in % root colonisation of nematode-free and nematode-infected plants; (ranges are given, Nd: no data presented).

Discussion

Plant responses to inoculation with PPN and AMF together differed among feeding types of nematodes. AMF plants suffered more from ectoparasites than non-AMF plants, while this was opposite for endoparasites. There is no obvious biological explanation why ectoparasites, in particular, are more damaging in the presence of AMF. In the absence of AMF, ectoparasites were not particularly damaging to the plants, the degree being comparable to that caused by sedentary endoparasitic nematodes. Possibly, it is not so much increased root damage by nematode feeding that causes the negative plant growth response, but nematode damage to mycorrhizal structures. The effect of ectoparasitic nematodes on AMF was more severe

than was the effect of root-knot nematodes. The browsing of ectoparasites may damage the extra-radical hyphal growth and possibly diminish fungal entry into the roots although disruption of extra-radical hyphae by earthworms did not affect AMF colonisation levels in leek (Tuffen, Eason, & Scullion, 2002). Although sample size is limited, the reviewed evidence does not support our hypothesis that interactions between ectoparasites and AMF are less strong than between other nematode feeding types and AMF.

The experiments with root-knot and cyst nematodes were similar in terms of nematode damage to the plant and the AMF effect on plant growth. The combined effect of nematodes and AMF on plant growth was also comparable between root-knot and cyst nematodes, but the reduction of nematodes by

Table 3. Summary of outcomes of interactions between arbuscular mycorrhizal fungi (AMF) infected plants and root-knot nematodes, published after 1996

