

## ABSTRACT

Title of Document: **SOIL NEMATODE COMMUNITIES AS INFLUENCED BY COVER CROPS, WITH A FOCUS ON BRASSICACEAE**

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The effect of brassicaceous cover crops (*Brassica juncea*/*Sinapis alba*, *B. napus*, and *Raphanus sativus*) on plant-parasitic and free-living soil nematode communities, in grain agroecosystems, was evaluated in three experiments, at two sites in Maryland. Brassicaceous cover crops alone did not suppress plant-parasitic nematodes, however when combined with rye (*Secale cereale*) or clover (*Trifolium incarnatum*), juvenile (J2) *Heterodera glycines* populations were lower in June, soybean yields were higher, or free-living nematode abundance was higher. Indices of free-living nematode community structure suggested that winter-kill of N-rich radishes activated the bacterivore community in early spring resulting in high populations of bacterivore dauer larvae and high community structure by summer. In contrast, nematode communities in spring-terminated rapeseed and rye plots had high abundances of fungivore nematodes and a plant associate/fungal feeder, *Coslenchus*. Brassicaceous cover crops in Maryland grain rotations may be more useful for managing soil ecology than for biofumigation of plant-parasitic nematodes.

SOIL NEMATODE COMMUNITIES AS INFLUENCED BY COVER CROPS,  
WITH A FOCUS ON BRASSICACEAE

By

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## **DEDICATION**

To all those who love the living soil.

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## CHAPTER I -- INTRODUCTION

### 1. Background and Problem Definition

Nematodes, being the most abundant multi-cellular organisms on the planet and with 15,000 species identified and estimates of 500,000 species extant (Poinar, 1983), are important contributors to agroecosystems. Of the eight feeding groups identified in terrestrial nematode communities--plant feeding, fungal feeding, bacterial feeding, substrate feeders, predators, eukaryote feeders, animal parasites, and omnivores (Yeates et al., 1993)--the plant-parasitic nematodes have received the most attention in terrestrial systems due to their direct economic impact on agriculture. Soybean cyst nematode, *Heterodera glycines*, is a major pest of soybeans, and affects about 40,500 ha of soybean on Maryland's eastern shore (W. Kenworthy, personal communication, 2002). *H. glycines* remains the leading cause of soybean yield loss in the United States (Wrather and Koenning, 2006). *Meloidogyne* (root-knot), *Pratylenchus* (lesion), *Tylenchorhynchus* (stunt), *Trichodorus* (stubby root), *Xiphinema* (dagger), and *Hoplolaimus* (lance) nematodes are also problematic for Maryland farmers and nursery growers (Kratochvil et al., 2003; S. Sardanelli, personal communication, 2003; Sindermann et al., 1993).

Incorporation of allelopathic cover crops is one of many ecological management tools that have come into use in the last thirty years, as chemical nematicides, high costs, and increased rates of biodegradation have narrowed options for chemical control of plant-parasitic nematodes (Halbrendt and LaMondia, 2004; Kratochvil et al., 2004; Matthiessen and Kirkegaard, 2006). Glucosinolate-containing brassicaceous cover crops

have long been studied in the laboratory for nematode suppression (Chitwood, 2002), and field research in Maryland, Pennsylvania and West Virginia showed that rapeseed (*Brassica napus*) was effective in suppressing re-plant disease in peach orchards (*Prunus* sp.) associated with the virus vector *Xiphinema* (Halbrendt, 1992). Biofumigation was first coined by J. A. Kirkegaard in the context of simulating chemical fumigation (metam sodium) with naturally derived compounds in brassicaceous cover crops (Matthiessen and Kirkegaard, 2006). However, it has since been loosely adopted to describe a pest suppressive effect that may be the result of a number of processes occurring after biomass incorporation. Organic matter addition to soil, feeds soil organisms, and pest suppressive services can be an effect of food web interactions (Watt et al., 2006; Sánchez-Moreno and Ferris, 2007). A number of indices available today enable use of nematode community analysis to interpret soil food web conditions as either fertile, stressed (by pollution), or structured (Bongers, 1990; Ettema and Bongers, 1993; Ferris et al., 2001). Indices have been used to interpret nematode community recovery after chemical fumigation (Yeates and van der Meulen, 1996), but there is little evidence in the literature of using nematode communities as indicators of biofumigation. Rather, interest has been focused on managing the soil food web via timed application of cover crops or management practices, like irrigation, to improve biological sources of fertility in synchrony with crop demands (Ferris et al., 2004; Wang et al., 2004).

## **2. Justification for Research**

Brassicaceous cover crops have several characteristics that make them particularly worthy of further investigation for plant-parasitic nematode control in

Maryland. Upon enzymatic hydrolysis of glucosinolates in brassicaceous tissue, toxic byproducts are released and have been shown to suppress weed seed germination (Brown and Morra, 1996; Vaughn and Boydston, 1997; Weil and Kremen, 2007), fungal pathogens (Smolinska et al., 2003) and nematodes (Akhtar and Mahmood, 1994; Halbrecht, 1996; Mojtahedi et al., 1991; Zasada and Ferris, 2003, 2004). Opportunities for biofumigation may be reduced in Maryland because no-till management predominates in grain rotations, precluding the normally recommended maceration and soil incorporation of cover crop tissue. However, winter-freeze of cover crops may provide total tissue rupture and enhance chemical reaction rates (Morra and Kirkegaard, 2002). The use of volatile winter cover crop decomposition products to directly suppress plant-parasitic nematodes, when the nematodes are less active in winter, may be transient, and additional mechanisms for suppression may be needed to maintain control during the cash crop season. Total nematode community analysis can aid in identifying other bio-mediated mechanisms of suppression.

Despite monetary incentives (\$30 to \$50/acre) in Maryland for cover crops planted before November 5, cover crop adoption in the state has been slow and limited almost exclusively to rye or winter grains. Cover crops with multiple benefits, including nematode suppression, may gain more rapid adoption. Other attributes of the brassicaceous cover crops, unrelated to allelopathy, include rapid establishment in fall, capacity to take up well over 150 kg/ha potentially leachable N in fall (Dean, 2006), rapid N mineralization in spring (Kremen, 2006), potential for soil macroporosity and compaction alleviation (Williams and Weil, 2004, Chen and Weil unpublished), very large phosphorous uptake and release (White and Weil, unpublished data), easy seed-bed

planting in spring (winter-kill types only) and coincidence of seasonal growth with periods of fallow in Maryland.

### **3. General Research Approach**

The research was conducted on two University of Maryland research stations, the Lower Eastern Shore Research and Education Center (LESREC) in Salisbury, MD and the Central Maryland Research and Education Center (CMREC) in Beltsville, MD from August 2003 through October 2005. These sites were chosen for their sandy soils which are often associated with infestations of plant-parasitic nematodes. One experiment was conducted for two years, and two experiments were conducted for a single year. Cover crop treatments were planted in August 2003 followed by soybean cash crops in spring 2004. In fall 2004, cover crops were broadcast seeded into standing soybeans for one experiment, while other experiments were initiated in fall 2004 by planting cover crops into prepared fields in late August. Corn or soybeans were planted in spring 2005 and were harvested in fall.

All plots were sampled for nematodes in the summer (June) and fall (August/September) after winter cover crop termination, in each experiment. Selected treatments from two experiments were also sampled in November and April. Nematodes were isolated using a modified Baermann extraction technique (Christie and Perry, 1951). Plant-parasitic nematode genera or families were enumerated for all dates, while total community analysis was conducted on selected treatments and dates. Genera and trophic group abundances were analyzed by date and tested for cover crop treatment effects. Community indices were used to interpret cover crop effects on soil ecology and when



available, data on soil or cover crop attributes were used to enhance community index interpretation. Bulk density and soil moisture were measured on every sample from which nematodes were extracted. Other soil properties were measured on selected samples or plots, including sand size distribution.

#### **4. General Research Objectives and Hypotheses**

The overall objective of this research was to evaluate the response of nematodes to cover crops, with emphasis on the brassicaceae family. The following hypotheses were tested:

1. Brassicaceous winter cover crops suppress plant-parasitic nematode populations.
2. Brassicaceous winter cover crops in combination with rye or clover suppress plant-parasitic nematodes.
3. Brassicaceous winter cover crops do not suppress free-living nematodes.
4. Brassicaceous winter cover crops or combinations thereof with rye and clover increase cash crop yields.
5. Different cover crop species affect nematode community indices differentially.

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## CHAPTER II – LITERATURE REVIEW

### 1. Plant-Parasitic Nematode Control

#### 1.1. Introduction to plant-parasitic nematode management

Plant-parasitic nematodes continue to cause major yield losses, despite decades of research on their control. *Heterodera glycines* (soybean cyst nematode), for example, remains the leading cause for soybean yield loss in the United States (Wrather and Koenning, 2006). In Maryland, soybean yield loss in 2003-2005 was estimated at 27.7 x 10<sup>3</sup> tonnes (Wrather and Koenning, 2006). Nematodes such as *Meloidogyne* (root-knot), *Pratylenchus* (lesion), *Tylenchorhynchus* (stunt), *Trichodorus* and *Paratrichodorus* (stubby root), *Xiphinema* (dagger), and *Hoplolaimus* (lance), *Helicotylenchus* (spiral) are other major plant-parasitic nematodes in Maryland, which have variable and often unknown yield impacts on grain, turf, fruit, nursery, and vegetable crops (Kratochvil et al., 2004; S. Sardanelli, personal communication, 2003; Sindermann et al., 1993).

In the last 20 years, suppression of plant-parasitic nematodes using ecological practices has received more attention. This is attributed to increased restrictions on nematicides, environmental and health concerns, increased microbial adaptation to chemicals (faster degradation), and increased evidence of the important role of biological diversity in nematode control (Cohen et al., 2005; Halbrecht and LaMondia, 2004; Lavelle et al., 2004). Today, integrated pest management advocates use of a cadre of practices to manage and prevent plant-parasitic nematode outbreaks, including practices such as rotation of cash crops, rotation of resistant cultivars, rotation into fallow, rotation

into non-host or trap cover crops, incorporation of allelopathic green manures, sanitation of equipment, and adjustment of planting dates (Halbrendt and LaMondia, 2004; Kratochvil et al., 2004; Wang et al., 2006). This review will focus on the use of brassicaceous cover crops as non-host cover crops, trap crops, and allelopathic green manures, with emphasis on species used in this study.

### *1.2. Mechanisms of control with brassicaceous cover crops*

Brassicaceous cover crops are well known for their potential in biocontrol via the glucosinolate compounds found in their tissues. Glucosinolates alone have not been shown to be toxic to organisms; it is the degradation products resulting from a reaction of glucosinolates with an enzyme, such as myrosinase or thioglucosidase, which are toxic (Donkin et al., 1995; Jing and Halbrendt, 1994). These hydrolysis products may include isothiocyanates (ITCs), thiocyanates, nitriles, and oxazolidine-2-thiones, though ITCs are considered the most toxic (Brown et al., 1991). Glucosinolate degradation products have been shown to suppress weed seed germination (Brown and Morra, 1996; Vaughn and Boydston, 1997; Weil and Kremen, 2007), fungal pathogens (Abawi and Widmer, 2000; Smolinska et al, 2003), and plant-parasitic nematodes (Akhtar and Mahmood, 1994; Halbrendt, 1996; Mojtahedi et al., 1991; Zasada and Ferris, 2003, 2004).

Glucosinolates are found in different physiological parts of plants and can vary in quantity based on environmental conditions (Agerbirk et al., 2001; Charron et al., 2004; Ciska et al., 2000). The concentrations and types of glucosinolates in root and shoot tissue may be influenced by grazing (Smith et al., 1991), attack by insects (Birch et al., 1990), plant maturity (Feeny and Rosenberry, 1982), and planting season (Lazzeri et al.,

2003). Gardiner et al. (1999) found higher concentrations of glucosinolate-degradation products from roots than shoot, despite accounting for only 25% of the plant biomass. They proposed that the prolonged release of hydrolysis products from the roots could contribute to the potential effectiveness of rapeseed (*Brassica napus* 'Humus' and 'Dwarf Essex') as a soil fumigant. In a greenhouse pot study root leachate, obtained by collecting water draining from pots with living rapeseed 'Dwarf Essex' plants, did not reduce the survival or egg hatching of *Rotylenchus reniformis* more than the control (Wang et al., 2001). Early studies, in petri dishes, pots, and the field, found that mustard root extracts or oil expressed from mustard (*B. nigra* or *Sinapis alba*) seed reduced hatch of *Globodera rostochiensis* (then thought to be *Heterodera*) and in the field increased potato yields (Ellenby, 1945; Ellenby, 1951). These results suggest variable mechanisms of nematode suppression from extracts of the living root. Few studies have macerated root material alone for evaluation of its effects on nematodes. Results from evaluation of 20 different brassicaceous varieties suggested that aboveground biomass was more toxic than belowground biomass and this toxicity increased with plant age, until senescence; seed extracts were the most toxic (Halbrendt, 1992).

The effectiveness of ITCs and other degradation products as biofumigants is dependent on many cultural factors, including the manner and environment in which the tissue is disrupted. It is recommended that tissues be macerated, incorporated, and irrigated so as to maximize the quantity and depth of soil matrix fumigation (Matthiessen et al., 2004). Options are limited for biofumigation in no-till agriculture, unless tissue is ruptured by freezing and thawing. Morra and Kierkegaard (2002) found high levels of ITC in soil (100 nmol/g soil) after freeze-thaw of mustard biomass. However, Price et al.

(2005) observed 81% less allyl-ITC production under cold conditions (15°C) compared to warm (45°C) when mustard was incorporated into soil.

The need for irrigation after incorporation is related to the volatile nature of the compounds in the soil. Gardiner et al. (1999) estimated that rapeseed degradation products remain in the soil for roughly three days. Brown et al. (1991) observed maximum isothiocyanate production within two hours of amending the soil and a 90% decrease within 24 hours, in bioassays using 30 g defatted rapeseed meal/kg soil. The volatile nature of degradation products may imply that suppression of plant-parasitic nematodes cannot be maintained over the length of the entire growing season, or that nematodes deeper in the soil may be unaffected. Research in Oregon on root-knot nematode, *M. incognita*, in potato production systems, suggests that mustard and oilseed radish may be effective in short-term suppression, but that complementary small doses of nematicide are required for full-season suppression (R. Ingham, personal communication, 2003).

The effectiveness of brassica cover crops as biofumigants is also largely dependent on the quantity of biomass grown. Commercial methyl isothiocyanates fumigants are applied at rates ranging from 517 to 1294 nmol per gram of soil (Brown et al., 1991), while incorporation of rapeseed as observed by Gardiner et al. (1999) would produce 30 nmol of isothiocyanate per gram of soil under the same hypothetical soil conditions. However, after conducting assays with commercial glucosinolate products on the nematode *M. javanica* to determine lethal concentrations, Zasada and Ferris (2003) estimate that 24 dry tons/ha of rapeseed material would be required to have effective biofumigation and is realistic in California. Other climates and producer reluctance to

fertilize cover crops may mean that brassica cover crops have less biofumigation potential in those regions.

