

WEED SPECIES AS HOSTS OF *MELOIDOGYNE*: A REVIEW

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ABSTRACT

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Over 226 weed species belonging to 43 botanical families have been studied for host suitability to different root-knot nematodes worldwide. *Meloidogyne incognita* was reported to reproduce on the largest number of weeds with over 138 weedy plant hosts throughout the world. Four other *Meloidogyne* spp., *M. javanica*, *M. arenaria*, *M. hapla*, and *M. graminicola* were found infecting 49, 48, 27, and 24 weed species, respectively, while *M. mayaguensis*, *M. chitwoodi*, and *M. floridensis* have been reported to reproduce on 24, 13 and 12 weed species, respectively. These data indicate that little is known about the exact weed host range of many species within the genus *Meloidogyne*. However, weed host status of *Meloidogyne* spp. reported herein indicates that weeds are a major reservoir of root-knot nematodes and should be considered as factors affecting the success of integrated nematode management programs.

Key words: host range, *Meloidogyne arenaria*, *M. chitwoodi*, *M. coffeicola*, *M. exigua*, *M. floridensis*, *M. graminicola*, *M. hapla*, *M. incognita*, *M. javanica*, *M. konaensis*, *M. mayaguensis*, *M. naasi*, *M. paranaensis*, *M. triticoryza*, root-knot nematodes, weeds.

RESUMEN

Rich, J. R., J. A. Brito, R. Kaur, and J. A. Ferrell. 2008. Especies de malezas como hospedantes de *Meloidogyne*. Revisión. *Nematropica* 39:157-185.

Se ha estudiado la susceptibilidad de más de 226 especies de malezas, pertenecientes a 43 familias botánicas, a diferentes nematodos agalladores. Se ha registrado a *Meloidogyne incognita* como la especie con la capacidad de reproducirse en la mayor cantidad de malezas, con más de 138 especies vegetales registradas como hospedantes en el mundo. Se han registrado cuatro otras especies de *Meloidogyne* spp., *M. javanica*, *M. arenaria*, *M. hapla*, y *M. graminicola* infectando 49, 48, 27 y 24 especies de malezas, respectivamente, mientras que *M. mayaguensis*, *M. chitwoodi*, y *M. floridensis* se han registrado en 24, 13 y 12 especies de malezas, respectivamente. Estos datos indican que se conoce poco acerca del rango de malezas hospedantes de muchas especies de *Meloidogyne*. No obstante, la lista de malezas susceptibles a *Meloidogyne* spp. que incluimos en esta revisión indica que las malezas son un importante reservorio de nematodos agalladores y que deben considerarse como factores que afectan el éxito de programas de manejo integrado de nematodos.

Palabras clave: malezas, *Meloidogyne arenaria*, *M. chitwoodi*, *M. coffeicola*, *M. exigua*, *M. floridensis*, *M. graminicola*, *M. hapla*, *M. incognita*, *M. javanica*, *M. konaensis*, *M. mayaguensis*, *M. naasi*, *M. paranaensis*, *M. triticoryza*, nematodos agalladores, rango de hospedantes.

INTRODUCTION

Weeds are a major constraint in agricultural production since they compete with

crop plants for water, soil nutrients, and light and also interfere with distribution of irrigation water and efficient fertilizer application (Anderson, 1996). Competi-

tion for resources with crop plants, particularly in the early stages of growth, can reduce crop yields more than 70% (Barentine 1974; Bendixen, 1986a; Smith 1968; Thurlow and Buchanan 1972). Due to their ubiquitous presence before, during, and after crop cycles, weeds serve as reservoirs for plant pathogens and nematodes that will cause damage in future crops (McWhorter 1989; Quénéhervé *et al.*, 1995; Quénéhervé *et al.*, 2006).

The problem of weed hosts to plant-parasitic nematodes is particularly severe in the subtropical and tropical environments where weeds grow year round (Crane *et al.*, 2008). Previous research has shown many common agricultural weeds to be excellent hosts of plant-parasitic nematodes (Asmus and Andrade, 1997; Bendixen *et al.*, 1986b; 1988a, b, c; Clements *et al.*, 2004; Diop *et al.*, 2000; Hogger and Bird, 1976; Sellami *et al.*, 1999). Weed species enable plant-parasitic nematodes to survive in the absence as well as the presence of a crop, providing a nematode inoculum source for the following season. For example, plant-parasitic nematodes including *Aphelenchoides besseyi*, *Ditylenchus angustus*, *Heterodera orizicola* and *M. graminicola* were found to reproduce on weeds that grow in fallow fields between rice crops, which perpetuate nematode problems (Rao *et al.*, 1986).

The root-knot nematodes, *Meloidogyne* spp., have been reported to survive and even thrive on weeds (Davidson and Townshend, 1967; Luc *et al.*, 2005; Zhang and Schmitt, 1994). This genus is considered the most important among plant-parasitic nematodes (Sasser and Freckman, 1987), mainly due to the wide host range which is known to exceed 3000 wild and cultivated plant species (Hussey and Janssen, 2002). To date, about 96 nominal species of *Meloidogyne* have been described (Brito *et al.*, 2008), but within the genus, *M. arenaria*, *M. hapla*, *M. incognita*, and *M. jav-*

anica represent 95% of all infestations in agricultural lands (Hussey and Janssen, 2002). The interaction of root-knot nematodes and weeds can magnify problems created by both pests in agricultural production systems compared to each acting alone. For example, the four weed species, *Ageratum conyzoides*, *Amaranthus spinosus*, *Eleusine indica* and *Portulaca oleracea* are considered among the world's worst weeds and are multiple hosts of *Meloidogyne* as well (Holm *et al.*, 1977). *Cyperus rotundus*, *Amaranthus* spp., *Chenopodium album*, and *Digitaria* spp. are also frequently encountered weed hosts of root-knot nematodes (Myers *et al.*, 2004). The weed species *Myrica faya* (*syn. Morella faya*) is a major threat to the natural ecosystem in Hawaii (Vitouseck and Walker, 1989) and was found to be a host of *Meloidogyne* spp. (Duffy and Gardner, 1999). Since weeds are ubiquitously present and many are good hosts of root-knot nematodes, controlling weeds would be a good initial step in reducing root-knot nematode populations worldwide (Das *et al.*, 1998).

The definition of a weed is 'any unwanted plant', essentially meaning any plant which interferes with growth and production of a desired plant species (Anderson, 1996). Using this definition, the concept of weeds can be broadened to include volunteer crops, such as peanut plants growing before or during a cotton crop. While these situations are important in rotations designed to minimize nematode damage, the weeds reported herein generally do not include agricultural crop plants that may be 'out of place'. Weed host status descriptions as related in this article, e.g. good or moderate host, in most instances are terms used by individual authors to define degree of nematode reproduction or galling on a particular weed. Also, some plants that are listed may or may not be weeds in the classical sense

but rather alternative hosts to *Meloidogyne* spp. which have been included for thoroughness. A number of references were found which described a weed or *Meloidogyne* genus without giving a species name. These references were not included in this article. All weeds described as hosts for individual *Meloidogyne* spp. are listed in Table 1, but references to this table are not made again in the text of this article.

WEEDS AS HOSTS OF MELOIDOGYNE SPP.

Meloidogyne arenaria

The peanut root-knot nematode is predominately found in warm-temperate and tropical environments and is highly virulent on numerous ornamental, vegetable, and agronomic crops. In weed host status studies in North Carolina USA, *Chenopodium album*, *Euphorbia maculata*, and *Vicia villosa* were described as good hosts while *Amaranthus hybridus*, *A. palmeri*, *Ambrosia artemisiifolia*, *Ipomoea hederacea* var. *integriscula*, *Setaria lutescens*, *Sida spinosa*, *Portulaca oleracea*, *Rumex acetosella* and *Rumex crispus* were moderate hosts of *M. arenaria* race 2 (Tedford and Fortnum, 1988). Brito *et al.* (2008) identified *Amaranthus spinosus*, *Ipomoea triloba*, *Jacquemontia tamnifolia*, *Macropodium lathyroides*, *Portulaca oleracea*, and *Physalis angulata* as weed hosts of *M. arenaria* in Florida. *Meloidogyne arenaria* was observed on *Solanum viarum*, which is an invasive perennial weed of pastures present predominantly in the southeastern USA (Church and Roskopf, 2005). Their work indicated that this weed species is a potential reservoir for *M. arenaria* in Florida and throughout the southern USA. Other weeds reported as hosts of *M. arenaria* include *Abutilon theophrasti*, *Amaranthus retroflexus*, *A. spinosus*, *Cnidoscolus stimulosus*, *Dichondra repens*, *Echinochloa muricata*, *Ipomoea triloba*, *Leontodon hispidus*, and *Phytolacca americana* (Kaur *et al.*, 2007).

