CROTALARIA AS A COVER CROP FOR NEMATODE MANAGEMENT: A REVIEW[†]

Koon-Hui Wang, B. S. Sipes, and D. P. Schmitt

Department of Plant and Environmental Protection Sciences, 3190 Maile Way, University of Hawaii, Honolulu, HI 96822-2279, U.S.A. Current address of senior author: Department of Entomology and Nematology, University of Florida, P.O. Box. 110620, Gainesville, FL 32611-0620, U.S.A. koon-hui@ufl.edu.

ABSTRACT

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Much of the research on *Crotalaria* has focused on nematode suppression in agricultural production systems. *Crotalaria* is a poor host to many plant-parasitic nematodes including *Meloidogyne* spp., *Rotylenchulus reniformis*, *Radopholus similis*, *Belonolaimus longicaudatus*, and *Heterodera glycines*. It is also a poor or non-host to a large group of other pests and pathogens, is competitive with weeds without becoming a weed, grows vigorously to provide good ground coverage for soil erosion control, fixes nitrogen, and is a green manure. However, most *Crotalaria* species are susceptible to *Pratylenchus* spp., *Helicotylenchus* sp., *Scutellonema* sp., and *Criconemella* spp. The objectives of this review are to summarize the knowledge of the efficacy of *Crotalaria* spp. for plant-parasitic nematode management, describe the mechanisms of nematode suppression, and outline prospects for using this crop effectively. *Crotalaria* species are used as preplant cover crops, intercrops, or soil amendments. Variation in nematode suppression by different *Crotalaria* cropping systems is discussed. The major impediment to using *Crotalaria* is its short-term effect in agricultural production systems. Integrating other pest management strategies with *Crotalaria* could offer promising nematode management approaches.

Key words: Allelopathy, *Crotalaria juncea*, nematode antagonistic fungi, plant-parasitic nematodes, sunn hemp.

RESUMEN

Wang, K.-H., B. S. Sipes, and D. P. Schmitt. 2002. Uso de *Crotalaria* como cultivo de cobertura para el manejo de nematodo: Una revision. Nematrópica 32:35-57.

Gran parte de la investigación en *Crotalaria* ha sido enfocada sobre la supresión de nematodos en sistemas de producción agrícola. *Crotalaria* es una hospedera inadecuada para muchos nematodos parásitos de plantas entre los cuales se incluyen *Meloidogyne* spp., *Rotylenchulus reniformis*, *Radopholus similis*, *Belonolaimus longicaudatus*, y *Heterodera glycines*. Un gran número de otros tipos de plagas y patógenos no logran hospedarse en ella, compite con malezas sin llegar a ser una maleza, crece vigorosamente proporcionando una buena cobertura del suelo que lo protege contra la erosión, fija nitrógeno, y es un abono verde. Sin embargo, muchas especies de *Crotalaria* son susceptibles a *Pratylenchus* spp., *Helicotylenchus* sp., *Scutellonema* sp., y *Criconemella* spp. Esta revisión tiene como objetivos resumir el conocimiento actual sobre la eficiencia de *Crotalaria* spp. para el manejo de nematodos fitoparásitos, describir los mechanismos de la supresión de nematodos, y esquematizar perspectivas para el uso de este cultivo eficientemente. Las especies de *Crotalaria* son usadas como cultivos de cobertura presiembra, cultivo intercalado o emiendas de suelo. Se discute la variación en la supresión de nematodos por diferentes sistemas de cultivos de *Crotalaria*. El mayor obstáculo para el uso de Cro-

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talaria es su efecto a corto plazo en los sitemas de producción agrícola. La integración de otras estrategias de manejo de plagas con Crotalaria podría ofrecer soluciones promisorias para el manejo de nematodo.

Palabras claves: Alelopatía, *Crotalaria juncea*, hongos antagonista de nematodos, nematodos fitoparásitos.

INTRODUCTION

Crotalaria possesses many characteristics of a cover crop, being a poor or non-host for a large group of pests and pathogens, competitive with weeds without becoming a weed, growing vigorously to provide good ground coverage, performing symbiosis with rhizobium to fix nitrogen, and being a green manure. This review will focus on growing *Crotalaria* for nematode management, and will provide an overview of the advantages and potential problems of this plant as a cover crop, a description of the mechanisms of nematode suppression, and prospects for using this crop effectively to suppress plant-parasitic nematodes.

Crotalaria

Crotalaria belongs to Fabaceae L. (syn. Leguminosae Juss.) and contains about 550 species (Purseglove, 1974). Growth habits vary from shrubs to herbs and the genus is common in the tropics and subtropics, with the greatest number of species occurring in Africa. One of the important fiber and green manure crops is *Crotalaria juncea* L. Several other economically important species are *C. intermedia* Kotschy, *C. mucronata* Desv (syn. *C. striata* DC.), and *C. retusa* L., which are grown as green manures, forages, and ornamentals.

Many species of *Crotalaria* contain alkaloids toxic to animals. For example, *C. burkeana* Benth causes crotalism (styfsiekte) in cattle in South Africa, an acute inflammation of the horn-forming membranes of the hoof. *Crotalaria dura* Wood & Evans causes pulmonary and liver diseases in horses and cirrhosis of the liver in cattle; *C. retusa* causes cirrhosis of the liver in humans and cattle in Jaimaica; *C. maypurensis* HBK is suspected of losses in cattle in Guyana (Purseglove, 1974); and *C. spectabilis* Roth. is toxic to livestock and can become a noxious weed (Good *et al.*, 1965).

Fortunately, numerous species are not toxic to livestock (Rotar and Joy, 1983), including *C. juncea*, commonly known as sunn hemp. It probably originated in India, is the fastest growing of the *Crotalaria* species, and is very effective at competitively displacing weeds (Purseglove, 1974). It is hardy, drought-resistant, and grows on almost all soil types. Although adapted to hot climates, the plant will endure slight frost. It is the most important fiber crop in India and is now widely grown as a green manure in Indonesia, Zimbabwe, Malaysia, Taiwan, Thailand, and China (Rotar and Joy, 1983). *Crotalaria juncea* was used in the manufacture of products such as twines, cords, fishing nets, sacks, and rope soles for shoes and sandals (Purseglove, 1974). In addition, since rhizobia that nodulate *C. juncea* are present in most soils, soil nitrogen improvement is expected (National Research Council, 1979). As a green manure crop, the plants can be tilled into the soil 2 months after planting to increase the soil organic matter. Therefore, *C. juncea* is grown in rotation with rice, maize, tobacco, cotton, sugar cane, pineapples (Hawaii), coffee (Brazil) and in

orchard crops (Purseglove, 1974). Its seeds have been fed to pigs in Zimbabwe and horses in the former Soviet Union without harm to the animals (Purseglove, 1974).