### *1.3. Nematode interactions with brassicaceous cover crops*

Brassicaceous cover crops may be used as a management tool for plant-parasitic nematodes through several mechanisms. Crop rotation with non-hosts or poor hosts is one of many practices used to decrease plant-parasitic nematode populations. A poor host is a plant that does not favor nematode reproduction in the rhizosphere ( $R_f = P_f/P_i < 0.1-1.0$ ;  $R_f$  = reproduction factor,  $P_f$  = final populations and  $P_i$  = initial populations). Cover crops as trap crops induce hatch (cyst forming nematodes) or allow penetration into the roots, but do not favor nematode reproduction, and can be incorporated or removed before completion of reproductive cycles to reduce populations. Brassicaceous cover crops, such as oilseed radish (*Raphanus sativus*) and mustard, bred to be resistant to *H. schachtii*, are effective trap crops ( $R_f < 0.5$ ) in Wyoming and throughout Europe, particularly in Germany (Smith et al., 2004). Finally, incorporation of cover crops with bio-toxic degradation products may directly suppress nematode populations (Chitwood, 2002). Optimum practices would involve more than one of these mechanisms simultaneously.

Host suitability of brassica cover crops has been evaluated for a variety of nematodes and will be reviewed here by nematode genera common in Maryland. Rapeseed cultivars 'Bridger', Gorazinska, and H-47 were poor hosts (females on root:  $R_f < 0.5$ ) for *H. glycines* (Bernard and Montgomery-Dee, 1993). However, in a screening of 46 cover crops for use in *H. glycines* management, rapeseed 'Dwarf Essex' and oilseed



radish (no cultivar given) had egg reproduction factors ( $R_f = \text{final egg count}/50 \text{ or } 100 \text{ cm}^3 \text{ of soil (Pf): initial egg count}/50 \text{ or } 100 \text{ cm}^3 \text{ (Pi)}$ ) of 0.90 and 0.85 respectively after 75 days of cover crop growth, averaged across two greenhouse studies that used clay loam soil from the field (Warnke et al., 2006).

Root knot nematodes, *M. incognita*, *M. javanica*, *M. chitwoodi*, and *M. hapla*, have reproduced ( $R_f > 1.0$ ; good host) on oilseed radish cultivars ‘Adagio’, ‘Trez’, ‘Melodie’, ‘Renova’, ‘Siletta’, ‘Nova’, ‘Ultimo’ or ‘Silentina’ and/or on mustard (*S. alba*) cultivars ‘Martigena’, ‘Albatross’, ‘Emergo’, ‘Maxi’, ‘Martigena’, ‘Metex’, ‘Serval’, or ‘ISCI 20’ (Al-Rehiyani and Hafez, 1998; Curto et al., 2005; Gardner and Caswell-Chen, 1994; Viaene and Abawi, 1998). However radish cultivar ‘Boss’ did not support reproduction of *M. incognita* in a greenhouse study (Curto et al., 2005).

Rapeseed (*B. napus*) cultivars ‘Bridger’, ‘Gorzanski’, and ‘H-47’ were good hosts ( $R_f > 1.0$ ) for root-knot nematode *M. incognita* (Bernard and Montgomery-Dee, 1993), but cultivars ‘Humus’, ‘Ceres’, ‘Westar’, and ‘Cascade’ were poor hosts ( $R_f = 0.1-1.0$ ) or non-host ( $R_f < 0.1$ ) for root-knot nematode *M. chitwoodi* race 1 or 2 (Al-Rehiyani and Hafez, 1998; Ingham et al., 1999). Rapeseed cultivars ‘Jupiter’ and ‘Liradonna’ were poor hosts for root-knot nematode *M. incognita* race 2 (Mojtahedi et al., 1991). In a microplot study oilseed radish cultivars ‘Trez’ and ‘Melodie’, as well as rapeseed cultivar ‘Humus’ were poor hosts for *M. chitwoodi* race 2, contrary to greenhouse study results (Al-Rehiyani and Hafez, 1998).

In a pot study, rapeseed cultivar ‘Humus’ and mustard cultivar ‘Martigena’ had the highest final nematode counts of lesion nematode, *Pratylenchus neglectus* (Al-Rehiyani and Hafez, 1998), though in another pot study rapeseed cultivars ‘Bridger’,

‘Gorazinska’, and ‘H-47’ were poor hosts for lesion nematode *P. scribneri* (Bernard and Montgomery-Dee, 1993). Oilseed radish and rapeseed were intermediate hosts for *P. penetrans* (Abawi and Ludwig, 1995). In a field study with potato rotations, populations of *P. penetrans* were sustained and not suppressed after cover cropping with rapeseed ‘Humus’ (LaMondia, 2006).

Brassica cover crops which host nematodes, but are also highly suppressive when incorporated as a green manure, may also be a viable option for producers. In Maryland, two successive plantings and incorporations of rapeseed cultivar ‘Dwarf Essex’ is recommended for pre-planting conditions for perennial small fruits and orchards (Fiola, 2007; Steiner, 2002). In a SARE project conducted in Maryland and Pennsylvania, rapeseed and mustard (white and black) suppressed *Xiphinema* sp. as effectively as nematicides, but it required a full year of two successive cover crop plantings. Jing and Halbrecht (1994) found that rapeseed cultivar ‘Humus’ extracts were the most toxic, from either the plant tissue or seed, in petri dish bioassays with *Caenorhabditis elegans*. In a greenhouse study mustard ‘Black Ebony’ was more effective than rapeseed and suppressed *Tylenchulus semipenetrans* by 76% compared to a control; however, in complementary field studies (Australian orchards) mustard had variable effects on *Paratrichodorus*, suppressing it by 58% compared to weeds in one experiment and having no effect, compared to weeds in another experiment (Walker and Morey, 1999). Another study showed no effective suppression by rapeseed on *Meloidogyne* juveniles, but low glucosinolate concentrations due to incorporation of six month old tissue may explain the lack of effect (Johnson et al., 1992). A vineyard inter-row field study found suppression of *M. javanica* across a large range of brassicaceous cover crops, but did not

find a correlation with tissue glucosinolate contents (McLeod and Steel, 1999). Potter et al. (1999) found a significant negative correlation between 2-phenylethyl glucosinolate in the root and host susceptibility to *P. neglectus*. These studies suggest that suppression of nematodes by brassicaceous cover crops is a complex interaction between plant properties and individual nematode genera sensitivities.

Despite numerous bioassays providing evidence of the direct chemical suppressive effects of brassicaceous cover crops on nematodes (Donkin et al., 1995; Jing et al., 1994; Zasada and Ferris, 2004), achieving these conditions in the field, where soil properties interfere with chemical availability, may be unrealistic. Results observed in the field may be misinterpreted as direct chemical effects. Increasing research suggests that complex interactions in the rhizosphere between various members of the food web may be the cause of observed pest suppression or provide potential for future opportunities of pest suppression (Bjørnlund et al., 2006; Dong and Zhang, 2006; Seigies and Pritts, 2006; Wang et al., 2001; Watt et al., 2006).

Apart from resistant trap crops bred to resist nematodes like *H. schachtii* (Smith et al., 2004), integrated biocontrol may be the only solution for suppression of cyst-forming nematodes. The Pf/Pi from a 56 day fallow period after brassicaceous cover crop amendment averaged 1.1 across two experiments, showing little potential for suppression of *H. glycines* by incorporation of brassicaceous cover crop biomass (Warnke et al., 2006). In another experiment, juvenile populations of *H. glycines* added to pots with freshly incorporated brassicaceous cover crops were sampled after 56 days of soybean growth in the same pots and were not lower than the control for oilseed radish, and mustard 'Domo', but were lower  $g^{-1}$  root for rapeseed 'Glacier' (Riga et al., 2001). In a

field experiment, *H. glycines* egg density after growth and incorporation of a canola rotation crop did not differ from the control (Miller et al., 2006). Niblack (2005) suggested that the only truly effective control for *H. glycines* is to rotate cash crops and susceptible cultivars, and soil sample for detection and monitoring.

To advance glucosinolate-pest suppression systems further, more research should be conducted in the field. Many nematodes are less active when soil temperatures are cooler (Al-Rehiyani and Hafez, 1998; Gardiner and Caswell-Chen, 1994), and greenhouse studies may not be simulating these conditions. The ability of microbes to adapt to chemicals and thereby enhance their degradation, is a serious concern, as farmers seek alternatives to methyl bromide (Matthiessen and Kirkegaard, 2006), and implies that even bio-fumigating cover crops need to be rotated.

#### *1.4. Conclusion*

In conclusion, the variability between studies may be the result of inconsistency in growing appropriate biomass quantity, glucosinolate production, or inappropriate plant/cultivar selection for the targeted pest. However, in the context of an era of glyphosate resistant crops, where less skill and knowledge are needed for production success, it is unlikely that a system requiring so much fine tuning will be adapted. More brassicaceous cover crop research should be conducted within the context of integrated pest management, within long-term rotations, and regionally focused. This would enable consideration of practical concerns related to the targeted cash crop rotations, the climate, the dominant soil types, and the likelihood of adoption.

## **2. Free-Living Nematode Community as Indicators**

### *2.1. Introduction to nematode community indicators*

Decades of research in plant-parasitic nematode ecology ultimately evolved into a growing interest in total nematode community ecology. Early interest (1970s) in the total nematode community, within an agricultural context, was partly inspired by studies relating net primary productivity to total nematode abundance within different ecosystem types, together with surprisingly little immediate effect on plant biomass response when nematicides killed large percentages of the nematode community (Yeates and Coleman, 1982). The role of nematodes in the soil food web became a topic of increasing importance. Simple microcosm studies with bacteria, protozoa and nematodes revealed that nematodes increased plant growth and/or N mineralization relative to microcosms without nematodes (Anderson et al., 1983; Ingham et al., 1985). It soon became evident that bacterivore nematodes were key regulators in organic matter decomposition both through transport of bacteria (on the cuticle and in the coelom), through predation and excretion of waste  $\text{NH}_4^+$ , and through grazing which stimulates compensatory bacterial growth (Freckman, 1988).

Subsequently, it became readily apparent that nematode communities would serve as good indicators of environmental quality in terrestrial ecosystems, whereas initially (1970s) nematode genera and total nematode abundance/copepod ratios were indicators in aquatic environments (Neher, 2001a). According to Schloter et al. (2003) faunal indicators in the soil food web should be ubiquitous across environments, abundant and

important in ecosystem function, and have high diversity. Nematodes, being the most abundant mesofauna on earth, being highly diverse (15,000 species to date) (Poinar, 1983), occupying primary through quaternary levels of the food chain, and being easily extracted from the soil, clearly meet the criteria for serving as an environmental indicator. Their inability to directly move soil particles, in contrast to “ecosystem engineers” (Jones et al., 1994), also makes them favorable indicators because their abundance and diversity is a direct reflection of the interaction between soil physical, chemical, and biological properties.

The 1990s was a progressive decade for research in nematode ecology, including such seminal works as the Maturity Index (MI) (Bongers, 1990) and classification of genera into trophic groups (Yeates et al., 1993). The Maturity Index was proposed in conjunction with categorization of nematode families into a colonizer-persister (cp) scale (1-5), representing a gradation of r- (opportunistic, fecund, generalists) and K- (persisters, low reproductive rates, specialists, large body sizes) selected strategies. The index was originally proposed for the Netherlands but has been adapted world-wide (Bongers, 2007). The MI is calculated by weighting the proportion of each cp group by their respective cp rank, thus the index is sensitive to high abundances of either low or high cp-ranked nematodes. The cp scores were assigned to nematode families primarily by sensitivity to pollution (toxicity or eutrophication) and secondarily by life-history characteristics such as reproductive capacity and strategy, under the assumption that as time increased after a disturbance a greater increase of cp-4 and -5 nematodes would be found (Bongers, 1990). Thus, the index is a broad measure of community succession after a disturbance. The intent of the index was to provide a signal about environmental

quality which would then require further investigation. Taxonomic resolution could then remain coarse and the index remain practical for quick environmental assessment.

A reference, or control, was recommended for correct assessment of the signal. In agricultural systems, native prairie, perennial agriculture systems, and organic systems have all been proposed as standards for undisturbed or sustainable environmental conditions (Neher, 2001b; Yeates and Bongers, 1999). However, standards have limited relevance at larger geographical scales where differences in climate result in greater variability. Neher et al. (1998) concluded that comparisons of index values in agricultural systems (annual v. perennial crops) were reliable within a state, but were not comparable between states, using North Carolina and Nebraska as models. In ecotoxicology research, it was suggested preferable to identify a local standard for each site of interest, since soil properties such as organic matter, pH, and texture have a strong influence on nematode communities and bioavailability of contaminants (Sochová et al., 2006). Since agriculture is a disturbance regime, it may be more informative to also have a local reference in agroecosystem studies.

The development of the enrichment index (EI), channel index (CI), and structure index (SI) in 2001 (Ferris et al.) magnified potential for use of nematodes as indicators in agricultural systems. The EI is calculated using a basal and enrichment component, which include cp-2 fungivores and bacterivores (persistent, stress tolerant decomposers) and cp-1 bacterivores and cp-2 fungivores (opportunistic enrichment responders) respectively. The enrichment component and basal component both include cp-2 fungivores because fungivores can contribute to N mineralization and respond rapidly to organic matter resources (Chen and Ferris, 1999). The enrichment and basal components

are weighted based on the expected response in abundance of cp-1 bacterivores (index weight of 3.2) relative to the other persistent enrichment responders, cp-2 bacterivores or fungivores (index weight of 0.8). The CI uses similar components and the same weightings as the EI, but reflects the dominance of the cp-2 fungivore activity. As the CI increases, it indicates a greater proportional activity of the fungal community.

The SI is calculated using the basal component and structure component, the latter comprised of cp 3-5 nematodes. Each cp level in the structure trajectory is weighted based on the relationship between connectance (potential food web linkages) and richness ( $\text{linkages} = \text{constant} \times (\text{richness})^2$ ) from several studies averaged together (Ferris et al., 2001). Diversity of genera within a cp group increased linearly (by 0.5) with each increase in cp value, inclusive of lower cp values. The constant in the relationship was derived from choosing 5 as representative of the highest level of connectance in a food web and dividing by the square of 2.5 (relative richness of the community with cp 2-5 compared to a community with only cp-2 nematodes). Correlation between nematode biomass and weightings in the EI and SI support the accuracy of the weightings in representing relative energy and carbon transfer among different trophic levels of the food web (Ferris et al., 2001).

Graphical viewing of cp groups or indices is advantageous for improving interpretation. Cp-triangles were introduced by de Goede et al. (1993) and were used to trace the relative shift in cp group dominance over time. Ferris et al. (2001) proposed the EI and SI as trajectories which could be graphed together. Index values could be graphed over time, and disturbances should be reflected in movement of values from one quadrant to another, signifying a range from stressed and disturbed (D) to enriched and stable (B).



More recently, Ferris and Bongers (2006) proposed using biomass estimations of bacterivore and fungivore nematodes in an Enrichment Profile (EP) to more accurately visualize the relative activity of bacterial and fungal decomposition pathways. Nematode biomass, and not abundance, was correlated with mineralized nitrogen in laboratory studies with different bacterivore genera (Ferris et al., 1998), and biomass depiction over time in a field study, revealed the relative impact of a single species (Ferris et al., 1996).

## *2.2. Applications in agriculture: organic matter amendments*

Attention to free-living nematodes as indicators in agricultural systems has been largely focused on understanding the decomposition food web dynamics. More specifically, there is interest in synchronizing biological fertility and crop needs, by understanding how amendments of varying C/N ratios alter the timing of C and N mineralization (Ferris and Matute, 2003). Ferris et al. (2004) observed increased EI values during the tomato season, when the soil food web was primed by cover cropping and irrigation the previous fall. Wang et al. (2004) recommended that sunnhemp (*Crotalaria juncea*) be grown so that incorporation of the amendment would precede crop needs by two weeks, based on decomposer succession of litterbags containing ground and dried sunnhemp material.