Reference	Plant	Nematode	AMF	AMF effect on nematode damage shoot (%)	AMF effect on nematode damage root (%)	Nematode response (%)	AMF response (%)
Pinochet et al. (1997)	<i>Musa AAA</i>	<i>Meloidogyne javanica</i>	<i>Glomus intraradices</i>	4	12	–63	10
Sankaranarayanan and Sundarababu (1997a)	<i>Vigna mungo</i>	<i>Meloidogyne incognita</i>	<i>Glomus mosseae</i>	14	–29	36	16
Sankaranarayanan and Sundarababu (1997b)	<i>V. mungo</i>	<i>M. incognita</i>	<i>Glomus fasciculatum</i>	Nd	Nd	70	22
Rao et al. (1997)	<i>Lycopersicon esculentum</i>	<i>M. incognita</i>	<i>Glomus deserticola</i>	Nd	Nd	30	Nd
Sharma and Trivedi (1997)	<i>Abelmoschus esculentum</i>	<i>M. incognita</i>	<i>G. mosseae</i>	54	47	2	7
			<i>G. fasciculatum</i>	54	46	3	8
Nagesh and Reddy (1997)	<i>Crossandra undulaefolia</i>	<i>M. incognita</i>	<i>G. mosseae</i>	Nd	Nd	25	Nd
Jaizme-Vega et al. (1997)	<i>Musa AAA</i>	<i>M. incognita</i>	<i>G. mosseae</i>	–12–20	30–57	–52–15	–8–1
Mishra and Shukla (1997)	<i>L. esculentum</i>	<i>M. incognita</i>	<i>G. fasciculatum</i>	–2–25	–11–19	40–51	–13–3
Jain et al. (1998a)	<i>Medicago sativa</i>	<i>M. incognita</i>	<i>G. fasciculatum</i>	–5–9	–28–4	14–41	4–21
Jain et al. (1998b)	<i>Trifolium alexandrinum</i>	<i>M. incognita</i>	<i>G. fasciculatum</i>	–18–2	–96–16	6–34	6–25
Ray and Dalei (1998)	<i>Vigna radiata</i>	<i>M. incognita</i>	<i>G. fasciculatum</i>	13	13	65	17
Rao et al. (1998)	<i>Solanum melongena</i>	<i>M. incognita</i>	<i>G. mosseae</i>	Nd	Nd	35	Nd
Rao and Gowen (1998)	<i>L. esculentum</i>	<i>M. incognita</i>	<i>G. deserticola</i>	Nd	Nd	45	Nd
Siddiqui and Mahmood (1998)	<i>L. esculentum</i>	<i>M. javanica</i>	<i>G. mosseae</i>	–5–4	–6–39	8–37	3–6
Sankaranarayanan and Sundarababu (1998)	<i>V. mungo</i>	<i>M. incognita</i>	<i>G. mosseae</i>	1–18	–48–30	18–34	6–19
			<i>G. fasciculatum</i>	4–26	–29–2	11–30	11–22
Reddy et al. (1998)	<i>L. esculentum</i>	<i>M. incognita</i>	<i>G. mosseae</i>	Nd	Nd	23–31	Nd
Santhi and Sundarababu (1998)	<i>V. unguiculata</i>	<i>M. incognita</i>	<i>G. fasciculatum</i>	Nd	Nd	33	Nd
Ranganatha et al. (1998)	<i>S. melongena</i>	<i>M. incognita</i>	<i>G. fasciculatum</i>	Nd	Nd	52	Nd
Habte, Zhang, and Schmitt (1999)	<i>Trifolium repens</i>	<i>M. incognita</i>	<i>Glomus</i>	17	12	Nd	–1
			<i>aggregatum</i>	48	60	Nd	–6
			<i>G. intraradices</i> , <i>G. mosseae</i>	48	60	Nd	–20
Pandey, Gupta, Singh, and, Kumar (1999)	<i>Hyoscyamus</i>	<i>M. incognita</i>	<i>G. aggregatum</i>	5	33	37	13
	<i>niger</i>		<i>G. fasciculatum</i>	4	3	20	12
			<i>G. mosseae</i>	4	2	12	16
Sankaranarayanan and Sundarababu (1999)	<i>V. mungo</i>	<i>M. incognita</i>	<i>G. mosseae</i>	19	–59	70	23
Nagesh et al. (1999a)	<i>L. esculentum</i>	<i>M. incognita</i>	<i>G. fasciculatum</i>	Nd	Nd	5–77	Nd
Nagesh et al. (1999b)	<i>C. undulaefolia</i>	<i>M. incognita</i>	<i>G. mosseae</i>	Nd	Nd	30	Nd
			<i>G. fasciculatum</i>	Nd	Nd	30	Nd
			<i>G. intraradices</i>	Nd	Nd	24	Nd
			<i>Acaulospora laevis</i>	Nd	Nd	15	Nd
Borah and Phukan (2000)	<i>S. melongena</i>	<i>M. incognita</i>	<i>G. fasciculatum</i>	5–27		3–87	
Bhat and Mahmood (2000)	<i>L. esculentum</i>	<i>M. incognita</i>	<i>G. mosseae</i>	2–0.18	15–19	6–12	–13–10
Bhagawati, Goswami, and Singh (2000)	<i>L. esculentum</i>	<i>M. incognita</i>	<i>Glomus etunicatum</i>	7	–5	60	13

Table 3. (continued)