Crotalaria juncea 'Tropic Sun', developed for use as a green manure, was released in 1982 by the National Resources of Conservation Seirra (NRCS), formerly the Soil Conservation Service, and University of Hawaii (Rotar and Joy, 1983). The source of the germplasm is uncertain, but it was probably collected by the Pineapple Research Institute in Hawaii since it was conducting research on *Crotalaria* species. In 1958, NRCS and University of Hawaii purchased seeds of *Crotalaria* from a farmer who was growing it as a cover crop on the island of Kauai. This germplasm was used to develop 'Tropic Sun'. The Agricultural Research Service's Poisonous Plant Laboratory and the University of Hawaii determined that seeds of this cultivar were not toxic to livestock, and that the plant was resistant to root-knot nematodes (Rotar and Joy, 1983).

In the tropics, 'Tropic Sun' grows and produces seed year round at elevations of 0 to 300 m, and in summer up to 600 m. It is grown in Guam and Puerto Rico under conditions similar to Hawaii. In the continental United States, *C. juncea* is adapted to spring and summer planting in the South and Southwest (Rotar and Joy, 1983) and can be grown as a winter cover crop in Alabama (Reeves *et al.*, 1996). It is suitable as a green manure crop as far north as Maryland, but may not seed well north of 30° latitude.

'Tropic Sun' is a rapidly growing crop that is good for use as a green manure and for adding organic matter and nitrogen to the soil. It suppresses weeds, slows soil erosion, and reduces root-knot nematodes populations (Rotar and Joy, 1983). When plowed under at early bloom stage, nitrogen recovery is the highest. It can produce 150 to 165 kg/ha of nitrogen and 7 t/ha air-dry organic matter at 60 days of growth under favorable conditions (Rotar and Joy, 1983). In southwestern Alabama, plants grown for 9 to 12 weeks will produce 5.9 t/ha dry-matter and 126 kg N/ha (Reeves *et al.*, 1996). Leaving the residue on the soil surface over winter resulted in the release of 75 to 80 kg N/ha (Reeves *et al.*, 1996).

The crop has a few pest and pathogen problems. Major diseases of *C. juncea* are Fusarium wilt caused by *Fusarium udum* var. *crotalariae* and anthracnose caused by *Collectotrichum curvatum* (Purseglove, 1974). In Brazil, the only disease reported on the crop is *Ceratocystes fimbriata* (National Research Council, 1979). The three most serious insect pests for *C. juncea* are larvae of the sunn hemp moth, *Utetheisa pulchell*a, the stem borer, *Laspeyresia pseudonectis*, and the pod borers (Purseglove, 1974). *Crotalaria juncea* was also a host to stink bug, *Nezara viridula* and African sorghum head bug, *Eurystylus oldi* (Davis, 1964; Malden and Ratnadass, 1998).

NEMATODE POPULATION SUPPRESSION BY *CROTALARIA*

Suppression of plant-parasitic nematodes by *Crotalaria* spp. has been known for decades. Godfrey (1928) noted that *C. juncea* had few root galls from infection with *Meloidogyne* spp. Most of the plant-parasitic nematodes suppressed by *Crotalaria* are sedentary endoparasitic nematodes. These include *Meloidogyne* spp. (Good *et al.*, 1965; McSorley *et al.*, 1994a; Taylor, 1985), *Heterodera glycines* (Rodríguez-Kábana *et al.*, 1992b) and *Rotylenchulus reniformis* (Robinson *et al.*, 1998; Araya and Caswell-Chen, 1994a). Some migratory nematodes such as *Belonolaimus longicaudatus* (Reddy *et al.*, 1986), *Paratrichodorous minor*, *Xiphinema americanum* (Good *et al.*, 1965; Brodie *et al.*, 1970), and *Radopholus similis* (Birchfield

and Bristline, 1956) were also suppressed by *Crotalaria* spp. (Table 1). Most of the plant-parasitic nematodes that are not suppressed by *Crotalaria* are migratory nematodes, including *Helicotylenchus* spp., *Mesocriconema xenoplax*, *P. minor*, *Pratylenchus* spp., *Radopholus similis*, *Scutellonema* spp. and *X. americanum* (Table 2).

Among the species tested, *C. spectabilis* and *C. juncea* are most frequently studied. These plants have been used as preplant cover crops, intercrops, and soil amendments. The suppressive effect of *Crotalaria* on nematodes is variable for all the application methods (Table 1). As suggested by McSorley (2002), this variation could be due to genetic variation within the nematode species, crop cultivars, cropping season, field history, cover cropping system, concurrent field practices or edaphic factors including various biological components associated with the *Crotalaria* rhizosphere or soil amendment. Accordingly, variation in nematode suppression by different *Crotalaria* application methods will be discussed.

Preplant cover crop: In general, when *Crotalaria* was used as a preplant cover crop, it suppressed population growth of most plant-parasitic nematodes except *Pratylenchus* spp. and *Helicotylenchus* spp. (Desaeger and Rao, 2000; Johnson and Campbell, 1980). Several studies demonstrated that *Crotalaria* suppressed *Meloidogyne* spp. better than nematicides, because it continued to suppress the nematode population development after a host was planted (Huang *et al.*, 1981; Aguillera *et al.*, 1984; Sharma and Scolari, 1984). *Crotalaria juncea* suppressed *R. reniformis* population densities better than weed cover when planted immediately after pineapple, with a nematode reproductive factor of 0.16 and 1.59 respectively (Wang, 2000). Although Johnson and Campbell (1980) suggested that *Crotalaria* treatment was not as effective as fallow, differences between those two treatments were not statistically significant.

Crotalaria species demonstrated variable resistance against different nematodes. For example, *C. juncea* supported moderate infection by *M. javanica*, whereas *C. intermedia* exhibited greater resistance, and *C. paulina* Schrank and *C. spectabilis* showed high resistance (Daulton, 1955; Martin, 1956). Similarly, *C. breviflora* DC., *C. lanceolata* E. Meyer and *C. mucronata* are very resistant, *C. retusa*, *C. grantiana* Harv., *C. spectabilis* and *C. juncea* are intermediate, and *C. striata* and *C. paulina* are less resistant to *R. reniformis* (Silva *et al.*, 1989b). Different susceptibility of *Crotalaria* species to *Pratylenchus* and *Helicotylenchus* spp. was also observed. Population densities of *P. coffeae* on tea were suppressed by *Crotalaria* (Visser and Vythilingam, 1959) but *P. zea* can penetrate roots of *C. breviflora*, *C. spectabilis*, *C. retusa*, and *C. juncea*, and *P. brachyurus* can penetrate roots of *C. juncea* and *C. spectabilis* at a lower rate than those penetrating roots of *Sorghum bicolor*, a standard host for *Pratylenchus* (Silva *et al.*, 1989a). Biomass production of several species of *Crotalaria*, including *C. paulina*, *C. pycnostachya*, and *C. striata*, was reduced by *P. zeae* (Desaeger and Rao, 2001). However, *C. mucronata* suppressed *P. zeae* and *P. brachyurus* (Endo, 1959) and *C. usaromoensis* decreased *P. brachyurus* population densities and improve pineapple yield. In another case, *P. brachyurus* survived in soil planted with *C. juncea*, but did not multiply (Charchar and Huang, 1981).