Nematode bacterivore dynamics during decomposition of amendments are similarly reported across studies, supporting the utility of the MI as an indicator for biological fertility. Bacterivores capable of forming dormant stages (cp-1), dauer larvae or *dauerlarvae* (Fuchs, 1914), generally peak 2-3 weeks after enrichment (Bouwman et al., 1993; Ettema and Bongers, 1993; Georgieva et al., 2005a; Wang et al., 2004). Dauer

formation has been reported in several studies using amendments with low C/N ratio (vetch roots and banana slices) (Georgieva et al., 2005a, 2005b; Ferris and Bongers, 2006). During succession cp-2 bacterivores replace cp-1 bacterivores, and this occurs when food supplies are too low to sustain the metabolic demands of cp-1 bacterivores (Ettema and Bongers, 1993). Fungivores, like *Aphelenchoides* and *Filenchus*, have been observed to respond like opportunists (McSorley and Frederick, 1999), and therefore their inclusion in the numerator of the EI is justified.

Decomposer succession is strongly influenced by the C/N ratio of the amendments. Bouwman et al. (1993) observed Cephalobidae (cp-2) nematodes replace Rhabditidae (cp-1) nematodes in glucose and proteose-peptone amended pots by week eight, while Aphelenchoididae (cp-2 fungivores) were dominant in wheat straw and decomposing wheat root amended pots by week eight of an incubation experiment. Ferris et al. (1998) predicted that residues with C/N ratios higher than 32:1 are likely to result in N limitation for plant growth in the presence of nematodes, and laboratory research with sand columns indicated that different C/N ratios of amendments resulted in different amounts of bacterivore-mediated mineralized N, though variation existed between species. In a field study, the slope of the CI, or rate of change from bacterial to fungal activity, was negatively correlated with the rate of change of cumulative N mineralized, and wheat straw amendments (with C/N ratios of 75.9) decreased N mineralization and increased the rate of change of the CI (Ferris and Matute, 2003). Georgieva et al. (2005b) observed correlation between bacterivore biomass and residue decomposition of vetch roots in early decomposition of a pot litterbag study, while fungivore nematodes correlated with rye decomposition in later stages of decomposition.

Conservation of carbon in the trophic food web is another research focus. The abundance of higher trophic feeding nematodes requires efficient carbon transfer from lower trophic levels to higher, which therefore may be enhanced through the metabolically slow fungal detrital pathway (Ferris and Bongers, 2006). Succession to higher cp groups (3-5) is also influenced by the C/N ratio of the organic amendment (McSorley and Frederick, 1999; Wang et al., 2004). Succession of omnivores was particularly rapid in the low C/N (19) ratio sunnhemp material (Wang et al., 2004), and in an apple orchard study the SI was highest over three years in an apple orchard mulch study where paper mulch or paper mulch and municipal compost were applied (Forge et al., 2003). Wang et al. (2004) observed that long term (5 yr., C/N 35) inputs of composted yard waste had significantly higher EI values and lower CI values compared to no inputs, but SI values were not different, despite 6% higher organic matter levels in plots receiving long term compost. These results may suggest that carbon quality, rather than quantity alone, is an important factor in stimulating the fungal decomposition pathway and ultimately greater succession. Additional motivation for feeding the soil food web carbon is for potential suppression of fungal pathogens by fungivores (Chen and Ferris, 1999; Okada et al., 2005).

The underlying assumption in managing for high SI values is that higher connectance, stability, and diversity, represented by the presence of higher abundances of omnivores and predators, increases food web resilience (rapid recovery from disturbance), potential for top-down food web regulation, and bio-control of plant-parasitic nematodes (Ferris and Bongers, 2006). Wang et al. (2006) observed 2.7 to 7.3 times higher percentages of plant-parasitic nematodes in anhydrous ammonia fertilized

plots compared to plots fertilized with sunnhemp, though no data about plant (squash) yields/biomass were provided. This hypothesis has yet to be clearly proven, and as Yeates and Wardle (1996) suggest, higher plant yields may be more related to better nutrient cycling than to reduced plant parasitism.

Weaknesses in index utility include inconsistent responses of genera or families within cp groups to disturbances. Yeates and van der Meulen (1996) showed that cp characterization of genera were not accurate when, for example, *Aporcelaimus* showed evidence of rapid recolonization when soils were sampled 52 months after fumigation. Fiscus and Neher (2002) identified that genera have different sensitivities to the direct and indirect effects of chemical and physical disturbances. For example, Ekschmitt and Korthals (2006) observed that fungivore decline was correlated with heavy metal contamination, but that it was an indirect effect of a decline in their food resource and not a response to direct toxicity. Other difficulties arise from knowledge gaps about feeding habits, particularly for the Tylenchidae. Feeding habits of higher trophic nematodes can also vary with life stage, risking mistaking algal, bacterial, or fungal feeding for successional maturity (Ettema and Bongers, 1993). Inclusion dauer larvae in EI calculation has not been proven appropriate, though it has been calculated as such (Okada and Harada, 2007).

Another weakness of indices is their calculation as proportions, whereby an increase in both lower and higher cp groups can prevent detection of treatment effects on food webs (Wang et al., 2003; Okada and Harada, 2007). This might be resolved through simultaneous graphical depiction of several indices, including trophic group maturity indices such as the FuMI (fungivores cp 2-4) and BaMI (bacterivores cp 1-4). The BaMI

has only been reported in a few studies (Ferris et al., 1996, Wasilewska 1998, 2004), but has shown lower BaMI values with either enrichment or early succession stages (disturbance). No treatment effects of the FuMI were found in the vetch amendment study by Ferris et al. (1996), and it has not been mentioned in other studies. Integration of these indices into graphical depiction with the EI, SI, and CI would enable better detection of treatment effects masked by proportions.

An alternative to indices is the use of nematode groups, genera or species as indicators. For agricultural systems, bacterivore, fungivore, and herbivore guilds (groups sharing the same resource base) are proposed as indicators of carbon flow (Ferris and Bongers, 2006). Fiscus and Neher (2002) identified nematode genera sensitive to direct and indirect chemical and physical disturbances. Ekschmitt and Korthals (2006) identified six genera whose presence (tolerance) reliably indicated various metal contaminants. Todd et al. (2006) identified ten genera best representing native prairie communities, though some species within a genus were better indicators than others.

One precaution in developing both indices and sentinel taxa is the importance of scale. The concept of a 'nematode community' in the soil implies an interacting group of nematodes across different trophic levels. Nematodes are often studied at a much larger scale than the scale at which nematodes interact. Decomposition dynamics in the rhizosphere are likely to be different than many of the studies focusing on decomposition in the bulk soil because of continuous labile C inputs from root exudates (Brussard, 1998; Ruf et al., 2006). The use of matric potential has enabled some interpretation of nematode dynamics at the pore scale (Görres et al., 1999; Neher et al., 1999; Savin et al., 2001, Yeates et al., 2002). Increasing interest in how environmental heterogeneity

influences decomposition and ecological function may propel more investigation of nematode communities as they exist and function in intact soil matrices (Bonkowski, 2000; Mikola and Sulkava, 2001), and this type of investigation may help to explain the strong influence of site properties (soil and climate) on nematode communities (Bjørnlund and Christensen, 2005; Frouz et al., 2001; Wardle et al., 2006; Yeates et al., 2006).

### *2.3. Conclusion*

In conclusion, nematode community analysis is useful for identifying enrichment of the food web through addition of organic amendments. Succession after enrichment disturbances has been verified in many studies, proving the MI useful at least for its original intent as an environmental signal. Indices at the resolution of family may be useful for long term monitoring of ecosystem recovery, while more knowledge about genera feeding habits, biomass, and sensitivities to disturbance may be necessary for developing a decision-making framework for biological fertility (and potentially pest) management. Future research may benefit from developing indices for isolated disturbances, using sentinel taxa or groups, and then viewing all the indices together for graphical interpretation. Verification of index relevance should continue to be done through use of current food web models. Potential for estimating, optimizing, and synchronizing biological fertility with crop demands exists, as field research across diverse soil properties, cropping systems, and climates continues to inform our knowledge about nematode response and behavior.

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### CHAPTER III –MANAGEMENT OF PLANT-PARASITIC NEMATODES IN MARYLAND GRAIN PRODUCTION SYSTEMS WITH BRASSICACEOUS AND RYE COVER CROPS

#### Abstract

Soil nematodes in grain crop agroecosystems were studied in three experiments at two sites in Maryland, to test the hypothesis that glucosinolate-containing brassicaceous cover crops would suppress plant-parasitic nematodes. Cover crops tested included mustard blend (*Brassica juncea* and *Sinapis alba*) ‘Caliente’, rapeseed (*B. napus*) ‘Essex’, rapeseed (*B. napus*) ‘Humus’, oilseed radish (*Raphanus sativus*) ‘Adagio’/‘Colonel’, and forage radish (*R. sativus*) ‘Dichon’. These were combined with rye (*Secale cereale*) ‘Wheeler’ and crimson clover (*Trifolium incarnatum*) in Experiment 1. *Heterodera glycines* increased more than ten-fold over the two years in which susceptible soybeans were grown; it was not suppressed by brassicaceous cover crops. Dolichodoridae nematodes declined over the two years in all treatments of the same experiment. Rye had opposite effects on Dolichodoridae in two experiments. Trichodoridae nematodes were 2-4 times higher in mustard plots than in other brassicaceous treatments during cover crop growth, and 1.8 times higher than in oilseed radish plots during the entire two years, in Exp. 1. In two of the three experiments, rye favored high abundances of Trichodoridae in June. Combination of brassicaceous cover crops with rye and clover decreased *H. glycines* J2 abundances, and/or increased soil moisture, or non-parasitic nematode abundances on one or more sample dates. In laboratory bioassays, all cover crop tissues reduced survival of *Meloidogyne incognita* or *H. glycines* J2 compared to unamended controls. Bioassays results suggested that

rapeseed biomass production in 2005 in Exp. 1 was insufficiently high for suppression of *H. glycines* J2. Bioassay results suggested radish biomass production was sufficient for suppression. The failure to observe suppression in the field with radish cover crops may have been related to freeze-termination of this cover crop, when soil temperatures depress nematode activity. Future brassicaceous biofumigation studies in Maryland should target high value production systems that allow for more intensive and flexible management of cover crops.

## **1. Introduction**

Cover crops are an important tool in integrated pest management and are beneficial to soil health (Abawi and Widmer, 2000; Vargas-Ayala and Rodriguez-Kabana, 2001). Brassicaceous cover crops have received more attention as reports of nematode suppression (Zasada and Ferris, 2003), soil pathogen suppression (Oliver et al., 1999; Smolinska et al., 2003), and weed suppression (Petersen et al., 2001) have increased. The agents of suppression appear to be volatile biotoxic degradation products that are released when glucosinolates in the plant tissue are hydrolyzed by myrosinase, either stored separately in the plant or located in the soil (Sarwar and Kirkegaard, 1998). The concentrations and type of glucosinolates in root and shoot tissue, however, may be influenced by cultivar (Eberlein et al., 1998), above-ground or below-ground grazing (Birch et al., 1990; Smith et al., 1991; van Darn et al., 2003), plant maturity at time of incorporation (Mojtahedi et al., 1991), and environmental factors like day length, season,

or climate (Ciska et al., 2000; Lazzeri et al., 2003; Charron et al., 2004). It is recommended that plant tissues be macerated to enhance biotoxic chemical production and irrigated to promote chemical penetration of the soil (Matthiessen et al., 2004). These environmental and management conditions have contributed to conflicting reports among studies regarding the practical efficacy of brassicaceous cover crops for pest management.

Nevertheless, research suggests that cultivars of brassicaceous cover crops possess suppressive qualities for specific nematodes and can be useful in plant-parasitic nematode management. Rapeseed cultivars ‘Humus’ and ‘Essex’ are known to produce 2-phenylethyl glucosinolate, which results in the toxic 2-phenylethyl isothiocyanate (ITC) upon degradation (Eberlein et al., 1998; Gardiner et al., 1999). Mustard (*Sinapis alba*) has been combined with radish (*Raphanus sativus*) as a green manure for suppression of *Heterodera schachtii* (Wilson et al., 1993) and mustard suppressed *Tylenchulus semipenetrans* by 76% compared to the control in a greenhouse study (Walker and Morey, 1999). Mustard (*B. juncea*) seed meal amendment suppressed *M. javanica* 100% when applied at a rate of 2.0% w/w, and *T. semipenetrans* showed 100% mortality at 0.9% w/w in a lab bioassay (Zasada and Ferris, 2004). Where oilseed radish ‘Adagio’, bred to resist *H. schachtii*, was grown in the field, populations of *H. schachtii* were reduced by 50-75% (Koch and Gray, 1997).

In the mid-Atlantic region, rapeseed was included in a rotation for suppression of *Meloidogyne* and *Pratylenchus*, however suppression was not observed in that rotation (Everts et al., 2006). In a regional small fruit study, two successional plantings and incorporations of rapeseed ‘Essex’ and mustard ‘Black Ebony’ suppressed *Xiphinema* sp.



as well as nematicides (Halbrendt, 1992), and rapeseed has been recommended for over a decade for suppression of replant disease for orchard renovation (Steiner, 2002).

Soybean cyst nematode, *H. glycines*, is a major pest of soybean (*Glycine max*), particularly on sandy soils in the mid-Atlantic region (Sindermann et al., 1993). Soybean cyst nematode affects approximately 40,500 ha of soybeans in Maryland (W. Kenworthy, personal communication, 2003), and *H. glycines* continues to be the leading cause for soybean yield loss in the United States (Wrather and Koenning, 2006). However, few studies have investigated the use of brassicaceous cover crops in the field to suppress *H. glycines* in the mid-Atlantic region or elsewhere (Miller et al., 2006).

The primary objective of this study was to evaluate the ability of brassicaceous cover crops to suppress plant-parasitic nematodes known to cause economic damage in soybean and corn in Maryland. The following hypotheses were tested: 1) brassicaceous cover crops will suppress populations of plant-parasitic nematodes, whether or not fresh biomass is incorporated into the soil, 2) combination with rye or clover will not decrease brassicaceous cover crop suppression of plant-parasitic nematodes, 3) cover crops will not suppress non-parasitic nematodes, 4) cover crops will increase grain crop yields. An additional objective was to use soil properties to help explain the results.

## **2. Materials and Methods**

### *2.1. Experiment 1*

Experiment 1 was conducted at the University of Maryland Lower Eastern Shore Research and Education Center (LESREC) in Salisbury, MD (N38°22', W75°39'). The

soil transitioned from a Hammonton series (coarse-loamy, siliceous, semiactive, mesic, aquic Hapludult) to a Galestown series (siliceous, mesic, psammentic Hapludult) from east to west across the field. The depth to subsoil clay (argillic horizon) in the eastern end was 20-60 cm closer to the soil surface than in the western end. Average (n=4) surface soil properties (0-15 cm) were loamy sand texture, pH 6.8, and organic matter 9.7 mg/g. Sand and clay contents ranged from 83% and 5% at the eastern end to 90% and 3% on the western end. Precipitation and temperature at LESREC during the study are shown in Figure 3.1; sprinkler irrigation was used to supplement rainfall at this site.