Reference	Plant	Nematode	AMF	AMF effect on nematode damage shoot (%)	AMF effect on nematode damage root (%)	Nematode response (%)	AMF response (%)
Ratti et al. (2000)	<i>Mentha arvensis</i>	<i>M. incognita</i>	<i>G. mosseae</i>	−14–1	−6–2	5–27	10–19
Jothi et al. (2000)	<i>A. esculentum</i> , <i>Pennisetum glaucum</i> , <i>V. radiata</i>	<i>M. incognita</i>		Nd Nd Nd	Nd Nd Nd	50–55 38 43	Nd Nd Nd
Jothi and Sundarababu (2000)	<i>S. melongena</i>	<i>M. incognita</i>	<i>G. fasciculatum</i> ,	1	−6	49	6
			<i>G. mosseae</i> , <i>G. intraradices</i> , <i>Glomus fulvum</i>	4 12 19	10 89 7	56 39 32	15 17 3
Waceke, Waudo, and Sikora (2001)	<i>Chrysanthemum cinerariifolium</i>	<i>Meloidogyne hapla</i>	<i>G. etunicatum</i> ,	5–24	−3–29	54–57	10–11
Talavera et al. (2001)	<i>L. esculentum</i>	<i>M. incognita</i>	<i>Glomus</i> sp. K14 <i>G. mosseae</i>	19–23 14	9–20 6	63–71 69	4–7 Nd
Siddiqui and Mahmood (2001)	<i>Cicer arietinum</i>	<i>M. javanica</i>	<i>G. mosseae</i>	12–25	Nd	53–63	2–4
Calvet et al. (2001)	<i>Prunus persica</i> x <i>P. dulcis</i>	<i>M. javanica</i>	<i>G. intraradices</i>	Nd	Nd	34–59	Nd
Sundarababu et al. (2001)	<i>Capsicum annuum</i>	<i>M. incognita</i>	<i>G. mosseae</i>	Nd	Nd	17–53	Nd
Jothi and Sundarababu (2001)	<i>S. melongenum</i> , <i>P. glaucum</i> ,	<i>M. incognita</i>	<i>G. mosseae</i>	−14–32 −47	−7–3 24	16–38 46	3–15 1
	<i>V. radiata</i>			2	−20	Nd	10
Cofcewicz, Medeiros, Carneiro, and Pierobom (2001)	<i>L. esculentum</i>	<i>M. javanica</i>	<i>G. etunicatum</i> ,	11	Nd	−15	3
			<i>G. margarita</i> <i>Glomus</i> sp. K14	−8 −46–10	Nd −199–−17	−10 35–71	9 0–5
Waceke et al. (2002)	<i>C. cinerariifolium</i>	<i>M. hapla</i>					
Talavera et al. (2002)	<i>L. esculentum</i>	<i>M. incognita</i>	<i>Glomus</i> sp.	−9–10	Nd	−10–30	−1–9
Jothi and Sundarababu (2002b)	<i>S. melongena</i>	<i>M. incognita</i>	<i>Glomus</i> sp.	Nd	Nd	17–44	Nd
Elsen, Declerck, and De Waele (2002)	<i>Musa AAA</i>	<i>M. javanica</i>	<i>G. mosseae</i> ,	Nd	Nd	29	6
			<i>Glomus macrocarpum</i> ,	Nd	Nd	39	−1
			<i>Glomus caledonium</i>	Nd	Nd	61	6
Labeena et al., 2002	<i>L. esculentum</i>	<i>M. incognita</i>	<i>G. fasciculatum</i> ,	−7	Nd	51	3
			<i>G. macrocarpum</i> ,	−5	Nd	43	1
			<i>G. margarita</i> ,	−5	Nd	36	−3
			<i>A. laevis</i> ,	−4	Nd	15	4
			<i>Sclerocystis dussi</i>	−9	Nd	21	6
Diedhiou et al. (2003)	<i>L. esculentum</i>	<i>M. incognita</i>	<i>Glomus coronatum</i>	−86–7	−10–19	−20–72	−6–22
Rao et al. (2003)	<i>S. melongena</i>	<i>M. incognita</i>	<i>G. fasciculatum</i>	Nd	Nd	18–29	Nd
Nehra et al. (2003)	<i>Zingiber officinale</i>	<i>M. incognita</i>	<i>G. mosseae</i> , <i>G. fasciculatum</i>			64 68	

AMF effect on nematode damage: nematode damage on non-AMF plants minus nematode damage on AMF plants. Nematode response: differences in numbers on non-AMF and AMF-plants relative to numbers on non-AMF plants; AMF response: difference in % root colonisation of nematode-free and nematode-infected plants; (ranges are given, Nd: no data presented).

AMF differed. Root-knot nematodes were reduced more than cyst nematodes. Possibly, this is related to differences in the way the nematodes move and where they induce their feeding cells. *Meloidogyne*

incognita juveniles invade roots moving between cells to the root tip and then migrate between cells up the differentiating central cylinder (and probably generally so do other root-knot nematodes)

Table 4. Summary of outcomes of interactions between arbuscular mycorrhizal fungi (AMF) infected plants and migratory endoparasitic nematodes published after 1996