Most reports have indicated that *C. spectabilis* suppressed *Meloidogyne* spp. However, a majority of the tests for *Crotalaria* were conducted in tropical or subtropical areas where *Crotalaria* is well adapted. A greenhouse experiment showed that *C. spectabilis* was not resistant to *M. hapla* (Good *et al.*, 1965), a nematode more com-

Table 1. Examples of positive effects of *Crotalaria* spp. on plant-parasitic nematodes management.

Species	Experimental conditions	Target nematode	Results	References
Crotalaria sp.	Host testing	*Meloidogyne* spp.	Poor host in tobacco fields of Florida.	Bratley, 1942
	Host testing	*Meloidogyne javanica*, *Pratylenchus coffeae*	Reduced nematodes on tea more efficiently than fallow.	Visser and Vythilingam, 1959
	Host testing	*R. reniformis*	Reduced nematode population densities.	Román, 1964
	Trap crop	*Meloidogyne* spp. on citrus (Asiatic pyroid citrus nematode)	Nematode invaded roots but no nematode reproduction.	Chitwood and Toung, 1960
C. agatiflora	Host testing in field soil	Majority of *M. javanica* mixed with *M. incognita*	No nematodes were recovered from soil or roots.	Desaeger and Rao, 1999
	Preplant cover crop for maize	*M. incognita*, *M. javanica*	Decreased nematode populations before and after maize planting compared to weed fallow.	Desaeger and Rao, 2000
C. breviflora	Field test	Ectoparasitic nematodes	Effectively reduced nematode numbers.	Ochse and Brewton, 1954
	Host testing	*M. incognita* race 3, *M. javanica*	No nematodes detected.	Santos and Ruano, 1987
	Host testing	*R. reniformis*	No nematodes detected.	Silva *et al.*, 1989b
C. breviflora	Host testing	*P. zea*	Low numbers compared to those in sorghum.	Silva *et al.*, 1989a
C. endecaphylla	Host testing	*M. incognita*, *M. javanica*	No nematodes recovered after 4 months.	Desaeger and Rao, 1999
C. fulva	Host testing	*M. incognita*, *M. javanica*	Non-host of these nematodes.	Netcher and Sikora, 1990
	Preplant cover crop for tobacco	*M. javanica*	Suppressed damage of *M. javanica* on tobacco.	Shepherd and Barker, 1993
C. grahamiana	Host testing	*M. incognita*, *M. javanica*	Non-host of these nematodes.	Netcher and Sikora, 1990; Desaeger and Rao, 1999
	Preplant cover crop for tobacco	*M. javanica*	Suppressed damage of *M. javanica* on tobacco.	Shepherd and Barker, 1993
C. greenway	Host testing	*M. incognita*, *M. javanica*	No nematodes recovered after 4 months.	Desaeger and Rao, 1999
C. grantiana	Host testing	*M. incognita* race 3, *M. javanica*	Resistant.	Santos and Ruano, 1987
	Host testing	*P. brachyurus*, *P. zea*	No nematodes were detected.	Silva *et al.*, 1989a
C. grantiana	Host testing	*R. reniformis*	Poor host.	Silva *et al.*, 1989b
C. incana	Host testing	*M. incognita*, *M. javanica*	No nematodes recovered after 4 months.	Desaeger and Rao, 1999
C. intermedia	Preplant cover crop for tobacco	*M. javanica*	Suppressed damage of *M. javanica* on tobacco.	Shepherd and Barker, 1993
C. juncea	Host testing	*Meloidogyne* spp.	Low root gall index.	Godfrey, 1928
	Host testing	*M. incognita* race 3, *M. javanica*	Resistant.	Santos and Ruano, 1987

Table 1. (Continued) Examples of positive effects of *Crotalaria* spp. on plant-parasitic nematodes management.

Species	Experimental conditions	Target nematode	Results	References
C. juncea	Host testing	*M. arenaria*, *M. incognita*, *M. javanica*	Only occasional egg masses observed on *M. incognita* infected plants.	McSorley, 1999
	Host testing	*M. exigua*	Highly efficient in suppressing the nematode.	Silva *et al.*, 1990a
	Host testing	*M. javanica*	Smaller giant cells; fewer giant cells per female; giant cells showed granular, dense cytoplasm, with small number of nuclei; large vacuoles frequently absent.	Silva *et al.*, 1990b
	Host testing	*M. javanica*	Some *M. javanica* reproduction but no galls observed and no juveniles found in soil; *M. javanica* extracted by mist chamber were significantly lower than that from the tomato.	Araya and Caswell-Chen, 1994a
	Host testing	*M. javanica*	Penetrate the roots but cannot develop into adult 45 days after inoculation.	Silva *et al.*, 1989c
	Host testing	*P. brachyurus*	Survived but failed to multiply.	Charchar and Huang, 1981
	Host testing	*P. brachyurus*, *P. zea*	Low numbers compared to those in sorghum.	Silva *et al.*, 1989
	Host testing	*Rotylenchulus reniformis*	Poor host, limited penetration, reduced *R. reniformis* at least as well as fallow.	Caswell *et al.*, 1991; Robinson *et al.*, 1998; Silva *et al.*, 1989b
	Leaf extract	*Radopholus similis*	Lethal at dilution of 1:5 at 24 hours after incubating the nematodes in the extract.	Jasy and Koshy, 1994
	Preplant cover crop for cotton	*M. incognita*	Suppressed population densities on cotton.	Robinson *et al.*, 1998
	Preplant cover crop for taro	*M. javanica*	Reduced nematode numbers on taro and increased taro corm weight better than continuous taro planting.	Sipes and Arakaki, 1997
	Preplant cover crop for tobacco	*M. javanica*	Suppressed damage by *M. javanica* to tobacco.	Shepherd and Barker, 1993
	Preplant cover crop for pineapple	*R. reniformis*	Reduced nematode population density compared to fallow.	Wang, 2000
	Intercropping with banana	*Helicotylenchus multicinctus*, *Hoplolaimus indicus*, *R. similis*, *R. reniformis*	Reduced the nematode population densities better than carbofuran treatment and increased banana yield.	Charles, 1995

Table 1. (Continued) Examples of positive effects of *Crotalaria* spp. on plant-parasitic nematodes management.