Experiment 1 was initiated in August 2003 and data collection was completed in fall 2005. A baseline survey of nematode populations and soil parameters across the experimental site was conducted and was used to establish the randomized complete block design with two blocks located on the Hammonton soil in the eastern and two blocks on the Galestown soil in the western end of the field site. Prior to the experiment, the field was cropped with a soybean-corn (*Zea mays*) -wheat (*Triticum aestivum*) rotation using conventional tillage. Plots were 3 x 9 m with all planting and tillage operations conducted parallel to (not across) the plot boundaries. The treatment structure was a 6 x 3 factorial, with brassicaceous and non-brassicaceous cover crops as the treatment factors. The six levels of brassica treatments were mustard blend (*S. alba* and *B. juncea*) 'Caliente', rapeseed (*B. napus*) 'Dwarf Essex' (hereafter referred to as 'Essex') and 'Humus', forage radish (*Raphanus sativus*) 'Dichon', oilseed radish (*R. sativus*) 'Adagio', and a weedy control. The three levels of the non-brassica cover crops were rye (*Secale cereale*) 'Wheeler', crimson clover (*Trifolium incarnatum*) 'Dixie', and a no cover crop, unweeded control. The dominant weeds in the control in summer 2004

were nutsedge (*Cyperus esculentus*), wild mustard (*Brassica* sp.), grasses, and cutleaf evening-primrose (*Oenothera laciniata*).

Cover crop seeds were broadcast by hand into bare tilled soil on 25 August 2003 and plots were then cultipacked to ensure good seed-soil contact. Seeding rates were 4.5 kg/ha mustard blend, 9 kg/ha rapeseed cultivars, 14.6 kg/ha radishes, 45 kg/ha for rye in combination, 126 kg/ha for rye alone, 34 kg/ha for crimson clover, and 17 kg/ha for crimson clover in combination. Cover crops were fertilized with 90 kg/ha N as ammonium sulfate and ammonium nitrate on 15 September 2003, to assure adequate nitrogen and sulfur nutrition for vigorous cover crop growth. A second application of 46 kg N/ha as ammonium sulfate was applied on 22 October.

Cover crop biomass in selected treatments was collected from 0.25 m<sup>2</sup> quadrats on 18 October 2003 and 28 April 2004. Cover crops were incorporated and killed with three passes of a disk harrow and a rear-mounted solid-wheel cultipacker on 28 April 2004. A soybean cyst susceptible, glyphosate tolerant soybean, cultivar 'NK/Syngenta S39Q4', was planted in 38 cm rows on 12 May 2004 at a seeding rate of 101 kg/ha. No further cultivation was performed after cover crop incorporation. To permit data collection on weed establishment for complementary studies, application of herbicide (N-(phosphonomethyl)glycine), at a rate of 0.96 L/ha active ingredient, was delayed until 15 June 2004. On 29 June 2004, a mixed fertilizer high in K was applied (36 kg N/ha, 22 kg P/ha, and 112 kg K/ha) in response to K deficiency symptoms on clover and low K levels on soil test reports.

On 15 September 2004 cover crop treatments for the second year were established by broadcasting seed into the standing soybean canopy (growth stage R7). Seeding rates

were 50% higher than in 2003 to compensate for lack of soil incorporation. On 22 September, 59 kg/ha N as ammonium sulfate was broadcast into plots. On 18 October 2004 soybeans were combine-harvested over living cover crops. Yield subsamples were taken to the laboratory and dried at 65°C for determination of moisture content. Biomass was collected for winter-susceptible cover crops on 13 December 2004 from two 0.25 m<sup>2</sup> quadrats per plot. On 13 and 14 April 2005, the biomass was determined for winter-surviving cover crops and weeds and then plants were rotary mowed to 7.6 cm above the soil surface. All plots then received one pass of a chisel plow (15 cm deep) followed by 2 passes of a disk harrow with solid wheel cultipacker. On 10 May 2005 the plots were fertilized with 12 kg P/ha, 84 kg K/ha, 28 kg S/ha, 1 kg B/ha, tilled with two passes of the disk harrow, and sown with soybeans (same cultivar as previous year) in 38 cm rows at a rate of 500,000 seeds/ha. On 10 June 2004, herbicide (N-(phosphonomethyl)glycine) was applied at 0.62 L/ha active ingredient. In response to spider mite infestation, the pesticide cyhalothrin, lambda ((RS)-alpha-cyano-3-phenoxybenzyl 3-(2-chloro-3,3,3-trifluoropropenyl)-2,2,-dimethylcyclopropanecarboxylate) was sprayed at a rate of 0.03 L/ha active ingredient on 15 July 2004. Soybeans were harvested with a combine on 2 November 2005, nearly a month after maturity because of rain. Yield sub-samples were taken to the laboratory and dried at 65°C for determination of moisture content.

## *2.2. Experiment 2*

Experiment 2 was located in the unused middle portion of the same field used for Exp. 1 and was also a randomized complete block design with plot size 3 x 9 m. Prior to planting, this area had been kept in fallow with repeated disking, since fall 2003.

Experiment 2 included six cover crop treatments: mustard blend ‘Caliente’, rapeseed ‘Essex’, forage radish ‘Dichon’, oilseed radish ‘Adagio’, cereal rye ‘Wheeler’, and an unweeded control. On 27 August 2004, cover crops were broadcast seeded (same rates as in Exp. 1) into tilled soil and then cultipacked. A total of 100 kg N/ha as ammonium nitrate was broadcast by hand on 1 September and 22 September 2004. Cover crop biomass was collected from 0.25 m<sup>2</sup> quadrats on 8 November 2004 for rapeseed, forage radish, and rye treatments and 15 November 2004 for oilseed and mustard treatments. Biomass collection of winter-surviving cover crops, and plot management was the same as in Exp. 1 (2005) for the rest of the season, apart from planting of glyphosate tolerant corn ‘Pioneer 34B62’ on 9 May 2005 in 76 cm rows at a rate of 64,467 seeds/ha. Corn plots also received two applications of nitrogen at a rate of 67 kg N/ha on both 4 and 13 June. Corn was harvested on 26 September 2004 with a combine.

### *2.3. Experiment 3*

An experiment was established at the Central Maryland Research and Education Center (CMREC), Laurel, MD (N39°1’, W76°51’). The soils transitioned from a Rosedale series (loamy, siliceous, semiactive, mesic Arenic Hapludult) at the northern end to an Evesboro series (mesic, coated-lamellic Quartzipsamment) at the southern end of the field. The significance of this transition was a difference in subsoil texture, with a sandy loam or finer, beginning at 60-80 cm and redoximorphic features beginning at 80-100 cm. This suggests more subsoil moisture in the northern half of the field. Surface soil texture was a loamy sand throughout the field (85.9 ± 1.2% sand, 9.8 ± 0.9% silt, 4.4

$\pm 0.3\%$  clay;  $n=4$ ) with pH 6.5 (June 2003) and organic matter 16.9 mg/g. The precipitation and temperature during the study is shown in Figure 3.1.

A randomized complete block design experiment was initiated in August 2004 and completed in fall 2005. The field was managed with no-till techniques for five years prior to the experiment and remained in no-till management during the experiment. The land was fallow the previous winter and was in soybean at early pod fill (growth stage R6) just before planting the cover crop treatments. Soybeans were mowed on 18 August 2004 and their residue was used as a source of fertility for fall planted cover crops (the tissue contained 208 kg N/ha). Plot size and orientation of operations was the same as in Exps. 1 and 2. Cover crop treatments were the same as in Exp. 2 except mustard blend was not included and oilseed radish cultivar 'Colonel' was used instead of 'Adagio'.

Cover crops were no-till drilled on 25 August 2004 at 16.5 kg/ha radish seed, 8 kg/ha rapeseed seed, and 126 kg/ha rye seed. Cover crop plant biomass (dry matter) was determined on 30 October 2004 for all treatments and on 23 April 2005 for winter-surviving cover crops (rapeseed and rye). The cover crops were then killed with herbicide (N-(phosphonomethyl)glycine) at 2.3 L/ha active ingredient on 27 April 2005. Lime was spread on 5 May 2005 at a rate of 1100 kg/ha based on soil test recommendation. Corn (Pioneer '34B62') was planted on 10 May 2005 in 76 cm wide rows using a no-till planter and a second application of herbicide was applied on 4 June at a rate of 1.7 L/ha active ingredient. Corn was fertilized with 146 kg/ha N using 30% urea-nitrate dribbled between the rows on 15 June 2005. Corn silage yield was determined on 12 September 2005 by cutting all corn plants at 2.5 cm above ground level

from two center rows of corn, 3 m in length, in each plot. This material was weighed in the field and a sub-sample was dried for several days at 65°C for moisture determination.

#### *2.4. Cover crop biomass determination*

Cover crop biomass (dry matter) was determined by harvesting plant material from an area of 0.25 m<sup>2</sup> on each end of the plot. Shoot biomass was harvested by clipping plants 1 cm above the soil surface. Under favorable moisture conditions, the fleshy roots were also harvested by gently pulling them out of the soil. During dry conditions, when pulling roots was not possible, only the shoots were collected. Roots were washed in the field or lab to remove adhering soil. Plant matter was either weighed fresh in the field and sub-samples collected, or if small enough, the entire sample was taken back to the lab. Samples were collected in cloth bags and placed in an oven to dry for several days at 65°C and weighed.

#### *2.5. Soil sampling and soil properties*

Soil samples to a depth of 15 cm of soil were collected in September and October 2003, April, June, September, and November of 2004, and April, June, and August of 2005 from selected treatments in Exp. 1. Samples were collected in June and August 2005 from Exp. 2 and 3. All soil samples were taken from the rhizosphere (0-8 cm distance from the plant) of the cover crops or cash crops and sampling in the edges of the plot was avoided to prevent edge effects. Twelve 2.3 cm cores were collected and combined from each plot. Samples were transported to the laboratory in coolers and kept at 6 °C for one to seven days before nematode extraction. To determine bulk density for

each sample, the entire composite soil sample was weighed and field water content determined on a small subsample. Sand content was determined for samples from brassicaceous treatment levels taken in September 2004 in Exp. 1. Sand fractions were then separated into coarse (0.5-1.0 mm), medium (250-500  $\mu\text{m}$ ), and very fine (53-106  $\mu\text{m}$ ) size fractions (modified from Kilmer and Alexander, 1949).

#### *2.6. Nematode/cyst extraction and identification*

Before opening the plastic bags, in which soil samples were sealed in the field, the soil inside was gently crumbled and mixed. Nematodes were extracted with a modified Baermann funnel technique (Christie and Perry, 1951). A volume of approximately 250  $\text{cm}^3$  of soil was weighed and submerged in approximately 1.6 L of tap water and stirred. Samples were allowed to settle for 135 seconds before the slurry was decanted into a 20- (850  $\mu\text{m}$ ) and 325-mesh (45  $\mu\text{m}$ ) stack of sieves. Nematodes on the 325-mesh sieve were washed onto a Baermann funnel, with tissue (Kleenex) supported by a plastic mesh grid. After 48 hours, nematodes were drained from the funnels into 20 ml glass vials. Samples were stored at 4°C for 12 to 72 hours before removing 15 ml of supernatant water. Five ml of 10% formalin (1 ml glycerol, 28 ml formaldehyde, 72 ml distilled water) was added to the remaining 5 ml of sample at 55-65°C (Grewal et al., 1990). Alternatively, 4 ml of 10% formalin and 1 ml of streptomycin (5g 100  $\text{ml}^{-1}$  water) (K.-H. Wang, personal communication, 2004) were added to a 5 ml sample, to deter bacterial degradation of samples. Preserved samples were stored at 4°C. In April 2005, samples were not fixed until 10 days after extraction because of their use in a laboratory bioassay.



For Exp. 1, cysts were extracted according to Krusberg et al. (1994) from all treatments in September 2004 and from selected treatments August 2005 (cover crops not in combination and the control). Ten percent of the sample was counted (Krusberg et al., 1994) on white filter paper under a dissecting microscope.

Vermiform nematodes for Exp. 1 were enumerated by placing a 0.5 ml aliquot in a three-dimensional cell counting slide. Additional water was added to fill the 2.3 ml capacity of the slide. An inverted microscope with up to 400x magnification was used to identify nematodes to genus or family. When total nematode count was less than 50, a second aliquot was counted. For Exps. 2 and 3, nematode aliquots were centrifuged at 1700 rpm for 3 minutes and prepared on a microscope slide for viewing at 400-1000x magnification with differential interference contrast microscopy (DIC) optics (Olympus BX51 microscope; Olympus America, Inc., Center Valley, PA). Because of use in a complementary total community study (Ch. IV), proportionally more nematodes were identified in Exps. 2 and 3 (at least  $150 \pm 15$  non-parasitic nematodes). Total sample counts for all experiments were calculated based on the soil bulk density, soil water content, volume of soil sampled in the field and lab (for nematode extraction), and the proportional volume of nematodes counted.

Nematodes identified as Dolichodoridae included species *Tylenchorhynchus claytoni* (Z. Handoo, personal communication, 2005) and genera *Quinisulcius*, were not distinguished at lower magnifications initially, and therefore were grouped for analysis. Trichodoridae nematodes included *Trichodorus* sp. and *Paratrichodorus* sp. which were also not distinguished initially.

## 2.7. Lab Bioassay 1

A nematode bioassay evaluating toxicity of macerated cover crop tissue was conducted using greenhouse-cultured *Meloidogyne incognita*. The experimental design was a randomized complete block design, with incubation petri dishes as the blocking factor. The treatment structure was an incomplete  $6 \times 2^2$  factorial, with treatment factors of biomass type (rapeseed 'Essex', mustard blend 'Caliente', forage radish 'Dichon', oilseed radish 'Adagio', a biomass control, rye 'Aroostock', and a 'no biomass' control), plant part (roots and shoots), and biomass rate (1% and 5% w/w). Three large and three small plants were collected of each cover crop type in late fall 2003. Roots of rye were not included and the same control (no biomass) was used for the two biomass rates, resulting in a total of 20 treatments.

Assay units were comprised of two small plastic cylinders, one fitting inside the other (3 cm diam.), with fine fabric (25  $\mu\text{m}$  mesh) stretched across the inner cylinder (Zasada and Tenuta, 2004). Fresh plant material was chopped with a small electric blender, and then weighed to  $0.05 \pm 0.01$  g and  $0.25 \pm 0.01$  g and mixed with  $5.0 \pm 0.01$  g of pre-weighed sand. The sand biomass mixture was poured into the assay unit and immediately followed by addition of 1 ml aliquot of nematode inoculum. Treatment applications were prepared and applied sequentially rather than by block, for efficiency. As a result, time of treatment application was recorded specifically for each assay unit and subsequent procedures were done according to the amount of time lapsed after aliquot application. Aliquots contained roughly  $270 \pm 15$  nematodes ( $n=5$ ). Each block or large petri dish with lid (containing 20 assay units) was placed in the same incubation chamber at 25 °C. At precisely 24 hours after addition of the nematode aliquot for each

unit, the unit was transferred to a small petri dish filled with water so that the cloth suspended sand-biomass mixture was just touching the surface of the water. This resulted in immediate saturation of the pore matrix. Over the course of the next 48 hr period, nematodes unaffected by the decomposition residues passed through the cloth and into the water of the petri dish. At the end of this period, assay units were removed from the small petri dishes, and nematodes were counted in each dish within two days.

### *2.8. Lab Bioassay 2*

In the second lab bioassay, plant material was collected from field blocks in Exp. 1 and the corresponding block number was maintained for the bioassay. The plant materials applied consisted of rapeseed 'Essex' and 'Humus' root and shoot material, and a biomass control of rye 'Wheeler' shoot, each at  $0.12 \pm 0.01$  g fresh plant matter/g dry sand. Two randomized complete block designs, one for each cultivar, were created, since the nematodes used for this assay consisted of a mixed community which was sampled and extracted from the field plots in which the brassicaceous plant material was grown. Each nematode community was added to the root and shoot of the corresponding brassicaceous cultivar and block from which it was extracted, as well as to rye shoot material, and a biomass-free control. On average  $210 \pm 14$  nematodes ( $n=3$ ) were added to each assay unit. Units and incubation procedure were the same as in Bioassay 1. Nematodes were identified to genera for plant-parasites and non-plant-parasitic nematodes were also counted.