Meloidogyne chitwoodi

The Columbia root-knot nematode was originally found in the Pacific Northwest USA infecting potato (Golden *et al.*, 1980). It has subsequently been reported in a number of other countries including Argentina, Belgium, Germany, Mexico the Netherlands, Portugal, and South Africa (Powers *et al.*, 2005). In an extensive host range study, O'Bannon *et al.* (1982) found that 53 of 68 weed and cultivated plant species were hosts to *M. chitwoodi*. Among the weed species listed as hosts were *Cirsium vulgare*, *Dactylis glomerata*, *Panicum capillare*, *Setaria viridis*, and *Sonchus asper*. Similarly, Griffin *et al.* (1984) reported several range grasses as hosts to *M. chitwoodi*, and these included *Agropyron desertorum*, *Bromis inermis*, *Dactylis glomerata*, and *Pascopyrum smithii*. Kutwayo and Been (2006) listed *Capsella bursa-pastoris*, *Senecio vulgaris*, and *Solanum nigrum* as hosts of *M. chitwoodi*, and *Solanum sarrachoides* was also reported as a host of this nematode (Boydston *et al.*, 2008).

Meloidogyne coffeicola

The common name for this nematode is the coffee root-knot nematode although another nematode, *M. exigua*, also has the same common name. This nematode has only been found in Brazil and has a very narrow host range. *Coffea arabica* is the major plant host of *M. coffeicola*, and it has only been reported infecting two weeds, *Eupatorium pauciflorum* and *Psychotria nitidula* (Jaehn *et al.*, 1980; Lordello and Lordello, 1972).

Meloidogyne exigua

This coffee root-knot nematode was first described by Goeldi (1887) from coffee in Brazil, and now is wide spread in central and south America. The nematode

Table 1. List of wild plant species, common names and botanical families occurring as hosts of *Meloidogyne* spp. worldwide.

Scientific name ^x	Common name ^y	Plant Family	<i>Meloidogyne</i> sp. ^z	Source/Reference
<i>Abutilon theophrasti</i>	Velvet-leaf	Malvaceae	<i>Mi</i>	Amin and Budai, 1994
			<i>Ma, Mf, Mi, Mj, Mm</i>	Kaur <i>et al.</i> , 2007
<i>Acalypha australis</i>	Australian acalypha	Euphorbiaceae	<i>Mi</i>	Ehwaeti <i>et al.</i> , 1999
<i>Acalypha setosa</i>	unknown	Euphorbiaceae	<i>Ma, Mi</i>	Brito <i>et al.</i> , 2008
<i>Achyranthes aspera</i>	Prickly chaff-flower	Amaranthaceae	<i>Mi</i>	Gowda <i>et al.</i> , 1995
			<i>Mi</i>	Mani and Hinai, 1996
<i>Aerva javanica</i>	Kapok bush	Amaranthaceae	<i>Mi</i>	Mani and Hinai, 1996
<i>Ageratum conyzoides</i>	Goat weed	Asteraceae	<i>Mi, Mj</i>	Mamaril and Aberto, 1989
			<i>Mg</i>	Khan <i>et al.</i> , 2004
			<i>Mp</i>	Roese and Oliveira, 2004
<i>Agropyron desertorum</i>	Crested wheatgrass	Poaceae	<i>Mc</i>	Griffin <i>et al.</i> , 1984
<i>Agropyron repens</i>	Quackgrass	Poaceae	<i>Mg</i>	Khan <i>et al.</i> , 2004
<i>Alternanthera sessilis</i>	Sessile joyweed	Amaranthaceae	<i>Mi</i>	Mani and Hinai, 1996
			<i>Mg</i>	Khan <i>et al.</i> , 2004
<i>Amaranthus angustifolius</i>	Prostrate pigweed	Amaranthaceae	<i>Mj</i>	Sellami <i>et al.</i> , 1999
<i>Amaranthus deflexus</i>	Low amaranth	Amaranthaceae	<i>Me</i>	Lima <i>et al.</i> , 1985
<i>Amaranthus graecizans</i>	Tumbleweed	Amaranthaceae	<i>Mi</i>	Mani and Hinai, 1996
			<i>Mi</i>	Velasquez-Valle, 2001
<i>Amaranthus hybridus</i>	Smooth pigweed	Amaranthaceae	<i>Ma, Mi</i>	Tedford and Fortum, 1988
			<i>Mj</i>	Lordello <i>et al.</i> , 1988
			<i>Mi, Mj</i>	Mani and Hinai, 1996

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^yCommon names listed herein were those given by the author or those found at the Weed Science Society of America website (Anonymous, 2007).

^zAbbreviations for the *Meloidogyne* spp.: *Ma* – *Meloidogyne arenaria*; *Mc* – *M. chitwoodi*; *Mco* – *M. coffeicola*; *Me* – *M. exigua*; *Mf* – *M. floridensis*; *Mg* – *M. graminicola*; *Mh* – *M. hapla*; *Mi* – *M. incognita*; *Mj* – *M. javanica*; *Mk* – *M. konaensis*; *Mm* – *M. mayaguensis*; *Mn* – *M. naasi*; *Mp* – *M. paranaensis*; *Mt* – *M. triticoryzae*.

Table 1. (Continued) List of wild plant species, common names and botanical families occurring as hosts of *Meloidogyne* spp. worldwide.

Scientific name ^x	Common name ^y	Plant Family	<i>Meloidogyne</i> sp. ^z	Source/Reference
			<i>Mj</i>	Asmus and Andrade, 1997
			<i>Mi</i>	Sellami <i>et al.</i> , 1999
			<i>Mm</i>	Souza <i>et al.</i> , 2006
<i>Amaranthus lividus</i> (syn. <i>Amaranthus blitum</i>)	Livid amaranth	Amaranthaceae	<i>Mi</i> , <i>Ma</i>	Amin and Budai, 1994
<i>Amaranthus palmeri</i>	Palmer amaranth	Amaranthaceae	<i>Ma</i> , <i>Mi</i>	Tedford and Fortum, 1988
<i>Amaranthus retroflexus</i>	Redroot amaranth	Amaranthaceae	<i>Mi</i>	Davidson and Townshend, 1967
			<i>Mi</i>	Sellami <i>et al.</i> , 1999
			<i>Ma</i> , <i>Mf</i> , <i>Mi</i> , <i>Mj</i> , <i>Mm</i>	Kaur <i>et al.</i> , 2007
<i>Amaranthus spinosus</i>	Spiny amaranth	Amaranthaceae	<i>Mg</i>	Sperandio and Amaral, 1994
			<i>Mp</i>	Roose and Oliveira, 2004
			<i>Ma</i> , <i>Mf</i> , <i>Mi</i> , <i>Mj</i> , <i>Mm</i>	Kaur <i>et al.</i> , 2007
			<i>Ma</i> , <i>Mi</i>	Brito <i>et al.</i> , 2008
<i>Amaranthus viridis</i>	Slender amaranth	Amaranthaceae	<i>Mi</i>	Mani and Hinai, 1996
			<i>Mi</i>	Myers <i>et al.</i> , 2004
<i>Ambrosia artemisiifolia</i>	Common ragweed	Asteraceae	<i>Ma</i> , <i>Mi</i>	Tedford and Fortum, 1988
<i>Anagallis arvensis</i>	Scarlet pimpernel	Primulaceae	<i>Mi</i> , <i>Mj</i>	Sellami <i>et al.</i> , 1999
<i>Anthemis cotula</i>	chamomile, mayweed	Asteraceae	<i>Mi</i>	Davidson and Townshend, 1967
<i>Arenaria serpyllifolia</i>	Thymeleaf sandwort	Caryophyllaceae	<i>Mi</i>	Ehwaeti <i>et al.</i> , 1999
<i>Axonopus affinis</i>	Carpetgrass	Poaceae	<i>Mi</i>	Davidson and Townshend, 1967
<i>Barbarea vulgaris</i>	Garden yellow rocket	Brassicaceae	<i>Ma</i> , <i>Mi</i>	Tedford and Fortum, 1988
<i>Bidens alba</i>	Common beggarticks	Asteraceae	<i>Mi</i>	Brito <i>et al.</i> , 2008

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<i>Bidens cernua</i>	Nodding beggarticks	Asteraceae	<i>Mh</i>	Belair and Benoit, 1996
			<i>Mh</i>	Leroux <i>et al.</i> , 1996
<i>Bidens frondosa</i>	Devil's beggarticks	Asteraceae	<i>Mh</i>	Belair and Benoit, 1996
			<i>Mi, Mh</i>	Kim <i>et al.</i> , 1998
<i>Bidens pilosa</i>	Hairy beggarticks	Asteraceae	<i>Mj</i>	Lordello <i>et al.</i> , 1988
			<i>Mj</i>	Asmus and Andrade 1997
			<i>Mm</i>	Willers, 1997
			<i>Mm</i>	Brito <i>et al.</i> , 2008
<i>Bidens vulgata</i>	Tall beggarticks	Asteraceae	<i>Mh</i>	Belair and Benoit, 1996
<i>Borreria hispida</i> (syn. <i>Spermacoce hispida</i>)	Ladaina	Rubiaceae	<i>Mi</i>	Gowda <i>et al.</i> , 1995
<i>Bothriochloa intermedia</i>	Caucasian bluestem	Poaceae	<i>Mg</i>	Khan <i>et al.</i> , 2004
<i>Brachiaria plantaginea</i> (syn. <i>Urochloa plantaginea</i>)	Alexandergrass	Poaceae	<i>Mp</i>	Roese and Oliveira, 2004
<i>Brachiaria ramosa</i> (syn. <i>Urochloa ramosa</i>)	Browntop millet	Poaceae	<i>Mg</i>	Khan <i>et al.</i> , 2004
<i>Bromus inermis</i>	Smooth Broom	Poaceae	<i>Mc</i>	Griffin <i>et al.</i> , 1984
<i>Bromus secalinus</i>	Cheat	Poaceae	<i>Mi</i>	Davidson and Townshend, 1967
			<i>Mc</i>	O'Bannon <i>et al.</i> , 1982
			<i>Mh</i>	Kutywayo and Been, 2006
<i>Capsella bursa-pastoris</i>	Shepherd's-purse	Brassicaceae	<i>Mc</i>	Belair and Benoit, 1996
			<i>Mc</i>	Belair and Benoit, 1996
			<i>Mh</i>	Belair and Benoit, 1996
<i>Cassia obtusifolia</i> (syn. <i>Senna obtusifolia</i>)	Sicklepod	Fabaceae	<i>Ma</i>	Rodriguez-Kabana <i>et al.</i> , 1977
<i>Caucalis platycarpus</i> (syn. <i>Caucalis lappula</i>)	Carrot bur parsley	Apiaceae	<i>Mi</i>	Amin and Budai, 1994
<i>Celosia argentea</i>	Celosia	Amaranthaceae	<i>Mi</i>	Gowda <i>et al.</i> , 1996

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Table 1. (Continued) List of wild plant species, common names and botanical families occurring as hosts of *Meloidogyne* spp. worldwide.