Species	Experimental conditions	Target nematode	Results	References
C. juncea	Crop rotation	*M. incognita*, *M. javanica*	A two-year corn and *C. juncea* rotation in a former sugarcane field reduced the nematode population densities.	Moura, 1991
	Crop rotation	*Meloidogyne* spp., *Pratylechus* spp.	Reduced the resurgence of these nematodes on sugar cane.	Moura, 1995
C. laburnifolia	Host testing	*M. incognita*, *M. javanica*	1 juvenile g^{-1} root recovered after 4 months.	Desaeger and Rao, 1999
C. lanceolata	Host testing	*P. brachyurus*, *P. zea*, *R. reniformis*	No nematode detected.	Silva *et al.*, 1989a, b
C. mucronata	Host testing	*M. incognita*, *M. javanica*	No nematodes recovered after 4 months.	Desaeger and Rao, 1999
	Host testing	*M. incognita* race 3, *M. javanica*	Resistant.	Santos and Ruano, 1987
	Host testing	*Pratylenchus zeae*, *P. brachyurus*	Poor host.	Endo, 1959
	Host testing	*P. brachyurus*, *P. zea*, *R. reniformis*	No nematode detected.	Silva *et al.*, 1989a, b
	Preplant cover crop	*P. brachyurus*	Reduced populations of *P. brachyurus*	Endo, 1959
	Preplant cover crop	*M. incognita*	Reduced the population densities of *M. incognita* below detectable levels in 1 to 3 years. Depends on the initial population density.	Murphy *et al.*, 1974
	Preplant cover crop	*M. incognita*, *P. brachyurus*, *Paratrichodorous christiei*	Combination of 6-week fallow and *C. mucronata* planting reduced these nematode population densities to almost undetectable levels on tomato and improved tomato yield.	Brodie and Murphy, 1975
C. ochroleuca	Host testing	Ectoparasitic nematodes	Effectively reduced nematode numbers	Ochse and Brewton, 1954
	Host testing	*M. incognita*, *M. javanica*	1 juvenile g^{-1} recovered after 4 months.	Desaeger and Rao, 1999
C. pallida	Host testing	*M. incognita*, *M. javanica*	Did not allow nematodes to reproduce.	Gonzaga and Ferraz, 1994
C. paulina	Host testing	*M. incognita*, *M. javanica*	No nematodes recovered after 4 months.	Desaeger and Rao, 1999
	Host testing and amendment effect	*M. incognita*	No egg masses were found on bean plants grown in the same pots after *C. paulina* was cultivated. Soil amendment did not suppress the nematode but enhanced bean growth.	Gonzaga and Ferraz, 1994
	Host testing	*M. incognita*	Life cycle not completed.	Gonzaga and Ferraz, 1994; Peacock, 1957
	Host testing	*M. incognita*, *M. javanica*	No nematodes recovered after 4 months.	Desaeger and Rao, 1999

Table 1. (Continued) Examples of positive effects of *Crotalaria* spp. on plant-parasitic nematodes management.

Species	Experimental conditions	Target nematode	Results	References
C. paulina	Host testing	*M. javanica*	Penetrate the roots but cannot develop into adult 45 days after inoculation.	Silva *et al.*, 1989c
	Host testing	*P. brachyurus*, *P. zea*	No nematode detected.	Silva *et al.*, 1989a
	Host testing	*R. reniformis*	Poor host.	Silva *et al.*, 1989b
	Preplant cover crop followed by bean and corn	Combination of *M. javanica*, *P. brachyurus*, *C. ornata* and *H. dihystera*	Reproductive factors of these nematodes on bean and corn planted after *C. paulina* were lower than those after fallow treatment.	Sharma and Scolari, 1984
C. recta	Host testing	*M. incognita*, *M. javanica*	No nematodes recovered after 4 months.	Desaeger and Rao, 1999
C. retusa	Host testing	Ectoparasitic nematodes	Effectively reduced nematode number.	Ochse and Brewton, 1954
	Host testing	*Meloidogyne* spp.	Resistant to five species of *Meloidogyne*.	Sasser, 1954
	Host testing	*M. javanica*	Penetrated the roots but did not develop to adult 45 days after inoculation.	Silva *et al.*, 1989c
	Host testing	*P. brachyurus*	No nematode detected.	Silva *et al.*, 1989a
	Host testing	*R. reniformis*	Poor host.	Silva *et al.*, 1989b
C. spectabilis	Host testing	*Meloidogyne* spp.	Resistant to five species of *Meloidogyne*.	Sasser, 1954
	Host testing	*M. arenaria*	High resistance and low root galling.	Good *et al.*, 1965; Taylor, 1985
	Host testing	*M. incognita* race 3 and *M. javanica*	Resistant.	Santos and Ruano, 1987
	Host testing	*M. arenaria*, *M. incognita*, *M. javanica*	No galls or egg masses were observed.	McSorley, 1999
	Host testing	*M. incognita*	High degree of resistance and low root galling.	Carneiro and Carneiro, 1982; Good *et al.*, 1965; Reddy *et al.*, 1986; Taylor, 1985
	Host testing	*M. arenaria*	No root gall symptoms.	Rodríguez-Kábana *et al.*, 1992a
	Host testing	*M. incognita*	Fewer nematodes invaded, development was delayed, and fecundity was low.	Anwar *et al.*, 1994
	Host testing	*M. incognita* race 1 and 3, *M. arenaria* race 1, *M. javanica*	No egg masses were observed.	McSorley and Dickson, 1995
	Host testing	*M. javanica*	High degree of resistance and low root galling.	Good *et al.*, 1965; Taylor *et al.*, 1985

Table 1. (Continued) Examples of positive effects of *Crotalaria* spp. on plant-parasitic nematodes management.