## 2.9. Statistical Analysis

Nematode genera, cyst counts, or summer crop yield were the response variables measured from at least one of the three randomized complete block design experiments. Analysis of variance (ANOVA) was performed using the MIXED procedure in SAS software version 9.1 (SAS Institute, Inc., Cary, NC, 2003), with block as a random factor. For Exp. 1, data collected from control plots and plots treated with the five brassicaeous treatment alone, were analyzed as a repeated measures ANOVA within each trial year and then were analyzed separately on each date. Data from Exp. 1, having a factorial treatment structure, were analyzed as a repeated measures over the two years if no interaction was detected, or analyzed by date separately. Data from Exp. 2, Exp. 3, and the bioassays were analyzed on each date.

In all experiments, data were  $\ln(x + 1000)$  or  $\sqrt{x + 1000}$  transformed if histograms and the Shapiro-Wilks test indicated that residuals were not normally distributed or if residuals increased variance with the mean. The GLIMMIX procedure was used when data fit a Poisson or negative binomial distribution. Pairwise multiple mean comparisons of the response variables were made after significant overall F-test using the Tukey (HSD) method. Differences were considered significant at  $P < 0.10$ . All data presented in tables are untransformed, arithmetic means and standard errors of the mean.

### 3. Results and Discussion

#### 3.1. Effects on *Heterodera glycines* and soybean yields

*Heterodera glycines* juveniles (J2) increased in abundance dramatically over the two years of susceptible soybean, whether or not brassicaceous winter cover crops were grown (Fig. 3.2A; Table 3.1). Among the five brassicaceous cover crop alone treatments and the control, oilseed radish ( $P < 0.03$ ) and forage radish ( $P < 0.09$ ) had higher abundances of *H. glycines* J2 compared to the control across dates in the second experiment year, though significant differences were only detected on the November sample date (Fig. 3.2A). Main effect means of *H. glycines* J2 abundances were higher in forage and oilseed radish in June 2005 ( $P \leq 0.07$ ) compared to treatments without brassicaceous cover crops (Table 3.1). In a greenhouse study, where *H. glycines* infected soil was collected in fall, brassicaceous cover crops had significantly higher egg densities at the end of the cover crop growing period than monocots, legumes, and other dicots (Warnke et al., 2006). Oilseed radish (0.88) egg density change after 75 days of cover crop growth was not significantly different than the control (0.70), however (Warnke et al., 2006). Sampling of J2 stages instead of egg density in this study, makes interpretation of results more difficult. Higher *H. glycines* J2 populations in radishes, for example, may not be more problematic than populations in other treatments, if egg production was equivalent or less. There were no treatment effects on cyst abundances in 2004 ( $139 \pm 13 \text{ } 10^3/\text{m}^2$ ) or in 2005 ( $78 \pm 8 \text{ } 10^3/\text{m}^2$ ). The lower abundance of *H. glycines* J2 across treatments in August (compared to June, Fig. 3.2A), is probably a temporal effect on J2 activity in soil rather than a decrease in reproductive potential, because soils in August were warm (25 °C) and dry (8.4 g water/g dry soil) and there was no rain or

irrigation for six days prior to sampling. Considering the more than ten-fold increase in *H. glycines* J2 over the two years, this study agrees with other studies that suggest brassicaceous cover crops do not decrease *H. glycines* reproductive potential either during cover crop growth or after green manure incorporation (Riga et al., 2001; Miller et al., 2006; Warnke et al., 2006).

Combination of brassicaceous cover crops with rye and crimson clover, however, resulted in lower *H. glycines* J2 abundances in June. Rye suppressed *H. glycines* J2 abundance compared to brassicaceous cover crops (main effect means) by 38% ( $P < 0.09$ ) in June 2004 and 57% ( $P < 0.0001$ ) in June 2005 (Tables 3.1). Clover main effect means for *H. glycines* J2 populations were 43% lower compared to brassicaceous main effect means in June 2005 (Table 3.1). However, neither rye nor clover alone was different from the weedy control plot alone in either year (simple effect means; Table 3.1).

There were no treatment effects on soybean yield in 2004, however main effects means of soybean yield were 59% and 25% higher in rye (1851 kg/ha) than in the control (1166 kg/ha,  $P < 0.001$ ; brassicaceous cover crops alone + weedy control) or crimson clover (1480 kg/ha,  $P < 0.10$ ), respectively in 2005. Low yields across treatments in 2005 (1503 kg/ha), compared to 2004 (3579 kg/ha), can be explained by only 10 cm total precipitation, including irrigation, during pod-fill (Brevedan and Egli, 2003) in August and September, followed by high rainfall in October (20 cm), which delayed harvest and caused bean rot. Soybeans at the same location, in maturity group III, matured by 1 October and yielded 4102 kg/ha on average (Kenworthy et al., 2006).

Some yield loss, however, may be attributable to damage from *H. glycines* (Fig. 3.3A). Nonlinear regression of soybean yield and *H. glycines* J2 suggests that yield decreases exponentially with increasing abundance of *H. glycines*. This supports current management recommendations in Maryland to take preventative measures if one cyst is found per 250 cm<sup>3</sup> of soil (Sardanelli et al., 1983). While the trend appears to be primarily a difference in years, reduced yields in the same plots in block 1 where *H. glycines* J2 populations were high in both years (Fig. 3.3B), suggests that the nematodes contributed to significant yield reductions in 2005. In both years, *H. glycines* J2 abundance in June was negatively correlated with yield (2004  $r=-0.451$ ,  $P < 0.0001$ ; 2005  $r=-0.436$ ,  $P < 0.0001$ ). Overall, more significant effects on *H. glycines* J2 and yield were detected in 2005 than in 2004, possibly as a result of weather, accumulated cover crop effects on soil properties, increased root density in continuous soybean (Nickel et al., 1995), or as a function of higher nematode densities, possibly already at equilibrium (Ferris, 1985; Chen et al., 2001).

*H. glycines* J2 populations were particularly low in Exp. 2 because of management in repeated disked fallow the year prior to treatment application (Table 3.2).

### 3.2. Effects on other plant-parasitic nematodes

Dolichodoridae nematodes declined over time in the brassicaceous cover crops alone and control plots in Exp. 1 (Fig. 3.2B). The opposing trends of *H. glycines* J2 and Dolichodoridae may be the result of intraspecific competition as described by Brinkman et al. (2004). However, strongly negative correlations between the genera were not observed on any single date. Analysis of data from all plots in Exp. 1 revealed cover

crop treatment effects on Dolichodoridae only in June 2005 when populations were two times higher in rye plots than clover plots ( $P < 0.03$ , Table 3.3). Dolichodoridae declined over time, probably because soybean is a poor food source for this nematode family in Maryland (S. Sardanelli, personal communication, 2007). No treatment effects on Dolichodoridae were found in Exp. 2. In contrast, Dolichodoridae populations in corn in Exp. 3, in June, were 2.6 to 3.4 times lower after rye than after no-cover and oilseed radish ( $P < 0.10$ ). In August, Dolichodoridae populations were 71% lower after rye than after no-cover ( $P < 0.03$ ). It is unclear what caused this suppression, but it is noteworthy considering the total non-parasitic nematode community abundance in rye was almost twice as high as the control (Table 3.4). Exp. 3 was the only experiment managed without tillage, and undisturbed soils have been shown to have more natural pest suppressive capacity than disturbed soils (Sánchez-Moreno and Ferris, 2007). However, populations of Dolichodoridae were sufficiently low that yield loss would not be expected, even in the control, and complementary research (Ch. IV) suggest that plant associates (fine root hair feeders not considered economic pests) dominated non-parasitic populations in rye.

Mustard and rye cover crops appeared to favor Trichodoridae nematodes at LESREC. In Exp. 1, populations were on average two times higher in mustard ( $484 \times 10^3/\text{m}^2$ ) in October 2003 compared to forage radish ( $P < 0.05$ ), oilseed radish ( $P < 0.07$ ), and the control ( $P < 0.03$ ) (rapeseed not sampled; simple effect means), and were on average 4 times higher ( $64 \times 10^3/\text{m}^2$ ) than all brassicaceous cover crops alone and the control ( $P < 0.05$ ) in April 2004 (not detected in rapeseed 'Essex') (Fig 3.2C). Averaged across two years, the brassicaceous main effect mean of Trichodoridae nematodes was



1.5 to 1.8 times higher in mustard compared to oilseed radish ( $P < 0.09$ ) (Table 3.5). In Exps. 1 and 2, rye (June 2004 main effect means for Exp. 1; June 2005 for Exp. 2) had higher abundances of Trichodoridae nematodes than the control (Tables 3.2 and 3.5). There were no treatment effects on Trichodoridae in Exp. 3.

### 3.3. *Effects on non-parasitic nematodes*

Cover crops did not have a biofumigation effect on non-parasitic nematodes, but instead a stimulatory effect. Sampling shortly after incorporation may have shown more of a biofumigation effect, however, compared to the 6 + weeks that elapsed before sampling in this study. Combination of brassicaceous cover crops with rye or clover in Exp. 1 resulted in greater abundances of the total nematode community, compared to the brassicaceous cover crops alone. Treatments including clover had on average 1.3 times more non-parasitic nematodes than brassicaceous cover crops alone from June 2004 to June 2005 (Table 3.6). Rye main effect means were 1.6 times higher in June 2005 than the control (brassicaceous cover crops and the weedy control). In Exp. 2, non-parasitic nematode abundances averaged 2.5 times higher than the control across June and August. In Exp. 3, non-parasitic nematode abundance was on average 1.6 times greater in rye plots than in the control plots, across June and August, though only significantly different in August (Table 3.6). These results may suggest that suppression of *H. glycines* J2 in rye was biologically mediated, rather than a direct chemical suppression.

### 3.4. Influence of soil properties

Soil moisture influenced results in Exp. 1. Soybean yield in Exp. 1 was strongly correlated with soil moisture, and *H. glycines* J2 populations were more strongly associated with yield in the wettest block than in the other blocks (Fig. 3.3B; Table 3.7). Soil moisture main effect means were higher in rye in June 2005 (14.3 g H<sub>2</sub>O/g dry soil), compared to the brassicaceous (13.1 g H<sub>2</sub>O g<sup>-1</sup> dry soil;  $P < 0.01$ ) and clover (13.7 g H<sub>2</sub>O/g dry soil) main effect means, which may explain the higher yields in rye in 2005. Previous studies show that rye cover crops have yield enhancing effects during droughty periods (Williams and Weil, 2004). These results confirm studies reporting environmental stresses, such as low soil moisture, to be either interactive with *H. glycines* or dominant in predicting soybean yield response (Donald et al., 2006; Koenning and Barker, 1995).

Dolichodoridae nematodes were strongly correlated with soil moisture, sand content, and sand grain sizes in Exp. 1 (Table 3.7). This may be the first report of correlations between sand grain sizes and abundance of a nematode genus in a field study. A laboratory study on nematode locomotion reported that sand contents greater than 80% increased locomotion of nematodes (Hunt et al., 2001), and early laboratory studies found that the movement of *H. schachtii* (18 µm wide) was restricted when particle sizes were <150 µm (Wallace, 1958). Dolichodoridae nematodes in this study (similar in width to *H. schachtii* juveniles) were positively correlated with particle sizes 53-106 µm in diameter, suggesting that the mixed grain sizes of field soil enabled movement (indicated by presence and survival) and that moisture retention, rather than habitable pore space, was the underlying association between Dolichodoridae and very

fine sand grains. McSorley (1997) reported correlations of cumulative rainfall (2 weeks) with nematode genera in an orchard and pasture, but did not find a significant correlation with *Tylenchorhynchus* (the dominant Dolichodoridae genera in this study), despite also being on a sandy soil (80-90% sand). The orchard soils were Pineda fine sands, and thus it is possible no correlation was observed because of smaller sand grain sizes capable of retaining moisture. The droughty conditions and coarser sand in Exp. 1 may have interacted with incompatible food resources for Dolichodoridae, in this study. The latter in particular may explain why these strong associations were not observed with other plant-parasitic nematodes in this study.

Bulk density measurements were used to express data on an area basis using field soil volumes. Table 3.8 illustrates how sampling after tillage (September 2003) and sampling after a period of soil settling can change the bulk density of the soil. If nematode abundance is not expressed on the basis of field soil volume, gross errors may be made by confounding changes in nematode abundances with changes in soil density.

### 3.5. *Why did bio-fumigation fail?*

Effectiveness of brassicaceous biofumigation is dependent on production of sufficient quantities of glucosinolates in plant tissue and sufficient rupture of tissue to facilitate hydrolysis and release of biotoxic degradation products (Zasada and Ferris, 2004). In a review on brassicaceous biofumigation (Matthiessen and Kirkegaard, 2006), biomass quantities between 3,000 and 17,000 kg/ha dry matter (*B. napus* and *B. juncea*) successfully suppressed nematodes compared to other biomass controls, however other studies in the review, with equal quantities of brassicaceous biomass, did not report

suppression. The sensitivity of glucosinolate production to environmental conditions (Ciska et al., 2000) and plant type or part (Kirkegaard and Sarwar, 1998), as well as conditions necessary for ITC evolution may account for the different rates of success among studies.

While cover crops were not analyzed for glucosinolate contents or isothiocyanate evolution potential, bioassays in the laboratory were conducted to assess potential for suppression. In the first bioassay, results suggested that a rate of 50 g fresh plant matter/kg dry soil should provide effective suppression of *M. incognita* (Fig. 3.4B,D). Assuming incorporation to a 15 cm depth and a bulk density of 1.5 g/cm<sup>3</sup>, the field biomass production needed, equivalent to the 1% and 5% rate (g fresh plant matter/kg dry soil) used in the bioassay, was approximately 3,400 and 16,900 kg dry matter/ha, respectively (85% tissue moisture content). Root tissue was generally more suppressive than shoot tissue, within an amendment application rate in bioassay 1. Rapeseed root suppressed *M. incognita* at the lower rate by 86% compared to the unamended control ( $P < 0.0007$ ). This supports studies showing higher glucosinolate concentrations in rapeseed roots than shoots (Eberlein et al., 1998; Gardiner et al., 1999). Lack of suppressive effects in the field by rapeseed, despite having sufficient quantities of biomass (if roots are included; Table 3.9) may be a result of ineffective incorporation practices.

In 2004 of Exp. 1, cover crops were not macerated prior to incorporation, and it did not rain until several days later. Cover crops were not incorporated in Exp. 3 because the field was in no-till management. Tissue maceration, irrigation, and incorporation are recommended practices for bio-fumigation with brassicaceous cover crops (Matthiessen et al., 2004). Brown et al. (1991) observed maximum ITC production within two hours

of amending the soil with rapeseed meal and a 90% decrease within 24 hours. Thus, volatilization of ITCs without water to improve penetration into the soil may have contributed to the lack of detectable effects on plant-parasitic nematodes. It is also possible that the bioassay may also have overestimated the potential for suppression in the field by rapeseed, because plants were collected in late fall, rather than in April when rapeseed was incorporated in the field. Plants that are two months old, have higher biofumigation potential than senescing plants (Mojtahedi et al., 1991).