Scientific name ^x	Common name ^y	Plant Family	<i>Meloidogyne</i> sp. ^z	Source/Reference
<i>Cenchrus incertus</i> (syn. <i>Cenchrus spinifex</i>)	Field sandbur	Poaceae	<i>Ma, Mi</i>	Tedford and Fortum, 1988
<i>Cerastium vulgatum</i> (syn. <i>Cerastium fontanum</i>)	Big chickweed	Caryophyllaceae	<i>Mi</i>	Davidson and Townshend, 1967; Ehwaeti <i>et al.</i> , 1999
<i>Chamaesyce hirta</i>	Garden spurge	Euphorbiaceae	<i>Mi</i>	Mani and Hinai, 1996
<i>Chamaesyce prostrata</i>	Ground spurge	Euphorbiaceae	<i>Mm</i>	Souza <i>et al.</i> , 2006
<i>Chenopodium album</i>	Common lambs-quarters	Chenopodiaceae	<i>Mm</i>	Brito <i>et al.</i> , 2008
			<i>Mi</i>	Davidson and Townshend, 1967
			<i>Ma</i>	Rodriguez-Kabana <i>et al.</i> , 1977
			<i>Ma, Mi</i>	Tedford and Fortum, 1988
			<i>Mn</i>	Amin and Budai, 1994
			<i>Mh</i>	Belair and Benoit, 1996
			<i>Mi, Mh</i>	Kim <i>et al.</i> , 1998
			<i>Mi</i>	Sellami <i>et al.</i> , 1999
<i>Chenopodium glaucum</i>	Oak-leaf goosefoot	Chenopodiaceae	<i>Mi</i>	Myers <i>et al.</i> , 2004; Brito <i>et al.</i> , 2008
			<i>Mh</i>	Amin and Budai, 1994
<i>Chenopodium hybridum</i> (syn. <i>Chenopodium simplex</i>)	Giantseed goosefoot	Chenopodiaceae	<i>Mi, Mh, Mn</i>	Belair and Benoit
			<i>Mi</i>	Amin and Budai, 1994
<i>Chenopodium murale</i>	Nettleleaf goosefoot	Chenopodiaceae	<i>Mi, Mj</i>	Sellami <i>et al.</i> , 1999
			<i>Mi</i>	Mani and Hinai, 1996
<i>Chloris gayana</i>	Rhodes grass	Poaceae	<i>Mi</i>	Sellami <i>et al.</i> , 1999
<i>Chloris gayana</i>	Rhodes grass	Poaceae	<i>Mi</i>	Mani and Hinai, 1996

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Table 1. (Continued) List of wild plant species, common names and botanical families occurring as hosts of *Meloidogyne* spp. worldwide.

Scientific name ^x	Common name ^y	Plant Family	<i>Meloidogyne</i> sp. ^z	Source/Reference
<i>Chrysanthemum leucanthemum</i> (syn. <i>Leucanthemum vulgare</i>)	Oxeye daisy	Asteraceae	<i>Mh</i>	Belair and Benoit, 1996
<i>Cirsium arvense</i>	Canadian thistle	Asteraceae	<i>Mc</i>	Kutywayo and Been, 2006
<i>Cirsium vulgare</i>	Bull thistle	Asteraceae	<i>Mc</i>	O'Bannon <i>et al.</i> , 1982
<i>Citrullus vulgaris</i> (syn. <i>Citrullus lanatus</i>)	Citronmelon	Cucurbitaceae	<i>Me</i>	Moraes <i>et al.</i> , 1972
<i>Cleome viscosa</i>	Jasmin del rio	Capparidaceae	<i>Mi</i>	Gowda <i>et al.</i> , 1996
<i>Cnidoscopus stimulosus</i>	Spurge nettle	Euphorbiaceae	<i>Ma, Mf, Mi, Mj, Mm</i>	Kaur <i>et al.</i> , 2007
<i>Cnidoscopus urens</i>	Devil nettle	Euphorbiaceae	<i>Mm</i>	Souza <i>et al.</i> , 2006
<i>Commelina benghalensis</i>	Benghal dayflower	Commelinaceae	<i>Mp</i>	Roesse and Oliveira, 2004
<i>Commelina diffusa</i>	Spreading dayflower	Commelinaceae	<i>Me</i>	Aragon <i>et al.</i> , 1978
<i>Convolvulus arvensis</i>	Field bindweed	Convolvulaceae	<i>Mj</i>	Mani and Hinai, 1996
			<i>Mi, Mj</i>	Sellami <i>et al.</i> , 1999
<i>Coronilla scopioides</i>	Crownvetch	Fabaceae	<i>Mn</i>	Vovlas and Inserra, 1979
<i>Crotalaria spectabilis</i>	Showy crotalaria	Fabaceae	<i>Ma, Mi</i>	Tedford and Fortum, 1988
<i>Cynodon dactylon</i>	Bermudagrass	Poaceae	<i>Ma, Mi</i>	Tedford and Fortum, 1988
			<i>Mi</i>	Sellami <i>et al.</i> , 1999
			<i>Mi</i>	Myers <i>et al.</i> , 2004
			<i>Mp</i>	Roesse and Oliveira, 2004
<i>Cynoglossum officinale</i>	Hound's Tongue	Boraginaceae	<i>Mi</i>	Davidson and Townshend, 1967
<i>Cyperus esculentus</i>	Yellow nutsedge	Cyperaceae	<i>Ma, Mi</i>	Tedford and Fortum, 1988
			<i>Mi</i>	Thomas <i>et al.</i> , 1997
			<i>Mi</i>	Schroeder <i>et al.</i> , 1999

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Table 1. (Continued) List of wild plant species, common names and botanical families occurring as hosts of *Meloidogyne* spp. worldwide.

Scientific name ^x	Common name ^y	Plant Family	<i>Meloidogyne</i> sp. ^z	Source/Reference
			<i>Mi</i>	Davis and Webster, 2003
			<i>Mi</i>	Meyers <i>et al.</i> , 2004
<i>Cyperus iria</i>	Rice flat sedge	Cyperaceae	<i>Mg</i>	Dabur <i>et al.</i> , 2004
<i>Cyperus rotundus</i>	Purple nutsedge	Cyperaceae	<i>Me</i>	Aragon <i>et al.</i> , 1978
			<i>Mk</i>	Zhang and Schmitt, 1994
			<i>Mj</i>	Mani and Hinai, 1996
			<i>Mt</i>	Gaur and Sharma 1998
			<i>Mi</i>	Sellami <i>et al.</i> , 1999
			<i>Mi</i>	Myers <i>et al.</i> , 2004
			<i>Mi</i>	Davis and Webster, 2003
			<i>Mi</i>	Thomas <i>et al.</i> , 2004
			<i>Mg</i>	Khan <i>et al.</i> , 2004
			<i>Mg</i>	Dabur <i>et al.</i> , 2004
			<i>Mp</i>	Roese and Oliveira, 2004
			<i>Mg</i>	Brito <i>et al.</i> , 2008;
<i>Dactylis glomerata</i>	Orchardgrass	Poaceae	<i>Mc</i>	Griffin <i>et al.</i> , 1984
<i>Dactyloctenium aegyptium</i>	Crowfootgrass	Poaceae	<i>Mg</i>	Khan <i>et al.</i> , 2004
<i>Daucus carota</i>	Wild carrot	Umbelliferae	<i>Mi</i>	Sellami <i>et al.</i> , 1999
<i>Datura metel</i> (syn. <i>Datura innoxia</i>)	Sacred datura	Solanaceae	<i>Mj</i>	Mani and Hinai, 1996
<i>Datura stramonium</i>	Jimsonweed	Solanaceae	<i>Ma, Mi</i>	Tedford and Fortum, 1988
			<i>Mi</i>	Ehwaeti <i>et al.</i> , 1999
<i>Descurainia sophia</i>	Herb sophia	Brassicaceae	<i>Mi</i>	Davidson and Townshend, 1967

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Table 1. (Continued) List of wild plant species, common names and botanical families occurring as hosts of *Meloidogyne* spp. worldwide.