Reference	Plant	Nematode	AMF	AMF effect on nematode damage shoot (%)	AMF effect on nematode damage root (%)	Nematode response to AMF (%)	AMF response to nematodes (%)
Jaizme-Vega and Pinochet (1997)	<i>Musa</i> AAA	<i>Pratylenchus goodeyi</i>	<i>Glomus intraradices</i>	Nd	Nd	38	Nd
			<i>Glomus mosseae</i>	Nd	Nd	18	Nd
			<i>Glomus aggregatum</i>	Nd	Nd	8	Nd
Pinochet et al. (1998)	<i>Prunus</i> sp.	<i>Pratylenchus vulnus</i>	<i>G. mosseae</i>	–10–48	–7–41	–93––21	14
Elsen et al. (2001)	<i>Musa</i> AAA	<i>Radopholus similis</i>	<i>G. mosseae</i>	Nd	Nd	50	Nd
Forge, Muelchen, Hackenberg, Neilsen, and Vrain (2001)	<i>Malus domestica</i>	<i>Pratylenchus penetrans</i>	<i>Glomus clarum</i> ,	Nd	Nd	–58	Nd
			<i>Glomus etunicatum</i> ,	Nd	Nd	–96––55	Nd
			<i>Glomus versiforme</i> ,	Nd	Nd	39	Nd
			<i>G. mosseae</i> ,	Nd	Nd	–54–42	Nd
			<i>G. intraradices</i> ,	Nd	Nd	–88––18	Nd
			<i>G. aggregatum</i>	Nd	Nd	–49	Nd
Talavera et al. (2001)	<i>Daucus carota</i>	<i>P. penetrans</i>	<i>Glomus</i> sp.	14	Nd	Nd	20
Elsen, Baimey, Swennen, and De Waele (2003a)	<i>Musa</i> AAA	<i>R. similis</i>	<i>G. mosseae</i>	–38–29	–31–25	–61–93	6–34
		<i>Pratylenchus coffeae</i>		–16–4	–10–0	58–63	17–24
Elsen et al. (2003b)	<i>Musa</i> AAA	<i>R. similis</i>	<i>G. mosseae</i>	–43–75	–75–67	–340–48	–5–22
Elsen et al. (2003c)	<i>D. carota</i>	<i>P. coffeae</i>		–8–33	–1–14	–116–0.2	0–16
		<i>P. coffeae</i>	<i>G. intraradices</i>	Nd	Nd	59	9

AMF effect on nematode damage: nematode damage on non-AMF plants minus nematode damage on AMF plants. Nematode response: differences in numbers on non-AMF and AMF-plants relative to numbers on non-AMF plants; AMF response: difference in % root colonisation of nematode-free and nematode-infected plants; (ranges are given, Nd: no data presented).

but their feeding cells and galls extend into the cortex, where they may interact with AMF. Cyst nematode juveniles generally cut their way through cortical cells towards the stele and their feeding cells may extend beyond or be confined within the endodermis. In the latter case, there is limited interaction with AMF. Apart from assuming that root-knot nematodes are more susceptible to

reduction by AMF, there are other explanations as most of the data on root-knot nematode populations were presented as a gall index. Comparisons of actual numbers of individuals did not separate root-knot and cyst nematode responses.

From an applied perspective, it is promising that migratory nematodes do less damage to AMF plants. Similar benefits of pathogens and parasites from