Winter-killing oilseed radish leaf tissue suppressed *M. incognita* by 57% compared to the unamended control at the lower rate (10 g/kg or 2,250 kg dry matter/ha, assuming 90% moisture,  $P < 0.0036$ ) in bioassay 1 (Fig. 3.4A). This rate of biomass production was achieved in all experiments (Table 3.9 and 3.10). It is possible that greenhouse cultured *M. incognita* is more sensitive to the breakdown products of brassicaceous oilseed radish leaf tissue than the nematodes in the field studies, however, it is likely that other factors also contributed to the ineffectiveness of biofumigation in the field. The advantages of total tissue rupture from freezing (Morra and Kirkegaard, 2002), may be offset by targeting a pest, such as nematodes, when they are least active because of cold temperatures. Also, Price et al. (2005) observed 81% less allyl-ITC production under cold conditions (15°C) compared to warm (45°C) when mustard was incorporated into soil. Low abundances of Trichodoridae in November and April of Exp. 1 may suggest that in Maryland summer and fall are better seasons for detection (and potentially for biofumigation), as was the case for *Pratylenchus* and *Meloidogyne* (Kratochvil et al., 2004).

In the second bioassay, nematodes used in this experiment were extracted from field plot soil in April 2005 from the rhizosphere of the rapeseed cultivar corresponding to that of the lab bioassay. Rapeseed cultivars 'Essex' and 'Humus' were similar in their suppressive effect on *H. glycines* J2 (Fig. 3.5A-D). Rapeseed roots suppressed non-parasitic nematodes as much as *H. glycines* J2, but shoots did not suppress non-parasitic nematodes as much as *H. glycines*. This bioassay shows that rapeseed biomass quantities in all experiments were insufficiently high (< 8,400 kg dry matter/ha) to result in *H. glycines* J2 suppression. In addition, this high rate of biomass amendment only reduced populations by about 50%, suggesting that either the tissue was not very chemically potent or *H. glycines* J2 are not very sensitive to the rapeseed and rye decomposition products. Suppression of *M. incognita* and *H. glycines* J2 with rye shoots in both bioassays may be the result of hydroxamic acids in rye residues (McBride et al., 2000; Zasada et al., 2005) or may indicate that oxygen was depleted during decomposition of the plant material (another possible way that the bioassay may overestimating fumigation potential in the field). Since biomass quantities of rye were low in 2005 of Exp.1, when suppression of *H. glycines* J2 was observed with rye (and clover), it is more likely that indirect green manure effects, such as soil moisture, were associated with suppression in that year.

#### **4. Conclusion**

Brassicaceous cover crops, as managed in these experiments, showed little potential for plant-parasitic nematode suppression. It should be noted that cover crops in

this study were not always mowed for maceration and were incorporated during flowering, were winter-freeze killed, or were no-till terminated with herbicide. These management practices were used because they were appropriate within the agronomic, economic, and environmental constraints of Maryland grain farmers. Successive planting of an *H. glycines* susceptible soybean cultivar, however, is not a standard practice and was done to increase infestations for testing biofumigation potential. The apparently higher *H. glycines* J2 populations in radish plots on some dates in this study suggest that future research should assess the reproductive potential of this nematode on radishes.

Other plant-parasitic nematodes in these experiments were particularly low in abundance. However, since prevention of population increase is the best nematode management practice, biofumigation studies on low populations are not irrelevant, especially prior to planting a crop favorable as a food source. Dolichodoridae nematodes declined over time in Exp. 1, apparently because soybean was an unfavorable food source.

Grain farmers in Maryland may best take advantage of N-scavenging attributes of radishes and rapeseed, while potentially ameliorating plant-parasitic nematode infestations, by combining brassicaceous cover crops with rye or clover. Combination of rye or clover with brassicaceous cover crops decreased *H. glycines* J2 in June 2005 (Exp. 1) and increased soybean yield or non-parasitic nematode abundance on other sample dates. Increased soil moisture in rye plots may have been associated with effects on *H. glycines* J2 and yield (Exp. 1). Dolichodoridae nematodes were lower in rye plots in Exp. 3 in June and August (during corn growth) compared to the control. Trichodoridae

nematodes, however, appeared to increase under rye cover cropping and this may be a concern for some production systems.

Soil properties were useful for explaining some results. Soybean yield was strongly correlated with soil moisture and *H. glycines* J2 were particularly negatively associated with yield in the wettest block of the field. Thus *H. glycines* J2 did not appear to be the leading cause for yield loss, but rather an interactive factor with soil moisture. Dolichodoridae nematodes were strongly associated with soil moisture and texture, including very fine sand grain sizes, and therefore dry conditions in the absence of a favorable food source may have fostered its decline. Expression of nematode abundance on an area basis, facilitated by measurement of bulk density with each sample, may improve the accuracy with which research can measure differences in nematode populations among seasons, sites and management regimes.

Amendment of fresh biomass to nematode populations in laboratory bioassays is an affordable and effective means of estimating biofumigation potential in field studies. Results suggested that sufficient quantities of rapeseed biomass were grown for *M. incognita* suppression. Since *M. incognita* was not present in field sites, lack of suppression of other plant-parasitic nematodes may have been due to differing sensitivities of genera to decomposition products. Interaction with soil properties, incomplete hydrolysis of glucosinolates, or insufficient penetration of degradation products into the soil may also explain the lack of effects in the field. The second bioassay suggested that insufficient biomass quantities of rapeseed were grown for suppression of *H. glycines* J2. Winter-freezing cover crops showed potential for biofumigation in lab bioassays, and sufficiently high biomass was grown in the field.



Therefore lack of suppressive effects suggests that winter freeze-fumigation is ineffective for nematode pests which are relatively inactive during cold conditions.

In conclusion, brassicaceous biofumigation of nematodes is an unlikely option for grain farming systems typical of the mid-Atlantic region. Laboratory bioassays suggest that brassicaceous cover crops have potential for nematode suppression, but this may require fall incorporation and management intensive practices. Therefore, future studies in brassicaceous bio-fumigation should target fruits, vegetables, and nursery plant systems that allow more flexibility in cover crop management.

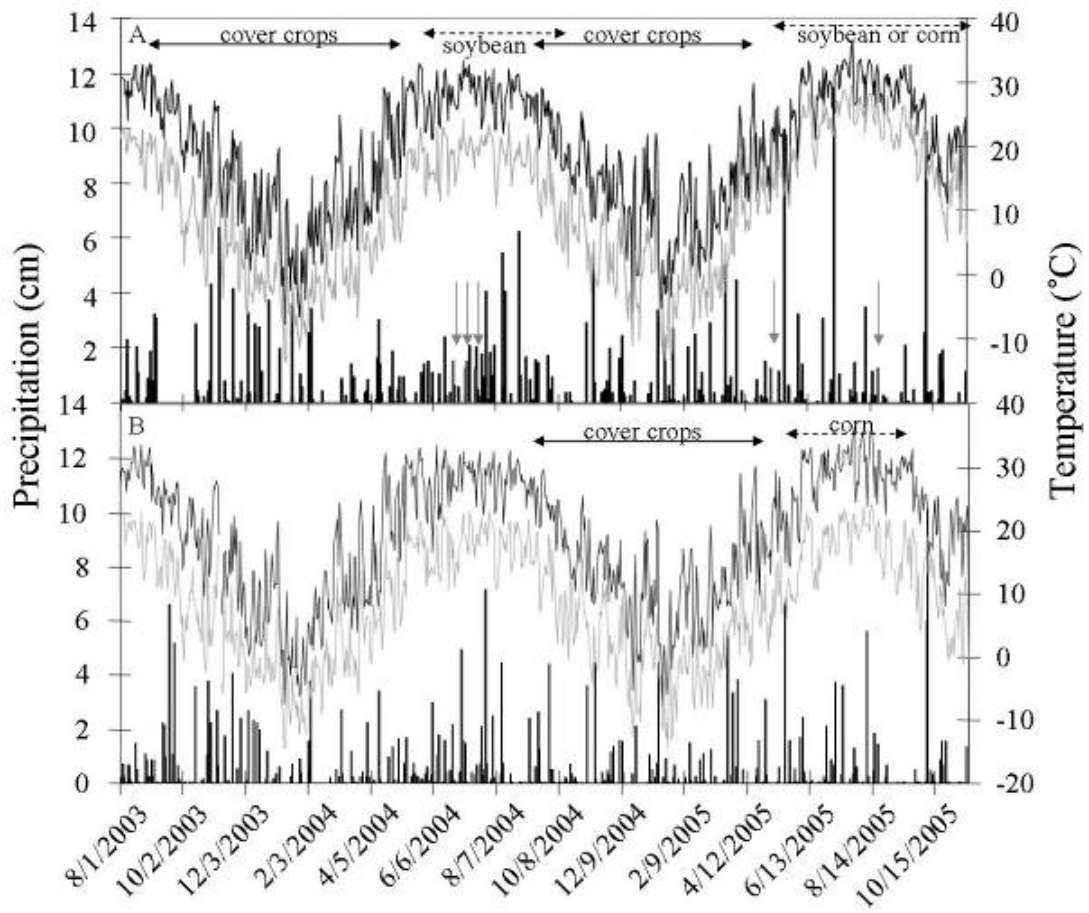
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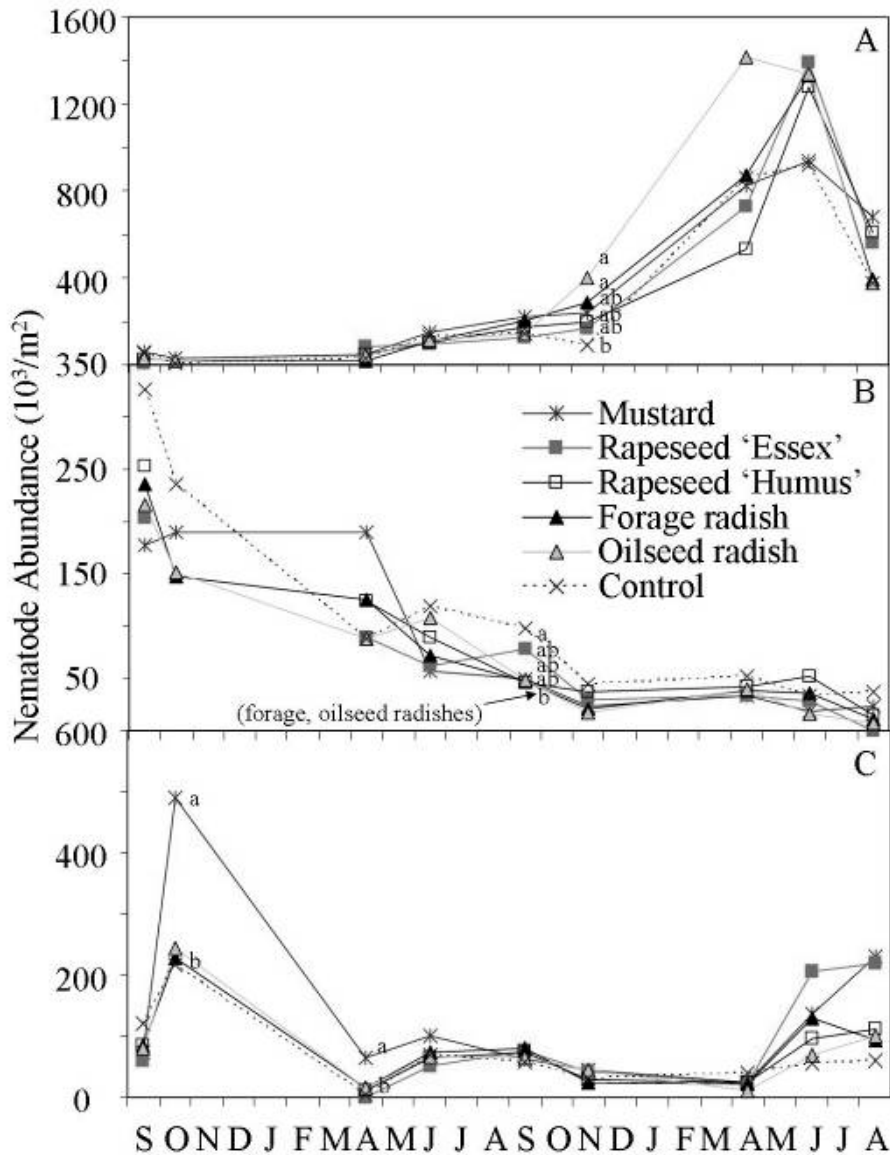
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**Figure 3.1.** Daily precipitation and average high and low temperatures at LESREC (A) and CMREC (B) over the two year experiment. Vertical arrows indicate irrigation events.



**Figure 3.2.** Abundance of *H. glycines* juveniles (J2) (A), Dolichodoridae nematodes (B), and Trichodoridae nematodes (C) in Exp. 1 from September 2003 to August 2005. Radish cover crops and mustard winter-killed in mid to late December, and rapeseed and weeds in the control were terminated by incorporation in mid to late April. September 2003 represents pre-treatment populations since cover crops were in cotyledon stage. Notice y axis values are different, and some treatments were not sampled in October 2003 or April 2004. Means presented with the same letter are not significantly different at ( $P < 0.10$ ) (HSD) ( $n=4$ ).

**Table 3.1.** Effects of winter cover crop treatments on *H. glycines* juvenile (J2) populations in Exp. 1 on four dates during the soybean cash crop season (n=4).

Year	Month	Mustard	Rapeseed 'Essex'	Rapeseed 'Humus'	J2 x 10 <sup>3</sup> m <sup>-2</sup> ± SEM		Oilseed Raidish	No Brassica	Non-brassica Main Effect Means
					Forage Radish	Radish			
2004	JUN	151±91 a	98±36 a	100±34 a	106±33 a	115±43 a	133±81 a	117±21 A	
	Rye	82±53 a	123±70 a	7.4±4 a	93±73 a	14±8 a	112±41 a	72±20 B	
	Clover	160±67 a	74±42 a	18±3 a	59±34 a	81±50 a	58±36 a	75±18 AB	
<b>Brassica Main Effect Means</b>		135±41 A	96±25 A	42±16 A	86±27 A	75±25 A	101±31 A		
2004	SEPT	219±44 a	125±30 a	173±39 a	202±36 a	145±30 a	145±27 a	168±14 A	
	Rye	136±11 a	209±150 a	146±58 a	183±42 a	241±80 a	138±37 a	176±27 A	
	Clover	106±18 a	129±33 a	140±26 a	166±30 a	194±64 a	193±32 a	155±15 A	
<b>Brassica Main Effect Means</b>		157±22 A	150±40 A	153±23 A	184±19 A	194±34 A	159±18 A		
2005	JUN	938±140 ab	1393±171 a	1277±407 abc	1332±245 ab	133±214 a	919±426 abc	1196±108 A	
	Rye	442±67 c	441±53 c	667±213 bc	747±190 abc	556±129 abc	402±42 c	513±49 B	
	Clover	764±262 ab	558±134 abc	617±169 abc	909±420 abc	831±47 abc	445±41 c	687±87 B	
<b>Brassica Main Effect Means</b>		715±111 AI	797±145 AB	775±170 AB	996±174 A	907±124 A	588±148 B		
2005	AUG	682±263 a	560±246 a	610±211 a	393±106 a	376±162 a	375±176 a	495±77 A	
	Rye	480±67 a	365±78 a	570±239 a	532±62 a	748±362 a	366±102 a	510±73 A	
	Clover	598±75 a	512±84 a	664±178 a	500±104 a	240±39 a	314±26 a	471±47 A	
<b>Brassica Main Effect Means</b>		587±88 A	479±85 A	615±111 A	475±52 A	455±136 A	352±62 A		

<sup>a</sup> Simple effect means followed by the same letter within a date and cover crop factor are not significantly different at  $P < 0.10$  (HSD).