Scientific name ^x	Common name ^y	Plant Family	<i>Meloidogyne</i> sp. ^z	Source/Reference
<i>Dichanthium annulatum</i>	Kleberg's bluestem	Poaceae	<i>Mg</i>	Dabur <i>et al.</i> , 2004
<i>Dichondra repens</i>	Dichondra	Convolvulaceae	<i>Ma, Mf, Mi, Mj, Mm</i>	Kaur <i>et al.</i> , 2007
<i>Digitaria horizontalis</i>	Jamaican crabgrass	Poaceae	<i>Mj</i>	Asmus and Andrade, 1997
<i>Digitaria sanguinalis</i>	Large crabgrass	Poaceae	<i>Ma</i>	Tedford and Fortum, 1988
			<i>Mn</i>	Amin and Budai, 1994
			<i>Mi</i>	Noling and Gilreath, 2002a
			<i>Mg</i>	Khan <i>et al.</i> , 2004
<i>Echinochloa colona</i>	Jungle-rice	Poaceae	<i>Mg</i>	Sperandio and Amaral, 1994
			<i>Mt</i>	Gaur and Sharma, 1998
			<i>Mg</i>	Dabur <i>et al.</i> , 2004, Khan <i>et al.</i> , 2004
			<i>Mp</i>	Roese and Oliveira, 2004
<i>Echinochloa crus-galli</i>	Barnyard-grass	Poaceae	<i>Mg</i>	Sperandio and Amaral, 1994
			<i>Ma, Mi</i>	Tedford and Fortum, 1988
			<i>Mt</i>	Gaur and Sharma, 1998
			<i>Mg</i>	Dabur <i>et al.</i> , 2004
<i>Echinochloa muricata</i>	Rough barnyard- grass	Poaceae	<i>Ma, Mi</i>	Kaur <i>et al.</i> , 2007
<i>Eclipta alba</i> (syn. <i>Eclipta prostrata</i>)	Eclipta	Asteraceae	<i>Mj</i>	Mani and Hinai, 1996
			<i>Mg</i>	Dabur <i>et al.</i> , 2004
<i>Eclipta prostrata</i>	Eclipta	Asteraceae	<i>Mm</i>	Brito <i>et al.</i> , 2008
<i>Eleusine indica</i>	Goosegrass	Poaceae	<i>Ma, Mi</i>	Tedford and Fortum, 1988
			<i>Mj</i>	Lordello <i>et al.</i> , 1988

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Table 1. (Continued) List of wild plant species, common names and botanical families occurring as hosts of *Meloidogyne* spp. worldwide.

Scientific name ^x	Common name ^y	Plant Family	<i>Meloidogyne</i> sp. ^z	Source/Reference
			<i>Mg</i>	Sperandio and Amaral, 1994
			<i>Mp</i>	Roese and Oliveira, 2004
<i>Emilia fosbergii</i>	Cupid's-shaving-brush	Asteraceae	<i>Mi, Mj</i>	Brito <i>et al.</i> , 2008
<i>Emilia sonchifolia</i>	Red tasselflower	Asteraceae	<i>Mi</i>	Gowda <i>et al.</i> , 1996; Nisha and Sheela, 2002
			<i>Mp</i>	Roese and Oliveira, 2004
			<i>Mm</i>	Souza <i>et al.</i> , 2006
			<i>Mf</i>	Brito <i>et al.</i> , 2008
<i>Epilobiurn hirsutum</i>	Hairy willowherb	Onagraceae	<i>Mi</i>	Ehwaeti <i>et al.</i> , 1999
<i>Erechtites hieracifolia</i>	American burnweed	Asteraceae	<i>Mj</i>	Mani and Hinai, 1996
			<i>Mi</i>	Brito <i>et al.</i> , 2008
<i>Erigeron annuus</i>	Fleabane	Asteraceae	<i>Mh</i>	Kim <i>et al.</i> , 1998
<i>Erigeron canadensis</i> (syn. <i>Conyza canadensis</i>)	Horseweed	Asteraceae	<i>Mh</i>	Leroux <i>et al.</i> , 1996
			<i>Mh</i>	Kim <i>et al.</i> , 1998
<i>Erysimum cheiranthoides</i>	Wormseed wallflower	Brassicaceae	<i>Mh</i>	Belair and Benoit, 1996
<i>Eupatorium maculatum</i>	Spotted joepeyeweed	Asteraceae	<i>Mh</i>	Belair and Benoit, 1996
<i>Eupatorium pauciflorum</i>	unknown	Asteraceae	<i>Mco</i>	Lordello and Lordello, 1972
			<i>Mco</i>	Jaehn <i>et al.</i> , 1980
<i>Euphorbia granulata</i>	unknown	Euphorbiaceae	<i>Mi, Mj</i>	Mani and Hinai, 1996
<i>Euphorbia hirta</i> (syn. <i>Chamaesyce hirta</i>)	Garden spurge	Euphorbiaceae	<i>Mi</i>	Gowda <i>et al.</i> , 1996
<i>Euphorbia maculata</i> (syn. <i>Chamaesyce maculata</i>)	Spotted spurge	Euphorbiaceae	<i>Ma</i>	Tedford and Fortnum, 1988
<i>Euphorbia peplus</i>	Petty spurge	Euphorbiaceae	<i>Mi</i>	Mani and Hinai, 1996

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Scientific name ^x	Common name ^y	Plant Family	<i>Meloidogyne</i> sp. ^z	Source/Reference
<i>Euphorbia supina</i> (syn. <i>Chamaesyce maculata</i>)	Spotted spurge	Euphorbiaceae	<i>Mi, Mi</i>	Davidson and Townshed, 1967; Tedford and Fortum, 1988
<i>Euphorbia tirucalli</i>	Indiantree	Euphorbiaceae	<i>Mp</i> <i>Mm</i>	Roese and Oliveira, 2004 Souza <i>et al.</i> , 2006
<i>Fatoua villosa</i>	Mulberryweed	Moraceae	<i>Mi</i>	Brito <i>et al.</i> , 2008
<i>Fimbristylis miliacea</i>	Globe fringerush	Cyperaceae	<i>Mg</i>	Sperandio and Amaral, 1994
<i>Flaveria trinervia</i>	Clustered yellowtops	Compositae	<i>Mi</i>	Mani and Hinai, 1996
<i>Fumaria capreolata</i>	White ramping fumitory	Fumariaceae	<i>Mi</i>	Sellami <i>et al.</i> , 1999
<i>Galinsoga ciliata</i> (syn. <i>Galinsoga quadriradiata</i>)	Hairy crabweed	Asteraceae	<i>Mp</i>	Roese and Oliveira, 2004
<i>Galinsoga parviflora</i>	Smallflower galinsoga	Asteraceae	<i>Mj</i> <i>Me</i> <i>Ma</i>	Lima <i>et al.</i> , 1985 Lordello <i>et al.</i> , 1988 Amin and Budai, 1994
<i>Glyceria fluitans</i>	Mannagrass	Poaceae	<i>Mn</i>	Sheridan and Grbavas, 1979
<i>Gnaphalium uliginosum</i>	Low cudweed	Asteraceae	<i>Mh</i>	Belair and Benoit, 1996
<i>Gutenbergia cordifolia</i>	unknown	Asteraceae	<i>Mj</i>	Desaeger and Rao, 2000
<i>Heliotropium bacciferum</i>	unknown	Boraginaceae	<i>Mj</i>	Mani and Hinai, 1996
<i>Hieracium pilosella</i>	Mouseear hawkweed	Asteraceae	<i>Mi</i>	Ehwaeti <i>et al.</i> , 1999
<i>Hordeum jubatum</i>	Foxtail barley	Poaceae	<i>Mi</i>	Davidson and Townshend, 1967
<i>Hypericum punctatum</i>	Spotted St. Johnswort	Guttiferae	<i>Mi</i>	Davidson and Townshend, 1967
<i>Impatiens balsamina</i>	Garden balsam	Balsaminaceae	<i>Mp</i>	Campos and Villain, 2005
<i>Ipomoea acuminata</i> (syn. <i>Ipomoea indica</i>)	Blue morning-glory	Convolvulaceae	<i>Me</i>	Lima <i>et al.</i> , 1985
<i>Ipomoea aristolochiaefolia</i>	unknown	Convolvulaceae	<i>Mj</i>	Lordello <i>et al.</i> , 1988

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Table 1. (Continued) List of wild plant species, common names and botanical families occurring as hosts of *Meloidogyne* spp. worldwide.