Species	Experimental conditions	Target nematode	Results	References
C. spectabilis	Host testing	*M. javanica*	Penetrated the roots but did not develop to adult; smaller giant cells and fewer giant cells per female; giant cells showed granular, dense cytoplasm, with few nuclei; large vacuoles frequently absent.	Silva *et al.*, 1989c; Silva *et al.*, 1990b
	Host testing	*M. javanica*	Few galls and no egg masses.	Martin, 1958
	Host testing	*Radopholus similis*	No reproduction.	Birchfield and Bristline, 1956
	Host testing	*P. brachyurus*, *P. zea*	Low numbers compared to those in sorghum.	Silva *et al.*, 1989a
	Host testing	*R. reniformis*	Poor host.	Silva *et al.*, 1989b
	Crop rotation with okra	*M. incognita*	Almost no *M. incognita* detected in okra roots when *C. spectabilis* was grown for 8 months prior to okra.	Huang *et al.*, 1981
	Preplant to coffee	*M. exigua*	No galls were formed and greatly reduced *M. exigua* numbers in the soil 6 months after planting. No nematodes detected in coffee roots 23 months after planting.	Almeida and Campos, 1991a, b.
	Crop rotation with squash and eggplant in two cropping seasons	*M. arenaria*	Suppressed the nematode only in the short season crop, squash, but still increased eggplant yield compared to peanut rotation.	McSorley *et al.*, 1994b
	Preplant cover crop for tomato	*M. incognita*	Reduced *M. incognita* on carrot; increased carrot yield compared to rotation with tomato.	Huang *et al.*, 1981
	Preplant cover crop for tobacco	*M. javanica*	Suppressed damage of *M. javanica* on tobacco.	Shepherd and Barker, 1993
	Preplant cover crop for snap bean	*Meloidogyne* spp.	Reduced populations of *Meloidogyne* spp. compared to fallowed plots.	Rhoades, 1964
	Preplant cover crop	Combination of *R. reniformis*, *Helicotylenchus* sp., *Pratylenchus* sp.	Reduced nematode population densities in soil.	Navarro, 1968
	Preplant cover crop	*Belonolaimus longicaudatus*, *Paratrichodorus minor*, *Xiphinema americanum*	Reduced nematode population densities in subsequent tomato field, enhanced tomato growth.	Good *et al.*, 1965; Brodie *et al.*, 1970

Table 1. (Continued) Examples of positive effects of *Crotalaria* spp. on plant-parasitic nematodes management.

Species	Experimental conditions	Target nematode	Results	References
C. spectabilis	Interplanted	*Meloidogyne* spp.	Nematodes controlled after *C. spectabilis* was interplanted in peach orchards for 2 years.	McBeth and Taylor, 1944
	Trap crop	*Meloidogyne* spp.	No galls developed.	Rodríguez-Kábana *et al.*, 1992a
	Soil amendment	*M. arenaria*	High degree of resistance.	Good *et al.*, 1965
	Soil amendment	*M. arenaria*	Reduced root galling on squash, nematicidal efficacy of amendments directly correlated with N content of the amendments.	Mian and Rodríguez-Kábana, 1982
	Ground seed amendment	*M. incognita*, *M. javanica*	Mixture at 1% level suppressed nematode reproduction better than non-amended soil. Mixture at 2% level almost completely suppressed nematode egg mass production but phytotoxic to tomato.	Rich and Rahi, 1995
C. striata	Host testing	*M. incognita*	Life cycle not completed.	Peacock, 1957
	Host testing	*M. incognita* race 3 and *M. javanica*	Resistant.	Santos and Ruano, 1987
	Host testing	*H. glycines*	Nematode population levels reduced and fresh weight of soybean increased.	Valle *et al.*, 1995
	Host testing	*P. brachyurus*, *P. zea*	No nematode detected.	Silva *et al.*, 1989a
	Host testing	*R. similis*	No reproduction.	Birchfield and Bristline, 1956
	Host testing	*R. reniformis*	Poor host.	Silva *et al.*, 1989b
C. usaramoensis	Host testing	*M. incognita*	Non-host.	Netcher and Sikora, 1990
C. usaramoensis	Crop rotation with pineapple	*P. brachyurus*	Decreased nematode population densities and improved pineapple yield.	Guérout, 1969
C. vallicola	Host testing	*M. incognita*, *M. javanica*	No nematodes recovered after 4 months.	Desaeger and Rao, 1999

Table 2. Examples of negative or no effects of *Crotalaria* spp. on plant-parasitic nematodes management.

Species	Experimental conditions	Target nematode	Results	References
Crotalaria sp.	Intercrop	*Pratylenchus brachyurus*	Control *Meloidogyne* spp. but increased *P. brachyurus* to damaging level on pineapple in Ivory Coast.	Luc *et al.*, 1993
C. agatiflora	Host testing	*Helicotylenchus* sp., *Scutellonema* sp.	As susceptible as maize.	Desaeger and Rao, 2001
	Preplant cover crop for maize	*Pratylenchus zeae*	Increased population densities of *P. zeae* to a level that can limit growth of maize.	Desaeger and Rao, 2000
C. grahamiana	Host testing	*Helicotylenchus* sp., *Scutellonema* sp.	As susceptible as maize.	Desaeger and Rao, 2001
	Host testing	*P. zeae, P. brachyurus*	As susceptible as maize.	Desaeger and Rao, 2001
	Host testing	*Trichodoridae*	5000 nematodes L^{-1} soil after 4 months.	Desaeger and Rao, 1999
C. incana	Host testing	*P. zeae, P. brachyurus*	As susceptible as maize.	Desaeger and Rao, 2001
C. juncea	Host testing	*M. arenaria* subsp. *thamesi, M. hapla, M. incognita* var *acrita, M. javanica*	These nematodes from South Africa were found penetrating and reproducing in roots. Data were not quantified.	Van der Linde, 1956
	Host testing	*M. hapla*	Roots almost totally galled, but few egg masses found.	Martin, 1958
	Host testing	*M. incognita* var. *acrita, M. javanica*	Galls visible.	Martin, 1958
	Host testing	*Radopholus similis*	Nematode numbers recovered not different from that in a standard host, *Sorghum bicolor.*	Inomoto, 1994
	Preplant cover crop	*Pratylenchus sefaensis*	Not effective against *P. sefaensis.*	Wilson and Caveness, 1980
C. laburnifolia	Host testing	*P. zeae, P. brachyurus*	As susceptible as maize.	Desaeger and Rao, 2001
C. mucronata	Preplant cover crop	*P. brachyurus, X. americanum*	Increased nematode population densities.	Murphy *et al.*, 1974
C. ochroleuca	Host testing	*M. incognita* var. *acrita*	Galls readily found.	Martin, 1958
	Host testing	*M. hapla*	Roots almost totally galled but no egg masses found.	Martin, 1958
	Host testing	*P. zeae and P. brachyurus*	As susceptible as maize.	Desaeger and Rao, 2001
	Preplant cover crop in microplot	*Meloidogyne* spp.	Not effective for nematode control.	Ijani *et al.*, 2000
	Host testing	*Trichodoridae*	5000 nematodes L^{-1} soil after 4 months.	Desaeger and Rao, 1999
C. paulina	Host testing	*P. zeae, P. brachyurus*	As susceptible as maize.	Desaeger and Rao, 2001

Table 2. (Continued) Examples of negative or no effects of *Crotalaria* spp. on plant-parasitic nematodes management.