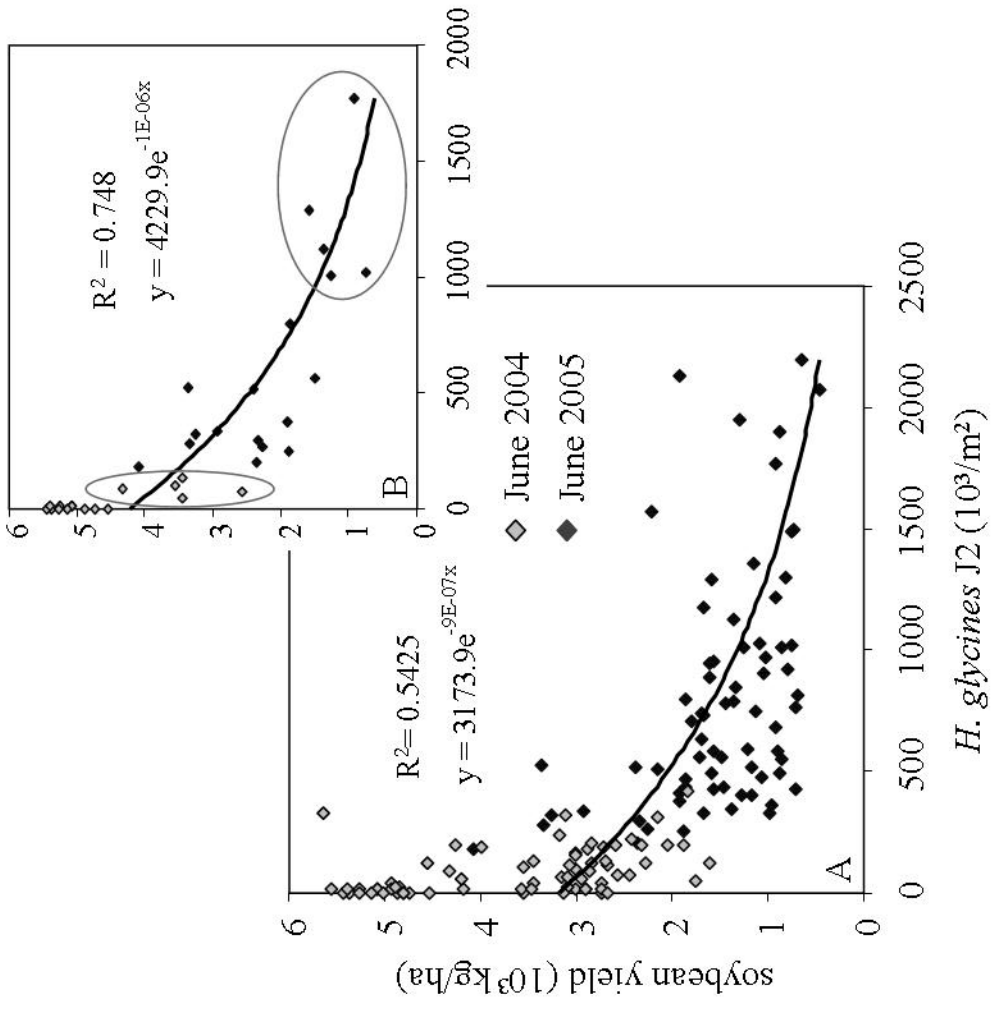
<sup>A</sup> Main effect means followed by the same letter within a date and cover crop factor are not significantly different at  $P < 0.10$  (HSD) (n=12 for brassicaceous main effects; n=24 for non-brassicaceous main effects).



**Table 3.2.** Effects of winter cover crop treatments on nematode abundances in Exp. 2 in June and August during the corn cash crop season of 2005.

Cover Crop <sup>a</sup>	<i>H. glycines</i> J2		Trichodoridae		Dolichodoridae		Non-parasitic	
	Jun	Aug	Jun	Aug	Jun	Aug	Jun	Aug
	----- nematodes x 10 <sup>3</sup> /m <sup>2</sup> ± SEM -----							
<b>Mustard</b>	14 ± 6 a	0 ± 0 b	83 ± 37 b	418 ± 127 a	10 ± 6 a	91 ± 72 a	2,110 ± 405 b	969 ± 175 ab
<b>Rapeseed 'Essex'</b>	2 ± 2 a	0 ± 0 b	118 ± 58 ab	350 ± 128 a	0 ± 0	35 ± 11 a	3,261 ± 393 b	1,535 ± 341 ab
<b>Forage Radish</b>	20 ± 9 a	6 ± 2 ab	112 ± 95 b	277 ± 59 a	6 ± 4	86 ± 41 a	2,792 ± 439 b	1,218 ± 214 ab
<b>Oilseed Radish</b>	22 ± 9 a	17 ± 13 a	29 ± 17 b	317 ± 122 a	0 ± 0	30 ± 10 a	2,293 ± 269 b	929 ± 104 b
<b>Rye</b>	27 ± 12 a	8 ± 4 ab	276 ± 63 a	105 ± 38 a	0 ± 0	5 ± 2 a	5,831 ± 158 a	1,673 ± 96 a
<b>Weedy Control</b>	6 ± 4 a	4 ± 4 ab	67 ± 41 b	292 ± 58 a	11 ± 7 a	24 ± 18 a	2,125 ± 359 b	773 ± 55 b

<sup>a</sup> Means followed by the same letter within a date and cover crop factor are not significantly different at  $P < 0.10$  (HSD) (n=4). June Dolichodoridae abundances were only analyzed for differences where nematodes were detected.



**Figure 3.3.** Nonlinear regression of *H. glycines* J2 and soybean yield in June 2004 and 2005 (A) and in block 1 (B) in Exp. 1. Circles indicate the same plots in 2004 and 2005.

**Table 3.3.** Main effect means and ANOVA tables of winter cover crop effects on Dolichodoridae population densities by date in Exp. 1 during the soybean cash crop season.

Main Effect Means <sup>a</sup>	2004		2005	
	June	September	June	June
	----- nematodes 10 <sup>3</sup> /m <sup>2</sup> ± SEM -----			
<b>Non-brassicaceous</b>				
None	84 ± 15 a	61 ± 14 a	30 ± 7 ab	
Rye	83 ± 18 a	66 ± 15 a	55 ± 13 a	
Clover	78 ± 15 a	66 ± 12 a	26 ± 7 b	
<b>ANOVA Source</b>	<b>df, F</b>	<b>P</b>	<b>df, F</b>	<b>P</b>
Brassicaceous	5, 48 0.25	0.9368	5, 49 0.39	0.8560
Non-brassicaceous	2, 8 0.22	0.8040	2, 49 1.03	0.3660
Brass*Non-brassicaceous	10, 48 0.70	0.7178	10, 49 1.30	0.2581
			10, 49 0.81	0.6162

<sup>a</sup> Main effect means followed by the same letter within a date and cover crop factor are not significantly different at  $P < 0.10$  (HSD). No means comparisons were significant for brassicaceous main effects. (n=12 for brassicaceous main effects; n=24 for non-brassicaceous main effects).

**Table 3.4.** Effects of winter cover crops on nematode abundance in Exp. 3 in June and August, during corn cash crop season of 2005.

Cover Crop	Dolichodoridae		Trichodoridae		Non-parasitic	
	Jun	Aug	Jun	Aug	Jun	Aug
	----- nematodes 10 <sup>3</sup> /m <sup>2</sup> ± SEM -----					
<b>Rapeseed 'Essex'</b>	49 ± 18 ab	218 ± 74 ab	86 ± 29 a	165 ± 85 a	2,082 ± 549 a	1,901 ± 271 ab
<b>Forage Radish</b>	36 ± 6 ab	190 ± 43 ab	85 ± 29 a	66 ± 27 a	2,024 ± 352 a	2,193 ± 406 ab
<b>Oilseed Radish</b>	76 ± 11 a	297 ± 52 ab	75 ± 58 a	52 ± 18 a	1,856 ± 402 a	2,223 ± 167 ab
<b>Rye 'Wheeler'</b>	33 ± 23 b	105 ± 50 b	135 ± 57 a	141 ± 57 a	2,051 ± 124 a	2,574 ± 722 a
<b>Weedy Control</b>	85 ± 34 a	366 ± 135 a	81 ± 42 a	128 ± 28 a	1,479 ± 382 a	1,358 ± 221 b

<sup>a</sup> Means followed by the same letter are not significantly different within a date at  $P < 0.10$  (HSD) (n=4).

**Table 3.5.** Main effect means and ANOVA tables of cover crop effects on Trichodoridae nematodes in Exp. 1 over two years, by date and across time.

Main Effect Means	June		Sept		June		Aug		Total Means	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
----- nematodes 10 <sup>3</sup> /m <sup>2</sup> -----										
<b>Brassicaceous</b>										
Mustard	147 ± 25 a		81 ± 13 a		143 ± 26 a		148 ± 48 a		130 ± 16 A	
Rapeseed 'Essex'	118 ± 37 a		75 ± 12 a		151 ± 31 a		148 ± 44 a		124 ± 17 AB	
Rapeseed 'Humus'	127 ± 24 a		74 ± 17 a		132 ± 29 a		160 ± 49 a		122 ± 16 AB	
Forage Radish	83 ± 22 a		66 ± 13 a		86 ± 20 a		105 ± 28 a		85 ± 11 AB	
Oilseed Radish	81 ± 15 a		55 ± 14 a		84 ± 17 a		69 ± 12 a		72 ± 7 B	
None	158 ± 48 a		74 ± 8 a		88 ± 17 a		119 ± 44 a		110 ± 17 AB	
<b>Non-brassicaceous</b>										
None	72 ± 9 b		69 ± 9 a		117 ± 20 a		137 ± 33 a		98 ± 10 A	
Rye	147 ± 22 a		60 ± 9 a		109 ± 12 a		100 ± 20 a		104 ± 9 A	
Clover	142 ± 27 a		81 ± 9 a		114 ± 19 a		136 ± 29 a		118 ± 11 A	
Monthly Means	119 ± 13 A		71 ± 5 B		113 ± 10 A		124 ± 16 A			
<b>Source</b>	<b>df/F</b>	<b>P</b>	<b>df/F</b>	<b>P</b>	<b>df/F</b>	<b>P</b>	<b>df/F</b>	<b>P</b>	<b>df/F</b>	<b>P</b>
Brassicaceous	5, 48.1	1.63	5, 49.2	0.92	5, 52	1.63	5, 52	1.15	5, 73.8	2.39
Non-brassicaceous	2, 48.1	4.85	2, 49.3	1.08	2, 52	0.09	2, 52	1.44	2, 73.8	0.51
Brass*Non	10, 48.1	0.89	10, 49.1	0.67	10, 52	1.37	10, 52	0.89	10, 73.7	0.93
Date									3, 70.9	7.52
Brassica*Date									15, 110	0.48
Nonbrass*Date									6, 88.3	1.64
Brass*Non*Date									30, 118	0.78

<sup>a</sup> Means followed by the same letter within a date and cover crop factor are not significantly different at  $P < 0.10$  (HSD) (n=12 for brassicaceous main effects; n=24 for non-brassicaceous main effects). Lower case letters represent main effect means within a date and capital letters represent main effect means across time.

**Table 3.6.** Main effect means of fall planted cover crops on non-parasitic nematode abundances during the soybean growing season in two years in Exp. 1, with ANOVA tables by date.

Main Effect Means <sup>a</sup>	2004		2005	
	June	September	June	August
	nematodes 10 <sup>6</sup> /m <sup>2</sup> ± SEM			
<b>Brassicaceous</b>				
Mustard 'Caliente'	2.5 ± 0.3 b	1.6 ± 0.2 a	2.0 ± 0.3 a	1.8 ± 0.2 b
Rapeseed 'Essex'	3.7 ± 0.6 a	2.0 ± 0.4 a	2.3 ± 0.4 a	2.1 ± 0.2 ab
Rapeseed 'Humus'	3.3 ± 0.4 ab	2.1 ± 0.3 a	2.3 ± 0.4 a	1.9 ± 0.3 ab
Forage Radish 'Dichon'	3.3 ± 0.3 ab	2.1 ± 0.2 a	2.0 ± 0.2 a	2.0 ± 0.2 ab
Oilseed Radish 'Adagio'	3.2 ± 0.4 ab	1.8 ± 0.3 a	2.1 ± 0.3 a	2.2 ± 0.2 ab
No Brassica	2.7 ± 0.2 b	1.8 ± 0.2 a	2.1 ± 0.4 a	2.8 ± 0.4 a
<b>Non-brassicaceous</b>				
None	2.9 ± 0.2 b	1.7 ± 0.1 b	1.6 ± 0.1 b	2.6 ± 0.2 a
Rye	3.1 ± 0.3 ab	1.9 ± 0.2 ab	2.6 ± 0.3 a	2.0 ± 0.3 b
Clover	3.4 ± 0.3 a	2.2 ± 0.2 a	2.2 ± 0.2 a	1.7 ± 0.1 b
<b>ANOVA</b>				
Brass	df, F	df, F	df, F	df, F
	5, 48 2.98	5, 49 0.90	5, 49 0.32	5, 50 2.14
Nonbrass	2, 48 2.58	2, 49 3.74	2, 49 7.62	2, 50 9.06
Brass*Nonbrass	10, 48 1.05	10, 49 0.59	10, 49 1.49	10, 50 1.21
				P
				0.076
				0.002
				0.307

<sup>a</sup> Main effect means followed by the same letter are not significantly different within a date and cover crop factor at  $P < 0.10$  (HSD). (n=12 for brassicaceous main effects; n=24 for non-brassicaceous main effects).

**Table 3.7.** Pearson correlation ( $\rho$ ) coefficients between Dolichodoridae, non-parasitic nematodes, and soybean yield with soil parameters or yield on four dates in Exp. 1.

	n=72		n=24			
	Moisture <sup>a</sup>	Yield <sup>b</sup>	Sand <sup>c</sup>	Coarse <sup>d</sup>	Medium <sup>d</sup>	Very Fine <sup>d</sup>
<b>June 2004</b>						
Dolichodoridae	0.437 <sup>***</sup>	0.491 <sup>****</sup>	-0.789 <sup>****</sup>	-0.709 <sup>****</sup>	-0.614 <sup>**</sup>	0.727 <sup>****</sup>
Non-parasitic	0.442 <sup>***</sup>	0.502 <sup>****</sup>	-0.444 <sup>*</sup>	-0.709 <sup>****</sup>	-0.358 <sup>†</sup>	0.440 <sup>*</sup>
Soil Moisture		0.330 <sup>**</sup>	-0.775 <sup>****</sup>	-0.307	-0.329	0.423 <sup>*</sup>
<b>September 2004</b>						
Dolichodoridae	0.719 <sup>****</sup>	0.628 <sup>****</sup>	-0.723 <sup>****</sup>	-0.739 <sup>****</sup>	-0.708 <sup>****</sup>	0.751 <sup>****</sup>
Non-parasitic	0.629 <sup>****</sup>	0.502 <sup>****</sup>	-0.514 <sup>*</sup>	-0.596 <sup>**</sup>	-0.626 <sup>**</sup>	0.551 <sup>**</sup>
Soil Moisture		0.655 <sup>****</sup>	-0.836 <sup>****</sup>	-0.677 <sup>****</sup>	-0.640 <sup>****</sup>	0.678 <sup>****</sup>
<b>June 2005</b>						
Dolichodoridae	0.636 <sup>****</sup>	0.519 <sup>****</sup>	-0.510 <sup>*</sup>	-0.410 <sup>†</sup>	-0.482 <sup>*</sup>	0.418 <sup>*</sup>
Non-parasitic	0.727 <sup>****</sup>	0.732 <sup>****</sup>	-0.500 <sup>*</sup>	ns	-0.415 <sup>*</sup>	ns
Soil Moisture		0.786 <sup>****</sup>	-0.836 <sup>****</sup>	-0.620 <sup>**</sup>	-0.700 <sup>****</sup>	0.680 <sup>****</sup>
<b>August 2005</b>						
Dolichodoridae	0.230 <sup>†</sup>	0.277 <sup>*</sup>	-0.399 <sup>†</sup>	ns	ns	ns
Non-parasitic	0.259 <sup>*</sup>	ns	ns	ns	ns	ns
Soil Moisture		0.586 <sup>****</sup>	-0.224	-0.238	-0.305	0.351 <sup>†</sup>

†, \*, \*\*, \*\*\*, \*\*\*\*, P < 0.10, P < 0.05, P < 0.01, P < 0.001, P < 0.0001

<sup>a</sup> g water/g dry soil in the composite sample from which a subsample was extracted for nematodes.