Scientific name ^x	Common name ^y	Plant Family	<i>Meloidogyne</i> sp. ^z	Source/Reference
<i>Ipomoea grandifolia</i>	Morning-glory	Convolvulaceae	<i>Mp</i>	Roese and Oliveira, 2004
<i>Ipomoea hederacea</i>	Ivyleaf morningglory	Convolvulaceae	<i>Ma</i> <i>Ma, Mi</i>	Rodriguez-Kabana <i>et al.</i> , 1977 Tedford and Fortum, 1988
<i>Ipomoea lacunosa</i>	Pitted morningglory	Convolvulaceae	<i>Ma</i>	Rodriguez-Kabana <i>et al.</i> , 1977
<i>Ipomoea pandurata</i>	Bigroot morningglory	Convolvulaceae	<i>Ma</i>	Rodriguez-Kabana <i>et al.</i> , 1977
<i>Ipomoea quamoclit</i>	Cypressvine morning-glory	Convolvulaceae	<i>Ma</i> <i>Mf</i>	Rodriguez-Kabana <i>et al.</i> , 1977 Stanley <i>et al.</i> , 2006
<i>Ipomoea triloba</i>	Three-lobed morning-glory	Convolvulaceae	<i>Ma, Mi, Mm,</i> <i>Mf, Mj</i>	Kaur <i>et al.</i> , 2007; Brito <i>et al.</i> , 2008
<i>Ipomoea violacea</i>	Heavenly blue morning-glory	Convolvulaceae	<i>Mf, Mm</i>	Kaur <i>et al.</i> , 2007
<i>Jacquemontia tamnifolia</i>	Smallflower morning-glory	Convolvulaceae	<i>Ma</i> <i>Mi</i> <i>Ma</i>	Rodriguez-Kabana <i>et al.</i> , 1977 Davis and Webster, 2003 Brito <i>et al.</i> , 2008
<i>Lactuca runcinata</i>	lettuce	Asteraceae	<i>Mi</i>	Gowda <i>et al.</i> , 1996
<i>Lamium amplexicaule</i>	Henbit deadnettle	Lamiaceae	<i>Mi</i>	Davidson and Townshed, 1967
<i>Launaea procumbens</i>	Procumbent launaea	Asteraceae	<i>Mi</i>	Mani and Hinai, 1996
<i>Leonotis nepetaefolia</i>	Lionsear	Lamiaceae	<i>Mf</i>	Kaur <i>et al.</i> , 2007
<i>Leontodon hispidus</i>	Bristly hawkbit	Asteraceae	<i>Mi</i> <i>Ma, Mf, Mi, Mj, Mm</i>	Ehwaeti <i>et al.</i> , 1999 Kaur <i>et al.</i> , 2007
<i>Leonurus cardiaca</i>	Common motherwort	Lamiaceae	<i>Mi</i>	Davidson and Townshend, 1967

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Table 1. (Continued) List of wild plant species, common names and botanical families occurring as hosts of *Meloidogyne* spp. worldwide.

Scientific name ^s	Common name ^v	Plant Family	<i>Meloidogyne</i> sp. ^z	Source/Reference
<i>Leonurus sibiricus</i>	Siberian motherwort	Lamiaceae	<i>Mj</i>	Moraes <i>et al.</i> , 1972
			<i>Me</i>	Lima <i>et al.</i> , 1985
<i>Leptochloa coloniculus</i>	Sprangletop	Poaceae	<i>Mt</i>	Gaur and Sharma, 1998
<i>Llex paraguariensis</i>	Mate	Aquifoliaceae	<i>Mp</i>	Santiago <i>et al.</i> , 2000
<i>Lotus corniculatus</i>	Bird's-foot trefoil	Fabaceae	<i>Ma, Mi</i>	Ehwaeti <i>et al.</i> , 1999
<i>Lucas aspera</i>	Thumba plant	Lamiaceae	<i>Mi</i>	Gowda <i>et al.</i> , 1995
<i>Macroptilium lathyroides</i>	Wild bushbean	Fabaceae	<i>Ma, Mi</i>	Brito <i>et al.</i> , 2008
<i>Malva neglecta</i>	Common mallow	Malvaceae	<i>Mi</i>	Davidson and Townshend, 1967
<i>Malva parviflora</i>	Cheeseweed mallow	Malvaceae	<i>Mj</i>	Sellami <i>et al.</i> , 1999
<i>Malva sylvestris</i>	High mallow	Malvaceae	<i>Mi</i>	Sellami <i>et al.</i> , 1999
<i>Matricaria indora</i> (syn. <i>Tripleurospermum perforata</i>)	Scentless chamomile	Asteraceae	<i>Mi</i>	Amin and Budai, 1994
<i>Matricaria matricarioides</i> (syn. <i>Matricaria discoidea</i>)	Pine-apple weed	Asteraceae	<i>Mh</i>	Belair and Benoit, 1996
<i>Medicago hispida</i> (syn. <i>Medicago polymorpha</i>)	California burclover	Fabaceae	<i>Mn</i>	Volvas and Inserra, 1979
<i>Medicago lupulina</i>	Black medic	Fabaceae	<i>Mi</i>	Davidson and Townshend, 1967
			<i>Mi</i>	Ehwaeti <i>et al.</i> , 1999
			<i>Mi</i>	Brito <i>et al.</i> , 2008
<i>Melilotus alba</i> (syn. <i>Melilotus officinalis</i>)	Yellow sweetclover	Fabaceae	<i>Mj</i>	Lorenzo <i>et al.</i> , 2002
			<i>Mg</i>	Dabur <i>et al.</i> , 2004
			<i>Mi</i>	Brito <i>et al.</i> , 2008
<i>Melilotus sulcata</i>	Melilot	Fabaceae	<i>Mn</i>	Volvas and Inserra, 1979
<i>Nasturtium officinalis</i>	English watercress	Brassicaceae	<i>Mf</i>	Stanley <i>et al.</i> , 2006
<i>Nepeta cataria</i>	Catnip	Labiatae	<i>Mi</i>	Davidson and Townshend, 1967

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Scientific name ^x	Common name ^y	Plant Family	<i>Meloidogyne</i> sp. ^z	Source/Reference
<i>Ocimum americanum</i>	Basil, besobla	Labiatae	<i>Mi</i>	Gowda <i>et al.</i> , 1996
<i>Ocimum canum</i>	Basil	Labiatae	<i>Mi</i>	Gowda <i>et al.</i> , 1996
<i>Oenothera biennis</i>	Common eveningprimrose	Onagraceae	<i>Ma</i>	Tedford and Fortum, 1988
<i>Oxalis europaea</i> (syn. <i>Oxalis stricta</i>)	Yellow woodsorrel	Oxalidaceae	<i>Mi</i>	Davidson and Townshend, 1967
<i>Panicum capillare</i>	Witchgrass	Poaceae	<i>Mc</i>	O'Bannon <i>et al.</i> , 1982
<i>Panicum miliaceum</i>	Wild-proso millet	Poaceae	<i>Mi</i>	Sellami <i>et al.</i> , 1999
<i>Panicum repens</i>	Torpedograss	Poaceae	<i>Mg</i>	Sperandio and Amaral, 1994
<i>Pascopyrum smithii</i>	wheatgrass	Poaceae	<i>Mc</i>	Griffin <i>et al.</i> , 1984
<i>Paspalum conjugatum</i>	Hilograss, sour paspalum	Poaceae	<i>Mk</i>	Zhang and Schmitt, 1994
<i>Paspalum notatum</i>	Bahiagrass	Poaceae	<i>Ma, Mi</i>	Tedford and Fortum, 1988
<i>Passiflora mucronata</i>	passion flower	Passifloraceae	<i>Mm</i>	Souza <i>et al.</i> , 2006
<i>Pastinaca sativa</i>	Wild parsnip	Apiaceae	<i>Mh</i>	Belair and Benoit, 1996
<i>Pennisetum purpureum</i>	Napiergrass	Poaceae	<i>Mi</i>	Mani and Hinai, 1996
<i>Phalaris minor</i>	Littleseed canarygrass	Poaceae	<i>Mt</i>	Gaur and Sharma, 1998
<i>Phyllanthus maderaspatensis</i>	unknown	Euphorbiaceae	<i>Mi</i>	Mani and Hinai, 1996
<i>Physalis angulata</i>	Cutleaf groundcherry,	Solanaceae	<i>Ma</i>	Brito <i>et al.</i> , 2008
<i>Physalis minima</i>	Wild groundcherry	Solanaceae	<i>Mi, Mj</i>	Mani and Hinai, 1996
	gooseberry		<i>Mg</i>	Khan <i>et al.</i> , 2004
<i>Phytolacca americana</i>	American pokeweed	Phytolaccaceae	<i>Ma, Mf, Mi, Mj, Mm</i>	Kaur <i>et al.</i> , 2007
<i>Pilea microphylla</i>	Artillery plant	Urticaceae	<i>Mi</i>	Brito <i>et al.</i> , 2008
<i>Poa annua</i>	Annual bluegrass	Poaceae	<i>Mg</i>	Sperandio and Amaral, 1994

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Table 1. (Continued) List of wild plant species, common names and botanical families occurring as hosts of *Meloidogyne* spp. worldwide.