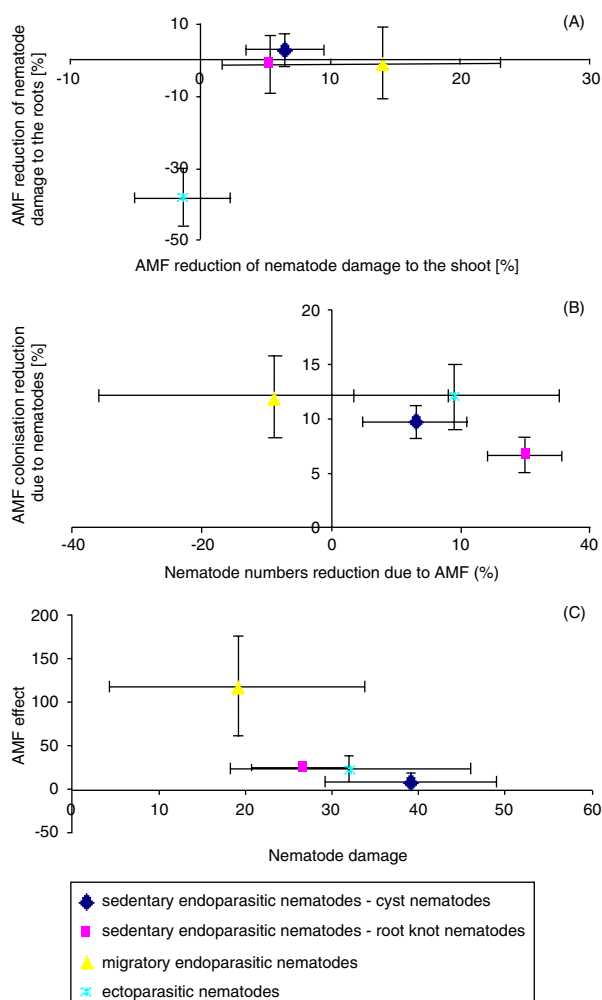


Figure 1. Responses to infection by arbuscular mycorrhizal fungi (AMF) and nematodes. Averages with 95% confidence intervals for nematode feeding classifications. Non-overlapping confidence intervals indicate significant differences between groups: (A) AMF effect on nematode damage: nematode damage on non-AMF plants minus nematode damage on AMF plants. Nematode damage: percentage reduction in plant biomass due to nematodes. (B) Nematode response and AMF response. Nematode response: differences in numbers on non-AMF and AMF-plants relative to numbers on non-AMF plants; AMF response: difference in % root colonisation of nematode-free and nematode-infected plants. (C) Nematode damage and AMF effect. Nematode damage: percentage reduction in plant biomass due to nematodes. AMF effect: percentage increase in plant biomass due to AMF.

AMF infection were found for performance of hemiparasitic plants and fecundity of aphids (Salonen, Vestberg, & Vauhkonen, 2001; Gange et al., 1999). However, despite the positive effect on plant growth, in the long term, the build up of nematode numbers could be problematic, especially in combination with their negative impacts on AMF. It is

not clear if the observed differences between feeding types and the exceptional results of migratory nematodes are due to some characteristics of the nematodes. The experiments with migratory nematodes were characterised by lower levels of damage to the plants than the other nematode groups, and larger positive effects of AMF on plant growth.

Most of these experiments with nematodes and AMF simply looked at endpoints, treating the actual interaction processes as taking place in a black box. Although mechanisms are suggested for how AMF could affect nematodes, there is very little evidence for these mechanisms. Changes in root exudates which decrease attraction are often suggested, but thus far no proof has been given. There are numerous studies showing that exudation patterns change under the influence of AMF, but none of them looked at the attraction of nematodes. The only published effect from mycorrhizal root exudates on nematodes that we could find was improved hatching of *Globodera pallida* (Ryan, Duffy, Cassells, & Jones, 2000). Changes in exudates not only affect nematodes, but also other rhizosphere organisms (Marschner & Baumann, 2003; Wamberg, Christensen, Jakobsen, Müller, & Sørensen, 2003), with possible antagonistic effects on nematodes, and plant growth promoting bacteria were attracted by root exudates from AMF plants (Sood, 2003).

Reduced penetration, as observed for *Meloidogyne* on AMF plants, (Mahanta & Phukan, 2000) could be due to changes in cell wall composition (van Buuren, Maldonado-Mendoza, Trieu, Blaylock, & Harrison, 1999), but no study actually demonstrated that penetration of mycorrhizal roots takes more time. There is no example of physical hindrance of nematode movement by AMF hyphae. Microscopic studies of nematode behaviour (Wyss, 2002) on AMF plants could fill these gaps.