Species	Experimental conditions	Target nematode	Results	References
C. pancira	Preplant cover crop in microplot	*M. incognita*	Did not reduce the nematode population densities sufficiently to protect following tomato crop.	Buente and Mueller, 1997
C. retusa	Host testing	*P. zeae*	Good host.	Jordaan and Waele, 1989
C. sphaerocarpa	Host testing	*M. hapla*	Not resistant to *M. hapla*, heavy root galling, sausage-shaped larvae found.	Good *et al.*, 1965
C. spectabilis	Crop rotation with okra	*H. dihystera*	Planted *C. spectabilis* for 8 months prior to okra, with no effect on *H. dihystera.*	Huang *et al.*, 1981
	Preplant cover crop	*Pratylenchus* spp.	Supported high population densities of *Pratylenchus* spp.	Robinson *et al.*, 1998
	Crop rotation with tomato	*Meloidogyne incognita* and *M. javanica*	Did not reduce *Meloidogyne* spp. sufficiently to meet USA certification regulation after 4 years of *Crotalaria*-tomato rotation.	Johnson and Campbell, 1980
	Intercrop with coffee	*M. javanica*	Did not reduce nematode infection on coffee sufficiently and did not improve coffee yield.	Jaehn and Rebel, 1984
	Crop rotation with tomato	*Criconemella* spp., *Paratrichodorus minor, P. brachyurus, P. zeae*	Supported large numbers of these nematodes after 4 years of *Crotalaria*-tomato cropping sequence.	Johnson and Campbell, 1980
	Intercrop with peach	*Criconemella xenoplax*	No effect.	Whittington and Zehr, 1992
C. striata	Host testing	*Helicotylenchus* sp., *Scutellonema* sp.	As susceptible as maize.	Desaeger and Rao, 2001
	Host testing	*P. zeae* and *P. brachyurus*	As susceptible as maize.	Desaeger and Rao, 2001

monly found in temperate regions. However, in South Africa, *C. spectabilis* allowed *M. hapla* penetration but not reproduction (van der Linde, 1956). Even though *C. spectabilis* suppressed most *Meloidogyne* spp., it did not reduce *M. incognita* and *M. javanica* population densities sufficiently to meet USA certification regulation after 4 years of *Crotalaria*-tomato rotation (Johnson and Campbell, 1980). However, *C. spectabilis*, as a preplant cover crop in Florida, suppressed *R. similis* successfully (Birchfield and Bistline, 1956). Duration of planting and field history might affect *Crotalaria* performance. For instance, 1 or 2 years of *C. mucronata* in land previously cropped to native pasture or okra, respectively, were required to achieve suppression of *M. incognita* population densities below detectable levels (Murphy *et al.*, 1974). Duration of crop growth after soil incorporation of *C. spectabilis* also influenced nematode control. Reduction of numbers of *M. arenaria* was adequate for squash but not eggplant which is a longer-term crop planted after *C. spectabilis* (McSorley *et al.*, 1994b). Nevertheless, *C. spectabilis* still increased eggplant fruit weight compared to that following peanut. The effect of *C. juncea* on *Radopholus similis* varied and may be related to the method of cover crop application (Inomoto, 1994; Jasy and Koshy, 1994). When *C. juncea* was applied as a preplant cover crop without soil incorporation, it failed to suppress *R. similis* (Inomoto, 1994), but was effective when its leaf extract was tested against the nematode (Jasy and Koshy, 1994). In another case, population densities of *P. brachyurus* increased considerably on *M. mucronata* after 3 years, but was not detectable if soil was fallow for 6 weeks prior to *C. mucronata* planting (Brodie and Murphy, 1975).

Intercropping: Intercropping refers to spatially mixed plantings of species in a field, usually by planting a row of one species next to the row of another. There has been little research on nematode populations when intercropping *Crotalaria* with cash crops. Successful examples of using *Crotalaria* as an intercrop against plant-parasitic nematodes were reported for peach and banana orchards (McBeth and Taylor, 1944; Charles, 1995). However, *Crotalaria* intercropped with peach had no effect on *Mesocriconema* spp. (Whittington and Zehr, 1992) and *C. spectabilis* intercropped with coffee did not suppress *M. incognita* (Jaehn and Rebel, 1984). This practice is constrained by the competition in growth between the cash crops and cover crops. Desaeger and Rao (2001) proposed to intercrop *C. grahamiana* with other leguminous cover crops such as *Sesbania sesban* and *Tephrosia vogelii* as these latter legumes are good hosts to *Meloidogyne* but poor hosts to *Pratylenchus* and *Helicotylenchus*. They found that intercropping *S. sesban* and *T. vogelii* with *Crotalaria* did not reduce the numbers of the vermiform stage of *Meloidogyne* but did reduce nematode egg mass production as compared to broadcast cropping of *S. sesban* and *T. vogelii* individually (Desaeger, 2001). However, intercropping with *C. grahamiana* resulted in higher *P. zeae* population densities than in cropping *S. sesban* and *T. vogelii* alone (Desaeger, 2001).

Wang (2000) intercropped *C. juncea* with pineapple and then alternated the *C. juncea* and pineapple planting bed in the next cropping cycle. This cropping system is similar to using *Crotalaria* as a preplant cover crop for pineapple except that *Crotalaria* was planted for a longer period of time. When pineapple was planted into the previously *C. juncea*-intercropped plots, *R. reniformis* population densities, egg production and mobility were lower than that in the previously weedy fallow plots (Wang, 2000). After one *C. juncea*-pineapple intercropping cycle (23 months), *C. juncea* enhanced bacterivorous nematode popula-

tion densities and nematode-trapping fungal propagules compared to weedy fallow or pineapple beds (Wang, 2000), indicating that microbial activities against *R. reniformis* may have been enhanced.

Soil Amendment: Incorporating biomass can play an important role in nematode suppression. Most *Crotalaria* preplant cover crops were followed by soil incorporation of the biomass and subsequent reduction of plant-parasitic nematode numbers. However, incorporation of *C. paulina* biomass did not suppress *M. incognita* better than allowing the biomass to remain on top of the ground as mulch (Gonzaga and Ferraz, 1994). Rich and Rahi (1995) found that soil amended with *C. spectabilis* seeds suppressed *M. incognita* and *M. javanica* better than non-amended soil.

MECHANISMS OF NEMATODE SUPPRESSION

Cover crops such as *Crotalaria* reduce plant-parasitic nematode populations by: 1) acting as a nonhost or a poor host (Rodríguez-Kábana *et al.*, 1988, 1989, 1990, 1992b, 1994), 2) producing allelochemicals that are toxic or inhibitory (Haroon and G. C. Smart, 1983; Gommers and Bakker, 1988; A Halbrendt, 1996), 3) providing a niche for antagonistic flora and fauna (Linford, 1937; Evans *et al.*, 1988; Caswell *et al.*, 1990; Kloepper *et al.*, 1991), and 4) trapping the nematode (Gallaher *et al.*, 1991; Gardner and Caswell-Chen, 1994; LaMondia, 1996).