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<i>Poinsettia heterophylla</i> (syn. <i>Euphorbia heterophylla</i>)	wild poinsettia	Euphorbiaceae	<i>Me</i> <i>Mj</i> <i>Mj</i> <i>Mm</i>	Lima <i>et al.</i> , 1985 Asmus and Andrade, 1997 Lordello <i>et al.</i> , 1988 Brito <i>et al.</i> , 2008
<i>Polygonum convolvulus</i>	Wild buckwheat	Polygonaceae	<i>Mh</i>	Belair and Benoit, 1996
<i>Polygonum persicaria</i>	Ladysthumb	Polygonaceae	<i>Mi</i> <i>Mn</i>	Davidson and Townshend, 1967 Sheridan and Grbavac, 1979
<i>Polygonum scabrum</i> (syn. <i>Polygonum lapathifolium</i>)	Pale smartweed	Polygonaceae	<i>Mn</i> <i>Mh</i>	Sheridan and Grbavac, 1979 Belair and Benoit, 1996
<i>Portulaca grandiflora</i>	Showy purslane	Portulacaceae	<i>Mi</i>	Mani and Hinai, 1996
<i>Portulaca oleracea</i>	Common purslane	Portulacaceae	<i>Ma, Mi</i> <i>Mh</i> <i>Mi</i> <i>Mi, Mj</i> <i>Mj</i> <i>Ma, Mi, Mm, Mj,</i>	Tedford and Fortum, 1988 Belair and Benoit, 1996 Mani and Hinai, 1996 Sellami <i>et al.</i> , 1999 Walker <i>et al.</i> , 2002 Brito <i>et al.</i> , 2008
<i>Potentilla norvegica</i>	Rough cinquefoil	Rosaceae	<i>Mi</i>	Davidson and Townshend, 1967
<i>Prunella vulgaris</i>	Common shelfheal, allheal	Labiatae	<i>Mi</i>	Davidson and Townshend, 1967
<i>Psychotria nitidula</i>	unknown	Rubiaceae	<i>Mco</i>	Jaehn <i>et al.</i> , 1980
<i>Raphanus raphanistrum</i>	Wild radish	Brassicaceae	<i>Mp</i>	Roese and Oliveira, 2004
<i>Richardia brasiliensis</i>	Brazil pusley	Rubiaceae	<i>Mp</i>	Roese and Oliveira, 2004
<i>Richardia scabra</i>	Florida pusley	Rubiaceae	<i>Mi</i>	Myers <i>et al.</i> , 2004

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Scientific name ^x	Common name ^y	Plant Family	<i>Meloidogyne</i> sp. ^z	Source/Reference
<i>Rorippa islandica</i> (syn. <i>Rorippa palustris</i>)	Yellowcress marsh	Brassicaceae	<i>Mh</i>	Belair and Benoit, 1996
<i>Rumex acetosella</i>	Red sorrel	Polygonaceae	<i>Ma, Mi</i>	Tedford and Fortum, 1988
<i>Rumex crispus</i>	Curly dock	Polygonaceae	<i>Mi</i>	Davidson and Townshend, 1967
			<i>Ma, Mi</i>	Tedford and Fortum, 1988
<i>Salpichroa origanifolia</i>	Lily of the valley vine	Solanaceae	<i>Mj</i>	Sellami <i>et al.</i> , 1999
<i>Senecio vulgaris</i>	Common groundsel	Asteraceae	<i>Mc</i>	Kutywayo and Been, 2006
<i>Senna alata</i>	Emperor's candlestick	Fabaceae	<i>Mj</i>	Moraes <i>et al.</i> , 1972
			<i>Mm</i>	Souza <i>et al.</i> , 2006
<i>Senna obtusifolia</i>	Sicklepod	Fabaceae	<i>Mf Mi., Mj, Mm</i>	Kaur <i>et al.</i> , 2007
<i>Senna occidentalis</i>	Coffee senna	Fabaceae	<i>Mm</i>	Souza <i>et al.</i> , 2006
<i>Sesbania aculeate</i>	Prickly sesbania	Fabaceae	<i>Mj</i>	Khan and Murmu, 2004
<i>Setaria lutescens</i>	Yellow foxtail	Poaceae	<i>Ma, Mi</i>	Tedford and Fortum, 1988
<i>Setaria media</i>	Foxtail grass	Poaceae	<i>Mi, Mh</i>	Kim <i>et al.</i> , 1998
<i>Setaria verticillata</i>	Bristly foxtail	Poaceae	<i>Mj</i>	Ciancio and Giudice, 1995
			<i>Mj</i>	Mani and Hinai, 1996
			<i>Mi</i>	Sellami <i>et al.</i> , 1999
<i>Setaria viridis</i>	Giant green foxtail	Poaceae	<i>Mi</i>	Davidson and Townshend, 1967
			<i>Mc</i>	O'Bannon <i>et al.</i> , 1982
			<i>Ma, Mi</i>	Tedford and Fortum, 1988
			<i>Mi</i>	Sellami <i>et al.</i> , 1999
<i>Sida acuta</i>	Southern sida	Malvaceae	<i>Mi</i>	Gowda <i>et al.</i> , 1996
<i>Sida rhombifolia</i>	Cuban jute	Malvaceae	<i>Mj</i>	Asmus and Andrade 1997

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<i>Sida spinosa</i>	Prickly sida	Malvaceae	<i>Mp</i>	Roese and Oliveira, 2004
			<i>Ma</i>	Rodriguez-Kabana <i>et al.</i> , 1977
			<i>Ma, Mi</i>	Tedford and Fortum, 1988
			<i>Mi</i>	Davis and Webster, 2003
<i>Silene dioica</i>	Red campion	Caryophyllaceae	<i>Mi</i>	Ehwaeti <i>et al.</i> , 1999
<i>Sisymbrium altissimum</i>	Tall tumble mustard	Brassicaceae	<i>Mi</i>	Davidson and Townshend, 1967
<i>Sium suave</i>	Water Parsnip	Umbeliferae	<i>Mh</i>	Belair and Benoit 1996
<i>Solanum americanum</i>	American black nightshade	Solanaceae	<i>Mj</i>	Asmus and Andrade, 1997
			<i>Mi</i>	Meyers <i>et al.</i> , 2004
			<i>Mp</i>	Roese and Oliveira, 2004
			<i>Mm</i>	Souza <i>et al.</i> , 2006
			<i>Mi, Mj, Mm</i>	Brito <i>et al.</i> , 2008
<i>Solanum dulcamara</i>	Climbing nightshade	Solanaceae	<i>Mi</i>	Davidson and Townshend, 1967
<i>Solanum nigrum</i>	Black nightshade	Solanaceae	<i>Mc</i>	O'Bannon <i>et al.</i> , 1982
			<i>Me</i>	Curi, 1973
			<i>Me</i>	Aragon <i>et al.</i> , 1978
			<i>Mj</i>	Ciancio and Giudice, 1995
			<i>Mi</i>	Mani and Hinai, 1996
			<i>Mi, Mh</i>	Kim <i>et al.</i> , 1998
			<i>Mi</i>	Zancada <i>et al.</i> , 1998
			<i>Mi</i>	Ehwaeti <i>et al.</i> , 1999
			<i>Mi, Mj</i>	Sellami <i>et al.</i> , 1999

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			<i>Mc</i>	Kutywayo and Been, 2006
<i>Solanum sarrachoides</i> (syn. <i>Solanum physalifolium</i>)	Hairy nightshade	Solanaceae	<i>Mc, Mh</i>	Boydston <i>et al.</i> , 2008
<i>Solanum torvum</i>	Turkeyberry	Solanaceae	<i>Ma</i>	Brito <i>et al.</i> , 2008
<i>Solanum viarum</i>	Tropical soda apple	Solanaceae	<i>Ma</i>	Church and Roskopf, 2005
<i>Sonchus asper</i>	Spiny sowthistle	Asteraceae	<i>Mc</i>	O'Bannon <i>et al.</i> , 1982
			<i>Ma</i>	Amin and Budai, 1994
<i>Sonchus oleraceus</i>	Common sowthistle	Asteraceae	<i>Mi, Mj</i>	Sellami <i>et al.</i> , 1999
<i>Sorghum arundinaceum</i>	Wild sorghum	Poaceae	<i>Mp</i>	Roose and Oliveira, 2004
<i>Sorghum halepense</i>	Johnsongrass	Poaceae	<i>Mj</i>	Lordello <i>et al.</i> , 1988
<i>Spananthe paniculata</i>	unknown	Apiaceae	<i>Me</i>	Lopez and Vilchez, 1991
<i>Spergula arvensis</i>	Corn spurry	Caryophyllaceae	<i>Mg</i>	Dabur <i>et al.</i> , 2004
<i>Sporobolus diander</i>	Tussock dropseed	Poaceae	<i>Mg</i>	Khan <i>et al.</i> , 2004
<i>Stachys arvensis</i>	Fieldnettle betony	Lamiaceae	<i>Me</i>	Lima <i>et al.</i> , 1985
<i>Stellaria media</i>	Common chickweed	Caryophyllaceae	<i>Mi</i>	Davidson and Townshend, 1967
			<i>Mi, Mh</i>	Kim <i>et al.</i> , 1998
<i>Talinum triangulare</i>	Waterleaf	Portulacaceae	<i>Mm</i>	Souza <i>et al.</i> , 2006
<i>Tamarix gallica</i>	Saltcedar	Tamaricaceae	<i>Mj</i>	Sellami <i>et al.</i> , 1999
<i>Taraxacum officinale</i>	Common dandelion	Asteraceae	<i>Me</i>	Lima <i>et al.</i> , 1985
			<i>Ma, Mi</i>	Tedford and Fortum, 1988
			<i>Mh</i>	Doucet <i>et al.</i> , 2000
<i>Thalictrum pubescens</i>	Tall meadow-rue	Ranunculaceae	<i>Mh</i>	Belair and Benoit, 1996
<i>Thlaspi arvense</i>	Field pennycress	Brassicaceae	<i>Mi</i>	Davidson and Townshend, 1967