No causes for slower development and reduced reproduction of nematodes on AMF plants have been identified. Root extracts of AMF tomato plants reduced the survival of *Meloidogyne* juveniles (Suresh, Bagyaray, & Reddy, 1985), but nematicidal compounds were not identified. However, not only AMF root extracts reduced survival of *Meloidogyne*, similar effects were caused by AMF-free root extracts, though slightly delayed. It would be a more elegant approach to look at changes in gene expression after AMF infection (Bestel-Corre, Dumas-Gaudot, & Gianinazzi, 2004), both localised and systemic expression, and compare these with gene expressions in plants infested by nematodes. Manipulation of gene expression is an important tool for the study of direct defenses of plants (Roda

& Baldwin, 2003). To test the hypothesis that nematode and AMF compete for photosynthates, Smith (1988) suggested using radioactive isotope labelling to study carbon and phosphorus flow in a AMF-sedentary endoparasitic nematode relationship. Stable isotopes may be more convenient to study the impacts of these interactions on carbon fluxes and sources and on nitrogen transfers (Dromph, Bardgett, & Cook, 2005).

Nematodes and AMF are unlikely to compete for space. Migratory nematodes and AMF are present in the same tissue (Pinochet et al., 1995; Lopez et al., 1997), but *M. incognita* was located in the central cylinder while AMF preferably colonised cortical parenchyma (Diedhiou et al., 2003). It is not known whether different AMF species also prefer to colonise different root parts. The study of Dickson (2004) showed that AMF differ in intercellular and extracellular colonisation, depending on fungus, host and possibly the environment. Plants colonised by fungi with mainly intracellular hyphae and coils will probably interfere much less with root-knot juveniles, which move intercellularly, but may severely hinder the movement of nematodes migrating intracellularly through cortical cells.

Increased root growth and function could make AMF plants more tolerant to nematode damage. In these cases the effect of AMF on nematodes can be mimicked by applying phosphorus or other nutrients. AMF may not only result in increased root systems as a whole, but also change root morphology. The increased root branching in AMF plants (Elsen, Beeterens, Swennen, & De Waele, 2003b) may counterbalance the impacts of nematodes that lead to less root branching.

Nematodes can directly affect AMF by killing cells that contribute to AMF nutrition. Some root cells are left necrotic after feeding by some nematode species while other nematodes induce cells to form specialised feeding structures. Some species of both root-knot and cyst nematodes induce root proliferation around the feeding site. If AMF colonised such proliferated roots, then this may have positive impacts on AMF resources. A more indirect way in which nematodes may affect AMF is an induced plant response which renders cells less susceptible/suitable for AMF. Since ectoparasitic nematodes have a stronger effect on AMF in comparison to root-knot nematodes, one might hypothesise that ectoparasites trigger more overall plant defence in comparison to the advanced and specialised feeding strategies of sedentary endoparasitic nematodes. In these interactions, co-evolution is presumed to have resulted in specific recognition mechanisms (the gene-for-gene interactions) and these are probably

associated with suppression or non-induction of general plant defence responses.

This survey has indicated that specific characteristics of nematode–plant interactions are important in determining the outcome of bitrophic interactions with AMF. Ectoparasitic nematodes did more damage to AMF plants than to non-AMF plants. For the endoparasites, AMF could contribute to nematode control. In general, nematode numbers were reduced by AMF while plants suffered less nematode damage in the presence of AMF. There were further differences within the broad feeding categories that were important in determining the characteristics of the interactions involving AMF. We have not taken into account specific features of AMF–plant relationships that may also affect the nature of the bitrophic relationships. Most studies used *Glomus* spp.; in the few studies that used other taxa (Abu-Elamayem, El-Shoura, Rabie, Ibrahim, & Fawaz, 1989; Vaast, Caswell-Chen, & Zasoski, 1998; Nagesh, Reddy, & Rao, 1999b; Labeena, Sreenivasa, & Lingaraju, 2002), there were no consistent differences among taxa. This review is based on studies that mainly use crop plants, which makes the results applicable to agricultural systems only.

To conclude, we need to know where the AMF and nematodes are, and when, in order to discern possible mechanisms. We should not only look at endpoints, but try to identify and characterise key phases in the interaction processes. This will mean a combination of classical and modern techniques, ranging from observations on histology and direct observations in Petri dishes to looking at the process of interaction through impacts on gene expression.

Acknowledgements

We thank Judith Webb, William Eason, Kirsten Leiss and two referees for valuable comments. This work is part of the EcoTrain project, which is funded by the European Union (RTN2-2001-0464). IGER is an Institute of the Biotechnology and Biological Sciences Research Council.

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