Poor or Non-host Effects: A non-host to a nematode species is a plant in which the nematode fails to reproduce (Trudgill, 1991). Seinhorst (1967) defined a poor host as having low a and M in the population increase equation, $P_f = M(1\text{-}e^{-a})$, where Pf is the final population, M is the maximum nematode population, a is the maximum multiplication rate, e is the natural logarithm (=2.1416). The criteria for host plant resistance are 1) failure of the nematode to live inside the host or early nematode death in the host, 2) decreased production of eggs, or 3) inhibition of nematode growth or development.

The mode of resistance in *Crotalaria* against different nematodes varies among plant and nematode species. *Meloidogyne javanica* is less attracted to *C. spectabilis* roots as compare to tomato roots (Silva *et al.*, 1989c). The life cycle of *M. incognita* was not completed in the roots of *C. striata* and *C. retusa* (Peacock, 1957). Development of *M. arenaria*, *M. incognita*, and *M. javanica* in the roots of *C. spectabilis* was arrested at the sausage-shaped late J_2 stage (Good *et al.*, 1965). Although the *Meloidogyne* spp. juveniles were able to penetrate the roots of *C. spectabilis*, *C. juncea*, *C. retusa* and *C. paulina*, none of them become adults within 45 days after inoculation (Silva *et al.*, 1989c). In other studies nematodes developed but produced few eggs (Rich and Rahi, 1995; McSorley, 1999). Giant cells of *C. spectabilis* and *C. juncea* induced by *M. javanica* were granular, had dense cytoplasm, few nuclei, lacked large vacuoles, and were smaller and fewer compared to those in tomato roots (Silva *et al.*, 1990b). Penetration of *M. javanica* into roots of *C. juncea* was suppressed (Araya and Caswell-Chen, 1994b). Although *C. juncea* supports *M. javanica* reproduction to some extent, galls did not develop (Araya and Caswell-Chen, 1994a). However, this effect can vary among nematode populations and species. One population of *M. javanica* from South Africa penetrated and reproduced on *C. juncea*, whereas only 5 out of 9 populations of *M. incognita* var. *acrita* penetrated and reproduced on *C. juncea* (van der Linde, 1956). Crotalaria juncea allowed *R. reniformis* infection but the nematode did not develop (Silva *et al.*, 1990b) or reproduce (Caswell *et al.*, 1991). How-

ever, when the observation time was prolonged, *R. reniformis* developed to female and eggs were produced, but at a slower rate than on a good host, cowpea (Wang, 2000a).

Allelopathic Effects: Allelopathy was originally designated for plant-plant and plant-microorganism biochemical interactions (Rice, 1984). Secondary plant metabolites are suspected as the allelopathic compound against nematodes. Several plant allelochemicals have effectively suppressed phytopathogens, including nematodes, with minimal environmental impact (Soler-Serratosa *et al.*, 1996).

Crotalaria spp. produce pyrrolizidine alkaloids and monocrotaline which have high vertebrate toxicity and could potentially be toxic to nematodes (Rich and Rahi, 1995). Upon exposure of root-knot nematode juveniles to monocrotaline solutions, their bodies began to jerk (Fassuliotis and Skucas, 1969). Infectivity of treated nematodes is therefore reduced. *Crotalaria juncea* leaf extract was lethal to *R. similis* at dilutions of 1:5 within 24 hours (Jasy and Koshy, 1994). *Crotalaria juncea* leaf leachate essentially stopped movement of *R. reniformis* (Wang, 2000a). However, Fassuliotis and Skucas (1969) did not find a relationship between the pyrrolizidine-containing plants and root-knot nematode resistance.

It is possible that the low C/N ratio of *Crotalaria* may also contribute to its allelopathic effect against nematodes (Fassuliotis and Skucas, 1969; Rich and Rahi, 1995). The nematicidal efficacy of *C. spectabilis* used as a soil amendment was related to the nitrogen content of the amendment (Mian and Rodríguez-Kábana, 1982). Materials with very low C/N or high content of ammonia will either result in plasmolysis of nematodes, or proliferation of nematophagous fungi due to the release of NH4+-N (Rodríguez-Kábana, 1986). Some of the nitrogenous amendments contain chitin. When added to the soil, enhanced soil chitinase activities could result in distortion of the chitin layer of the nematode eggshell (Rodríguez-Kábana, 1986). Mechanisms involved in the action of low C/N ratio remain complex.

Enhancement of Nematode Antagonistists: Nematode antagonist is a general term for parasites, predators, pathogens, competitors, and other organisms that repel, inhibit, or kill plant-parasitic nematodes. Antagonists, most likely favored by selected cover crops, include fungal egg parasites, trapping fungi, endoparasitic fungi, fungal parasites of females, endomycorrhizal fungi, plant-health promoting rhizobacteria, and obligate bacterial parasites (Sikora, 1992). Other antagonists including mites, collembola, tardigrades, oligochaetes, predatory nematodes, turbellarians, and protozoans that reduce nematode population densities are seldom discussed because data relevant to their management are insufficient (Sikora, 1992). For practical plant-parasitic nematode control to be successful in agricultural soils, the antagonists need the ability to proliferate under intensive farming practices (Morgan-Jones and Rodríguez-Kábana, 1987).

There are several hypotheses on how cover crops can enhance nematode-antagonistic activities. Linford (1937) speculated that incorporation of organic matter provides an environment that favors population growth and activities of nematophagous fungi. A series of ecological events may be involved. The decomposing organic material is a significant event because the bacteria which proliferate after organic matter incorporation become a food base for microbiovorous nematodes. In turn, these nematodes serve as a food source for nematophagous fungi (van den Boogert *et al.*, 1994b). For example, incorporation of *C. juncea* enhanced *Acrobeloides bodenhei-*

meri, one of the most susceptible bacterivorous nematodes to parasitism by *Hirsutella rhossiliensis* (a nematode-endoparasitic fungus) (Venette *et al.*, 1997).

Mycostasis, the inability of fungal spores to germinate in natural soils when temperature and moisture condition are favorable for germination, may also be involved in the enhancement of nematode antagonistic fungi following the incorporation of organic matter (Stirling, 1991). Nematode-trapping fungal activity is enhanced when N is limiting (Barron, 1982). During the early stages of incorporation of organic matter into the soil, the C/N ratio increases. This high C concentration may aid spore germination (Ko and Lockwood, 1967).

Leguminous crops enhance nematophagous fungi better than other crops. Root-knot symptoms were reduced more by alfalfa amendments in a 4-year microplot test than by chemical fertilization of plots (Mankau, 1968). *Meloidogyne incognita* was suppressed in soil amended with alfalfa inoculated with *Arthrobotrys conoides* (Al-Hazmi *et al.*, 1982). Microplots amended with alfalfa meal increased nematode-trapping fungal activity of two efficient nematode-trapping fungal species, *A. dactyloides* and *Dactylellina ellipsospora* (van den Boogert *et al.*, 1994a). Pea enhanced the densities and species diversity of nematode-trapping fungi more than white mustard or barley (Persmark and Jansson, 1997). In addition, formation of conidial traps of nematode-trapping fungi was more prevalent in the pea rhizosphere than in root-free soil (Persmark and Nordbring-Hertz, 1997).