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<i>Tridax procumbens</i>	Coatbuttons	Asteraceae	<i>Mp</i>	Roese and Oliveira, 2004
<i>Trifolium repens</i>	White clover	Fabaceae	<i>Mi</i>	Ehwaeti <i>et al.</i> , 1999
<i>Trigonella polyceratia</i>	Fenugreek	Fabaceae	<i>Mg</i>	Dabur <i>et al.</i> , 2004
<i>Urena lobata</i>	Cadillo	Malvaceae	<i>Mi</i>	Brito <i>et al.</i> , 2008
<i>Verbena officinalis</i>	Vervain	Verbenaceae	<i>Mi</i>	Sellami <i>et al.</i> , 1999
<i>Vernonia cinerea</i>	Inflammation bush	Asteraceae	<i>Mi, Mj</i>	Mani and Hinai, 1996
<i>Veronica agrestis</i>	Green field speedwell	Scrophulariaceae	<i>Mh</i>	Belair and Benoit, 1996
<i>Veronica peregrina</i>	Purslane speedwell	Scrophulariaceae	<i>Mi</i>	Davidson and Townshend, 1967
<i>Veronica serpyllifolia</i>	Thymeleaf speedwell	Scrophulariaceae	<i>Mi</i>	Davidson and Townshend, 1967
<i>Vicia villosa</i>	Hairy vetch	Fabaceae	<i>Mn</i>	Vovlas and Inserra, 1979
			<i>Ma, Mi</i>	Tedford and Fortum, 1988
<i>Withania somnifera</i>	Ashwagandha	Solanaceae	<i>Mi, Mj</i>	Mani and Hinai, 1996
<i>Xanthium strumarium</i>	Common cocklebur	Asteraceae	<i>Ma, Mi</i>	Tedford and Fortum, 1988
<i>Youngia japonica</i>	False hawksbeard	Asteraceae	<i>Mi, Mj</i>	Brito <i>et al.</i> , 2008

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is highly damaging to coffee (Barbosa *et al.*, 2004), but only a few weed hosts have been described. Lima *et al.* (1985) found that weed hosts of *M. exigua* included *Amaranthus deflexus*, *Poinsettia heterophylla*, *Ipomoea acuminata*, *Leonurus sibiricus*, *Stachys arvensis*, and *Taraxacum officinale*. Other weed hosts of *M. exigua* include *Commelina diffusa*, *Cyperus rotundus*, and *Solanum nigrum* (Aragon, 1978), *Citrullus vulgaris* (Moraes *et al.*, 1972) and *Spananthe paniculata* (Lopez and Vilchez, 1991).

Meloidogyne floridensis

This root-knot nematode was recently described as a new species infecting peach in Florida, USA (Handoo *et al.*, 2004) and is known to occur only in the United States (Brito *et al.*, 2008). The nematode was reported by Brito *et al.* (2008) to infect *Emilia sonchifolia*, while Stanley *et al.* (2006) found that two other weeds, *Ipomoea quamoclit* and *Nasturtium officinalis*, were hosts of *M. floridensis*. In another study, Kaur *et al.* (2007) found that *Amaranthus spinosus*, *A. retroflexus*, *Cnidocolus stimulosus*, *Dichondra repens*, *Ipomea triloba*, *I. violacea*, *Leonotis nepetaefolia* and *Phytolacca americana* were good hosts.

Meloidogyne graminicola

The rice root-knot nematode has been reported from several rice growing countries of the world, especially in light textured soils and irrigated upland conditions where it causes damage to rice in both nurseries and field plantings (Panwar and Rao, 1998; Rao *et al.*, 1986). This nematode had been found infecting weed species associated with rice cultivation including *Cyperus deformis*, *C. iria*, *Dichanthium annulatum*, *Echinochloa colona*, *E. crus-galli*, *Eclipta alba*, *Melilotus alba*, and *Trigonella polyceratia* (Bajaj and Dabur 2000; Dabur *et al.*, 2004; Sperandio and Amaral, 1994), and also

Echinochloa colonom (Khan and Murmu, 2004). Khan *et al.* (2004) studied the weeds harboring *M. graminicola* in India and found 17 weeds associated with this nematode in rice fields, eight of which were new host records (*Agropyron repens*, *Alternanthera sessilis*, *Bothriochloa intermedia*, *Brachiaria ramosa*, *Dactyloctenium aegyptium*, *Digitaria sanguinalis*, *Physalis minima*, and *Sporobolus diander*). The egg-laying behavior of females of *M. graminicola* differed with the weed host species. In some of the weeds, the female nematode produced egg masses within the galls, while others such as *Cyperus rotundus*, *Echinochloa colonom*, *Physalis minima* and *Sporobolus diander* had small egg masses on the root gall; however in *Ageratum conyzoides*, heavy root galling and large egg masses were observed (Khan *et al.*, 2004). This nematode was also found infecting *Cyperus rotundus* in Florida (Brito *et al.*, 2008).

Meloidogyne hapla

The northern root-knot nematode is an important vegetable crop pest and is a major limiting factor in temperate regions of the world (Melakeberhan *et al.*, 2007; Mitkowski *et al.*, 2002; Potter and Olthof, 1993; Vrain, 1982). Many weed species are highly susceptible to *M. hapla* and serve as alternative hosts in agricultural areas (Bendixen, 1986b; Edwards and Jones, 1984; Gaskin and Crittenden, 1956). In greenhouse tests, Belair and Benoit (1996) found high populations of *M. hapla* on *Bidens cernua*, *B. frondosa*, *B. vulgata*, *Matricaria matricarioides*, *Pastinaca sativa*, *Polygonum scabrum*, *Sium suave*, and *Thlaspi arvense*. Moderate reproduction of *M. hapla* was supported by *Capsella bursa-pastoris*, *Chrysanthemum leucanthemum*, *Gnaphalium uliginosum*, *Stellaria media*, *Thalictrum pubescens*, and *Veronica agresti* while *Chenopodium album*, *C. glaucum*, *Erysimum cheiranthoides*,

Eupatorium maculatum, *Polygonum convolvulus*, *Portulaca oleracea*, and *Rorippa islandica* reportedly sustained low reproduction of this nematode. Roots of *Eupatorium maculatum* and *Thalictrum pubescens* exhibited no distinct galling caused by *M. hapla* but supported low and moderate populations of the nematode on the two weed species, respectively. Interestingly, *M. hapla* induced galls on *Senecio vulgaris* but no eggs or juveniles were produced. Some non-host weed species of *M. hapla* were *Amaranthus retroflexus*, *Ambrosia artemisiifolia*, *Echinochloa crus-galli*, and *Setaria viridis*. *Taraxacum officinale* was also reported as a good host of *M. hapla* (Doucet *et al.*, 2000) and poses a serious threat to agriculture production in Argentina since it is widely disseminated in the country.

Meloidogyne incognita

The southern root-knot nematode is widely distributed throughout the world and has a wide range of weed hosts (Alam and Khan, 1976; Brito *et al.*, 2008; Krishna-Murthy and Elias, 1968). In greenhouse tests, 34 species of weeds in 32 genera belonging to 19 botanical families were found to be good hosts of *M. incognita* (Davidson and Townshend, 1967). In large greenhouse tests, Gaskins (1958) found that 70 out of 103 weed species tested were hosts to *Meloidogyne incognita* as measured by presence of mature females. Among the most highly susceptible weeds were *Ampelamus albidus*, *Amaranthus graecizans*, *A. retroflexus*, *Ipomoea hederacea*, *Lactuca scariola*, *Plantago lanceolata*, *Polygonum aviculare*, *P. persicaria*, and *Solanum dulcamara*. Gowda *et al.* (1995) assessed the susceptibility of the 22 common weeds found to grow in tobacco fields in India and observed that *Celosia argentea* and *Ocimum canum* were highly infected and showed gall sizes ranging from small to medium while *Cleome vis-*

cosa and *Sida acuta* supported moderate galling and small to large galls, respectively. Other weeds (*Achyranthes aspera*, *Borreria hispida*, *Emelia sonchifolia*, *Euphorbia hirta*, *Lactuca runcinata*, and *Lucas aspera*) also were found to be hosts of *M. incognita*. In an extensive survey in the Sultanate of Oman, Mani and Hinai (1996) observed 30 weeds as hosts of *M. incognita* and *M. javanica*. Among those found as hosts of *M. incognita* were *Achyranthes aspera*, *Aerva javanica*, *Alternanthera sessilis*, *Amaranthus hybridus*, *A. graecizans*, *Chamaesyce hirta*, *Chenopodium murale*, *Datura metel*, *Portulaca grandiflora*, *P. oleracea*, *Phyllanthus maderaspatensis*, *Solanum nigrum* and *Withania somnifera*. *Cyperus esculentus* and *C. rotundus* were reported as hosts of *M. incognita*, and these weeds produced a pest complex that is a serious threat to cotton in Georgia (Bird and Hogger, 1973) and chile pepper production in New Mexico USA (Schroeder *et al.* 1999; Thomas *et al.* 1997; 2004). Myers *et al.* (2004) found *M. incognita* associated with major weeds in Florida USA, especially, *Cyperus esculentus*, *C. rotundus*, *Cynodon dactylon*, *Richardia scabra* and *Solanum americanum*. In Mexico, *M. incognita* and unidentified *Meloidogyne* spp. were found on *Amaranthus graecizans* in irrigated and dry lands of the states of Aguascalientes, San Luis Potosi and Zacatecas (Velasquez-Valle, 2001). Nisha and Sheela (2002) reported *Emilia sonchifolia* as a new host of *M. incognita* in India and suggested that *M. incognita* was the major nematode infesting crops and weeds in that country.