Being a legume, *Crotalaria juncea* has characteristics that may make the crop useful for nematode antagonism. For example, *C. juncea* has soil enzymatic activity correlated with microbial activity and suppressiveness to soil borne plant pathogens (Quiroga-Madrigal *et al.*, 1999). Plant exudates from *Crotalaria* spp. were selective for microbial species antagonistic to phytopathogenic fungi and nematodes (Rodríguez-Kábana and Klopper, 1998).

Nematode-trapping fungi are a major group of nematode antagonists that can be enhanced by incorporation of residues of *C. juncea* (Wang, 2000). These fungi have been categorized into two groups: parasitic and saprophytic (Cooke, 1963). The saprophytic group consists of predators characterized by sticky three-dimensional networks and non-spontaneous trap formation. These fungi have a saprophytic and a predatory (trap formation) phase. In the presence of nematodes, or even exudates and homogenates of nematodes, trap formation is induced (Nordbring-Hertz, 1973). The parasitic group consists of nematode-trapping fungi that form constricting rings, adhesive knobs, or adhesive branches. These fungi form traps spontaneously, and thus are more effective trappers. Among these two groups of nematode-trapping fungi, the population densities of parasitic fungi are more likely to be enhanced by organic matter due to the rich microbial flora and fauna (Gray, 1983). The nematode trapping by these fungi are not nematode species- or trophic group-specific, therefore the enhancement of nematode-trapping fungi by organic matter incorporation should lead to increased trapping of plant-parasitic nematodes (Jansson and Nordbring-Hertz, 1980).

Soil amended with *C. juncea* to give a 1:100 (w:w) concentration, enhanced parasitic nematode-trapping fungi, nematode egg parasitic fungi, vermiform stage parasites, and bacterivorous nematode population densities more efficiently than soil amended with chopped pineapple tissues or non-amended soil (Wang, 2000). *Crotalaria juncea* amendment enhanced the population densities of nematode-trapping fungi and the percentage of eggs parasit-

ized by the fungi. Enhancement of nematode-trapping fungi was most effective in soils that had not been treated with 1,3-dichloropropene for at least 5 months (Wang, 2000). Suppression of *R. reniformis* by *C. juncea* amendment was correlated with parasitic nematode-trapping fungi, fungal egg parasites, and bacterivorous nematodes (Wang, 2000). Nematode-trapping fungi population densities were higher in *C. juncea* planted plots than weed fallow plots (Wang, 2000). However, four months after removal of *C. juncea*, and replacement with pineapple plants, the population densities of nematode-trapping fungi greatly decreased (Wang, 2000b).

PROSPECTS

Nematode management is rarely successful in the long term with unitactic approaches. It is important to integrate multiple-tactics into a strategy. *Crotalaria* offers the potential to be one of the tactics. Some *Crotalaria* species are potential cover crops for managing several important plant-parasitic nematodes including *Meloidogyne* spp. and *R. reniformis*. Unfortunately, the residual effects are short term (a few months). *Crotalaria*, a poor host, generally helps reduce nematode population densities, but the number of nematodes will resurge on subsequent host crops. The damage threshold level, especially on longer-term crops, will often be reached or exceeded (McSorley *et al.*, 1994b). This scenario strongly suggests that integrating the *Crotalaria* rotation system with other nematode management strategies is necessary. Among the possibilities for integration are crop resistance, enhanced crop tolerance, selection for fast growing crop varieties, soil solarization, and biological control.

Solarization of soil amended with *Crotalaria* tissues may enhance nematode control over either tactic alone. Pyrrolizidine alkaloids and monocrotaline are released from *Crotalaria* tissues upon decomposition (Rich and Rahi, 1995). Soil solarization could enhance the "biofumigation" process. Nematodes will be affected by the sublethal heat in conjunction with the nematicidal effects from *Crotalaria*.

Chemical nematicides should be avoided in a cropping system if the objective is to enhance nematode-antagonistic microorganisms in the cropping system. Several studies have demonstrated the destructive effect of fumigation treatments to nematode antagonistic microorganisms. For example, formaldehyde treatment increased the multiplication of *Heterodera avenae* as compared to non-fumigated nematode-suppressive soil after the chemical degenerated in Rothamstead (Kerry *et al.*, 1995). Preplant treatment with metam sodium, methyl bromide, methyl iodide, or formaldehyde reduced suppressiveness of soil against *H. schachtii* (Westphal and Becker, 1999). *Crotalaria juncea* amendments failed to enhance nematode-trapping fungi populations in soils that were recently treated with 1,3-dichloropropane (Wang, 2000).

We hypothesize that intercropping *Crotalaria* with a longer term cash crop will allow the nematode-antagonisitc microorganisms associated with *Crotalaria* to establish after one cycle of the cash crop. Previous research had demonstrated that *C. juncea* could enhance nematode-trapping fungi activities in the rhizosphere (Wang, 2000). However, development of microbial populations to a density needed to control nematodes has occurred only under perennial crops or those grown in monocultures (Kerry, 1987). Prolonged culture of *Crotalaria* in an intercropping system enhanced the nematode suppressive effect in both peach (McBeth and Taylor, 1944) and pineapple systems (Wang, 2000).

Another approach worth exploring is the search for biocontrol agents compati-

ble with *Crotalaria* cropping systems. Introduction of biocontrol agents to manage plant-parasitic nematode has met with limited success in the field (Stirling, 1991). This might be due to microbiostasis properties of the soil (Ho and Ko, 1986) and the legume rhizosphere may overcome fungistasis against the nematode-trapping fungi better than that of root-free soil (Persmark and Nordbring-Hertz, 1997). Although several attempts have failed to enhance some nematophagous fungi by *Crotalaria* (Venette *et al.*, 1997), *in situ* nematode-antagonistic microorganisms associated with the *Crotalaria* rhizosphere and *Crotalaria* amended soils have not been studied in depth. Such research might improve the prospect of prolonging the nematode suppressive effect of *Crotalaria* cropping systems.

In summary, *Crotalaria*, besides being an efficient green manure, is a poor host to many important plant-parasitic nematodes, producing allelopathic compound toxic to nematodes, and is able to enhance some nematode-antagonisitc microorganisms. Therefore using *Crotalaria* as a cover crop may offer alternatives to nematicides. Integrating the use of *Crotalaria* with other pest management strategies offers promise for the development of new sustainable agricultural cropping systems.

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