Meloidogyne javanica

The Javanese root-knot nematode is tropical and subtropical in distribution and has a broad host range (Taylor and Sasser, 1978). Asmus and Andrade (1997) found that *Amaranthus hybridus*, *Bidens pilosa*, *Digitalis horizontalis*, *Euphorbia heterophylla*, *Sida*

rhubifolia and *Solanum americanum* served as reservoir hosts for *M. javanica*. Since this nematode multiplied on all the weed species, control of weeds, especially *A. hybridus*, *E. heterophylla* and *S. americanum*, was of high importance for preventing multiplication of *M. javanica*. Other weeds reported as hosts of *M. javanica* are *Gutenbergia cordifolia* in Kenya (Desaeger and Rao, 2000), *Melilotus alba* in Argentina (Lorenzo *et al.*, 2002), *Portulaca oleracea* in Australia (Walker *et al.*, 2002), and *Sesbania aculeata* in India (Khan and Murmu, 2004).

Meloidogyne konaensis

The Kona coffee root-knot nematode was first found infecting coffee plantations in Hawaii (Eisenback *et al.*, 1994) but also reproduced heavily on tomato over a wide temperature range (Zhang, 1994). Only one weed species, *Cyperus rotundus*, has been observed as host of this nematode (Zhang and Schimtt, 1994). Further studies of host suitability of this nematode among plants should be useful for crop selection in areas adjacent to coffee plantings.

Meloidogyne mayaguensis

The guava root-knot nematode (Souza *et al.*, 2006) was originally described from eggplant (*Solanum melongena*) collected in Puerto Rico (Rammah and Hirschmann, 1988). Since then, this nematode has been found to be pathogenic to many economically important crops including coffee, guava, pepper, tomato, soybean and also ornamental plants in several regions of the world (Brito *et al.*, 2007; 2008; Carneiro *et al.*, 2001; Decker and Fuentes, 1989; Fargette *et al.*, 1996; Molinari *et al.*, 2005; Willers, 1997). *Biden pilosa* was the first weed species identified as a host of *M. mayaguensis* (Willers, 1997). Recently, 14 additional weed species in 12 botanical families were

reported as hosts of *M. mayaguensis* (Souza *et al.*, 2006). Similarly, 10 other weed species were identified as good hosts of this nematode including *Abutilon theophrasti*, *Amaranthus retroflexus*, *A. spinosus*, *Cnidioscolus stimulosus*, *Dichondra repens*, *Ipomoea triloba*, *I. violacea*, *Leontodon hispidus*, *Phytolacca americana* and *Senna obtusifolia* (Kaur *et al.*, 2007). *Meloidogyne mayaguensis* was also found infecting *Eclipta prostrata* and *Portulaca oleracea* under field conditions (Brito *et al.*, 2008).

Meloidogyne naasi

The barley root-knot nematode has only been studied as a host of a few weed species. It was found infecting *Coronilla scopioides*, *Medicago hispida*, *Melilotus sulcata*, and *Vicia villosa* in a wheat field in Italy (Vovlas and Insera, 1979) and was present on *Glyceria fluitans* and *Polygonum persicaria* in New Zealand (Sheridan and Grbavac, 1979) and *Chenopodium hybridum*, *C. album* and *Digitaria sanguinalis* in Hungary (Amin and Budai, 1994).

Meloidogyne paranaensis

This nematode was first found infecting coffee plants in Parana state, Brazil, and as such, was named the Parana coffee root-knot nematode (Carneiro *et al.*, 1996). The major weed hosts of *M. paranaensis* include *Cyperus rotundus*, *Echinochloa colonum*, *Eleusine indica*, *Galinsoga ciliata*, *Ipomoea grandifolia*, *Raphanus raphanistrum*, *Solanum americanum* and *Sorghum arundinaceum* while *Acanthospermum australe*, *Biden pilosa*, *Cenchrus echinatus*, *Conyza bonariensis*, *Desmodium tortuosum*, *Digitaria horizontalis*, *Mimosa invisa*, *Sonchus oleraceus* and *Spermacoce latifolia* were non-hosts of this nematode (Roese and Oliveira, 2004). *Impatiens balsamina* was also found to be a host of *M. paranaensis* (Campos and Villain, 2005).

Meloidogyne triticoryzae

This root-knot nematode was first described from India and was found infecting wheat and rice (Gaur *et al.*, 1993). Weeds known to be good hosts of this nematode are *Cyperus rotundus*, *Echinochloa colonum*, *Echinochloa crus-galli*, *Leptochloa colonicus* and *Phalaris minor* (Gaur and Sharma, 1998).

DISCUSSION

Information on the host range of *Meloidogyne* spp. is very incomplete and sometimes contradictory; and many additional studies are necessary to adequately describe this subject. For example, published research to determine weed hosts was only found on about 14 of the 96 nominal species of *Meloidogyne*. In addition, there are 3479 recognized weed species in the Weed Science Society of America database (Anonymous, 2007), thus adding tremendously to the work for Nematologists. Weeds, like crop plants, differ widely in their host status to individual *Meloidogyne* spp. For example, *Crotalaria spectabilis* was found to be a good host of *M. arenaria* and *M. incognita* (Tedford and Fortnum, 1988) but immune to *M. mayaguensis* (Guimarães *et al.*, 2003). Two other factors, *Meloidogyne* spp. race and weed biotypes, also complicate the host status designation of weeds to *Meloidogyne* spp.; therefore, localized observations and tests will be needed in addition to simple host range tests (Griffin, 1982). For example, different authors have found differing results on host ranges of weeds such *Senna obtusifolia*. Rodriguez-Kabana *et al.* (1977) found *M. arenaria* race 1 causing severe root galling on this weed, but others have reported that *M. arenaria* race 1 (Kaur *et al.*, 2007) and *M. arenaria* race 2 (Tedford and Fortnum, 1988) were not found to reproduce on *Senna obtusifolia*. Similarly,

Digitaria sanguinalis was reported to be a host of *M. incognita* (Myers *et al.*, 2004; Noling and Gilreath, 2002), but no reproduction of *M. incognita* race 4 was reported in another study (Kaur *et al.*, 2007).

It is important to also remember that some weeds are NOT hosts of plant-parasitic nematodes, a fact that may be useful in management programs. For example, Rhoades (1976) reported that a summer cover crop of hairy indigo (*Indigofera hirsuta*) was a non-host to *Meloidogyne incognita* and *M. javanica* as well as the sting nematode (*Belonolaimus longicaudatus*). In field experiments, hairy indigo was as effective as soil fumigation for control of those nematode species in subsequent vegetable crop production.

Knowledge about weeds as hosts of *Meloidogyne* spp., particularly weeds known to be highly symptomatic hosts of root-knot nematodes, makes it possible to use existing weeds to monitor fields for those nematodes. This is especially important when laboratory assay is impractical or when more data points on *Meloidogyne* infestation are needed than can be derived by laboratory soil assay alone. For instance, a wild *Citrullus* sp. has been used to monitor *Meloidogyne arenaria* race 2 in North Florida, USA, and several Leguminosae were used to index a *Meloidogyne* sp. infestation in fields to be planted to melons *Cucumis melo* in Guatemala where laboratory soil assay was unavailable (R. A. Dunn, pers. comm.).

The host status and ultimately the degree of nematode reproduction on weeds should be a major concern in integrated nematode management recommendations since weeds are almost universally present during crop growth and afterwards in fallow periods. This statement seems contrary to modern agricultural perceptions of many scientists and farmers who now consider that weeds are not major con-

straints in commercial production due to the excellent control provided by herbicides. However, weed control is often conducted relative to weed populations and threshold levels established for weed/crop competition. If weed populations are relatively low, it may be viewed as unprofitable to perform weed control, regardless of whether these weeds host parasitic nematodes. More commonly, limited resource growers, particularly those in the subtropics and tropics, often are not able to manage weeds as effectively during the cropping season. Additionally, both large-scale commercial and limited resource growers routinely have long fallow periods between crops, when weeds continue to grow. These fallow periods may last from 3-6 months and are natural in most crop production cycles. For example, in northern Florida USA, thousands of acres of cotton and peanut are harvested in September and October each year, and the land is then not used for crop production for over 6 months until planting commences the following May.

Hence, agricultural land devoted to annual crops remains idle for periods of several months between crops, allowing prolific weed growth. A solution that may seem simple is to control weeds, particularly in the off-cropping season. However, this could lead to increased grower cost, greater soil erosion potential, less nutrient recycling, and lower soil organic matter levels. Research is necessary to develop nematode management options such as selectively eliminating major weed hosts with herbicides, encouraging the growth of non-host weeds, or planting cover crops that could suppress weed populations. Results from this review indicate that the presence of weeds any time during the year are likely to compromise carefully documented and effective rotation systems for nematode management. This review pro-

vides further evidence that weed management both within and after the normal cropping cycle is an overlooked yet critical component of nematode management systems. Without a strong weed management program, the benefits of crop rotation for nematode management can be quickly annulled by weed hosts of plant-parasitic nematodes. Recommendations for crop rotation by Nematologists should also include clear statements about the necessity of controlling weeds, particularly in those periods between cropping cycles.

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