<sup>b</sup> kg/ha for the plot at the end of the growing season.

<sup>c</sup> g sand/g dry soil for the plot from which soil was sampled for nematodes.

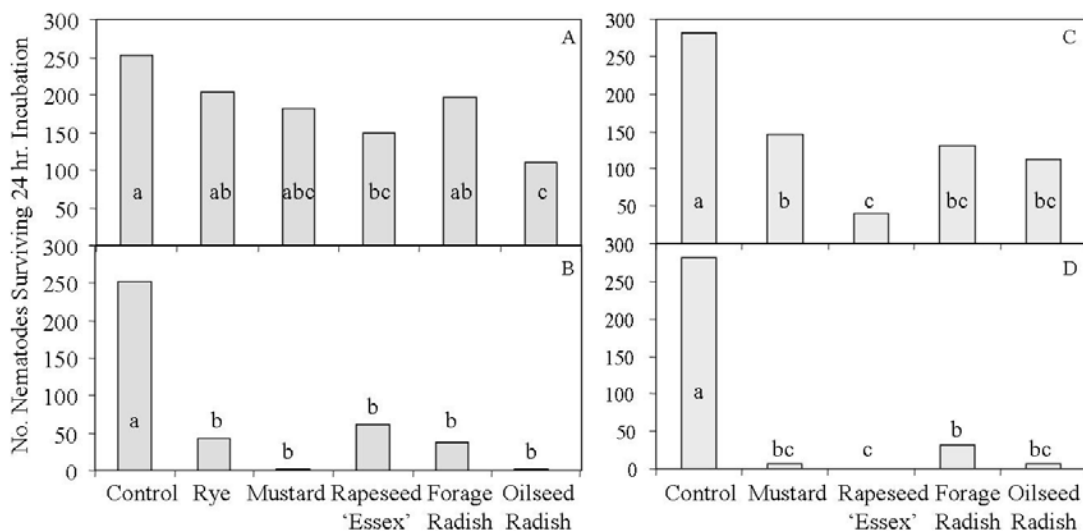
<sup>d</sup> total sand was sieved into separate sand size fractions: coarse (0.5-1.0 mm), medium (250-500  $\mu$ m), and very fine sand (53-106  $\mu$ m).

**Table 3.8.** Changes in nematode abundances between two sample dates for data are reported as abundance/250 cm<sup>3</sup> lab extracted soil volume, abundance/g dry soil, and abundance/300 cm<sup>3</sup> field soil volume.

LOC	DATE	BLOCKS	BD g/cm <sup>3</sup>	lab cup ~300 cm <sup>3</sup>		g <sup>-1</sup> dry soil		300 cm <sup>3</sup> field soil	
				Count ± SEM	% change <sup>a</sup>	CountSEM ±	% change <sup>a</sup>	CountSEM ±	% change <sup>a</sup>
<b>Exp. 1</b>	9/1/2003	1	1.36	986 ± 119		3.43 ± 0.40		1394 ± 153	
		2	1.40	856 ± 60		2.80 ± 0.17		1174 ± 64	
		3	1.42	548 ± 171		1.76 ± 0.55		747 ± 223	
		4	1.48	178 ± 53		0.58 ± 0.17		256 ± 73	
	9/19/200								
		4	1.50	563 ± 78	-75.22	1.96 ± 0.27	-74.64	881 ± 125	-57.75
		2	1.55	618 ± 23	-38.44	2.12 ± 0.07	-31.97	992 ± 41	-18.19
		3	1.60	364 ± 39	-50.50	1.24 ± 0.14	-41.21	595 ± 66	-24.63
		4	1.54	302 ± 43	41.15	1.01 ± 0.14	42.82	462 ± 55	45.70

<sup>a</sup> change in abundance between September 2003 and September 2004 for the method listed above.





**Figure 3.4.** Effect of cover crop tissue on survival of *Meloidogyne incognita* in Bioassay 1. An aliquot of nematodes was applied to bioassay units containing a mixture of sand and plant shoot material at a rate of 10 g kg<sup>-1</sup> fresh biomass (A) or 50 g kg<sup>-1</sup> fresh biomass (B). Root material was applied at the same rates, respectively (C,D). Nematodes were incubated in 3 cm d.m. plastic cylinders with the sand/fresh plant biomass mixture for 24 hours before contact with water (48 hours) enabled them to move out of the cylinder. Means represented with the same letter are not significantly different at  $P < 0.10$  (HSD) (n=3).

**Table 3.9.** Experiment 1 dry plant matter yields in fall (mustard, forage radish, oilseed radish) and in spring (rapeseed 'Essex' and 'Humus'), weedy control, rye (alone and averaged when planted with brassicaceous), and clover (alone and averaged when planted with brassicaceous) (n=4).

Cover Crop	2003-2004			2004-2005		
	Shoot Biomass	Root Biomass	Total Biomass	Shoot Biomass	Total Biomass	Shoot Biomass
Mustard Blend	3,995 ± 70	736 ± 105	4,731 ± 40	2,342 ± 228		
Rapeseed 'Essex'	7,474 ± 901	2,070 ± 364	9,544 ± 1062	1,985 ± 432		
Rapeseed 'Humus'	5,943 ± 630	1,134 ± 379	7,078 ± 1005	2,319 ± 411		
Forage Radish 'Dichon'	3,948 ± 651	1,254 ± 120	5,202 ± 759	1,921 ± 252		
Oilseed Radish 'Adagio'	4,807 ± 556	913 ± 36	5,720 ± 551	2,294 ± 301		
Control (weeds)	4,637 ± 969	ND	ND	1,546 ± 305		
Rye	5,379 ± 498	ND	ND	2,318 ± 415		
Rye (planted w/ brassicas)	2,545 ± 320	ND	ND	1,736 ± 134		
Clover	5,477 ± 358	ND	ND	2,353 ± 488		
Clover (planted w/ brassicas)	3,138 ± 279	ND	ND	1,897 ± 209		

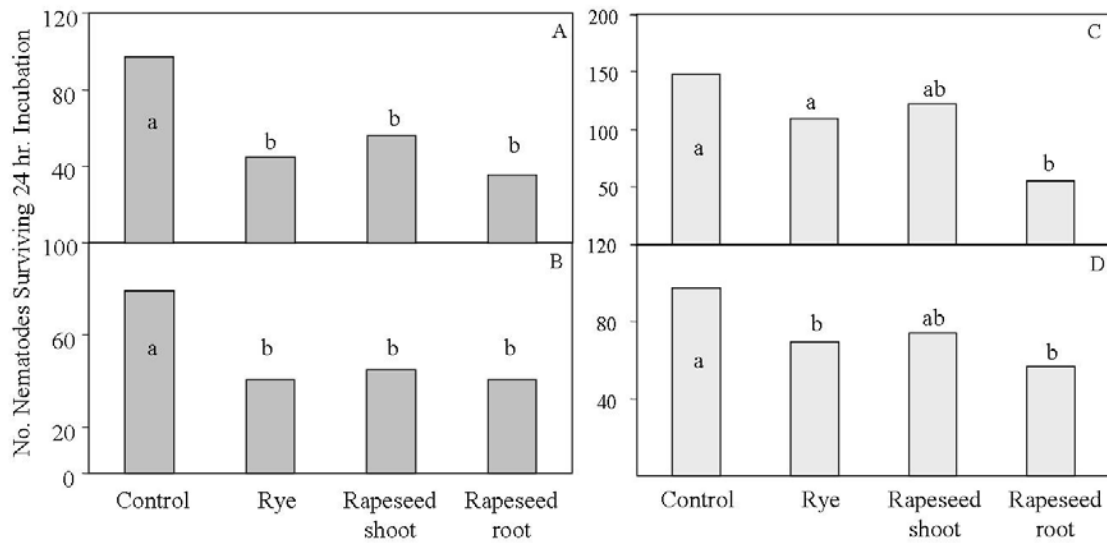
ND Not determined.

**Table 3.10.** Experiment 2 and Experiment 3 dry matter data prior to cover crop termination. Cover crops were planted in late August and harvested on 8 November and 30 October 2004 for Exp. 2 and 3, respectively (n=3 or 4).

Cover Crop	Experiment 2		Experiment 3	
	Shoot	Root	Shoot	Root
	----- kg/ha dry matter -----			
<b>Rapeseed 'Essex'</b>	4,620 ± 474	ND	3,140 ± 406	1,533 ± 788
<b>Forage radish 'Dichon'</b>	3,647 ± 441	2258 ± 75	3,758 ± 322	2,224 ± 500
<b>Oilseed radish 'Colonel'</b>	5,026 ± 346 <sup>a</sup>	ND	3,139 ± 629	996 ± 84
<b>Control (weeds)</b>	894 ± 160	ND	678 ± 99	ND
<b>Rye 'Wheeler'</b>	3,634 ± 676	ND	4,658 ± 818	ND

<sup>a</sup> oilseed radish and mustard was harvested seven days after other cover crops. Mustard data was not available.

ND not determined



**Figure 3.5.** Effects of cover crop tissues on survival of *H. glycines* (A,B) and non-parasitic nematodes (C,D) in Bioassay 2. Nematodes used in the bioassay were mixed communities extracted from field plots growing rapeseed ‘Essex’ (A,C) and rapeseed ‘Humus’ (B,C) and then treated with corresponding macerated rapeseed tissue at a rate of 25 g/kg dry sand. Nematodes were incubated in 3 cm diam. plastic cylinders with the sand/fresh plant biomass mixture for 24 hours before contact with water (48 hours) enabled them to move out of the cylinder. Means represented with the same letter are not significantly different at  $P < 0.10$  (HSD) (n=4).

## CHAPTER IV-- NEMATODE COMMUNITY RESPONSE TO BRASSICACEOUS AND RYE WINTER COVER CROPS

### Abstract

Fall planted cover crops have the potential to benefit cash crops in the following year by altering the soil ecology. This study evaluated the effects of cover crops (forage radish (*Raphanus sativus*) 'Dichon', oilseed radish (*Raphanus sativus*) 'Adagio'/'Colonel', rapeseed (*Brassica napus*) 'Essex', mustard blend (*Sinapis alba* and *B. juncea*) 'Caliente', rye (*Secale cereale*) 'Wheeler') on the soil nematode communities at two sites in Maryland. Samples were taken from the upper 15 cm of soil two or three times per year and extracted nematodes were identified to genera or family. The enrichment index (EI), channel index (CI), structure index (SI), bacterivore and fungivore maturity indices (BaMI, FuMI), and total community maturity index 2-5 ( $\Sigma$ MI25, MI25) were calculated as measures of the nematode community response to cover crops. Large populations of dormant (dauer) bacterivore Rhabditidae nematodes were found in radish cover crop plots four to eight months after radish winter freeze-kill, and EI values in radish plots were higher than in control plots in 2005 experiments, six months after radish winter freeze-kill. Spring-terminated cover crops favored fungivore decomposition channels, evidenced by high CI values. Large abundances of the plant associate (potentially facultative hyphal feeder), *Coslenchus*, in rapeseed and rye plots contributed to this effect. Despite repeated agronomic disturbances such as tillage, N applications, and herbicide treatments, SI, BaMI, FuMI, and  $\Sigma$ MI25 values were frequently higher in winter-terminated cover crop plots than spring-terminated cover crop plots. Future research should investigate the ecological niches of dauer larvae and *Coslenchus*. In

addition, a cover crop combination of radish, plus rye or rapeseed, should be investigated for potential to optimize simultaneously both bacterial and fungal decomposition pathways and both basal and structured components of the nematode community.

## **1. Introduction**

Cover crops continue to receive attention for their ability to suppress pests and improve soil health (Fageria et al., 2005). Brassicaceous cover crop green manures have been used to successfully suppress pests (Matthiessen and Kirkegaard, 2006), including plant-parasitic nematodes (Halbrendt, 1996; Aballay et al., 2004; Rahman and Somers, 2005), diseases (Smolinska et al., 2003; Seigies and Pritts, 2006), and weeds (Petersen et al., 2001; Ercoli et al., 2007). Other benefits such as nitrogen capture in late fall and winter (Kristensen and Thorup-Kristensen, 2004; Dean, 2006; Kremen, 2006) and compaction alleviation (Williams and Weil, 2003; Weil and Kremen, 2007), make brassicaceous cover crops an attractive tool for farmers in Maryland. Many studies have reported the ecological effects of cover crops or biomass amendments on the free-living nematode community (McSorley and Frederick, 1999; Porazinska et al. 1999; Bullock III et al., 2002; Forge et al., 2002; Ferris and Matute, 2003; Ferris et al., 2004; Wang et al. 2004; Wang et al. 2006), but none have monitored total nematode communities during brassicaceous cover crop growth or after application of brassicaceous cover crops as green manures.

Several nematode community indices have been developed to detect ecological changes in the soil, and these have proven useful for interpreting the ecological impacts of agricultural management practices such cover cropping. The maturity index (MI)

(Bongers, 1990) was proposed to use nematode communities as signals of environmental disturbance, either through enrichment or pollution. The MI is derived from classification of nematodes into guilds, or groups of different genera that perform similar ecosystem functions. Nematodes are grouped into different numerical categories, 1-5, based on their tendency to behave like an opportunistic r-selected colonizer (1) or a generalist K-selected persister (5), and weighted with their respective colonizer-persister (c-p) rank. Elements used to determine their c-p rank included sensitivities to physical or chemical disturbance, reproductive rates, body size, and adaptations to adverse environmental conditions (Bongers and Bongers, 1998). Hundreds of published articles have utilized the free-living and total community MI to interpret environmental conditions (Bongers, 2007), supporting its utility as a measure of ecosystem change, disturbance, or succession. During succession or maturation of the nematode community, cp-1 enrichment responders decline and are replaced by cp-2 generalists (Ettema and Bongers, 1993), who are better adapted to scavenge food from surfaces, compared to the cp-1 filter feeders (Bouwman and Zwart, 1994). As abundances of cp-3-5 nematodes increase, cp-2 nematodes remain as the basal part of the food web, though this guild may be represented by other organisms than nematodes (Bongers and Ferris, 1999). The ecological interpretation of high MI values may include stability (less disturbance), diversity, more niche partitioning, leveling in resource availability after N rich amendment, and/or a less stressed habitat (Ettema and Bongers, 1993; Bongers and Ferris, 1999; Háněl, 2003; Neher et al., 2005; Darby et al., 2007).

Various adaptations of the MI have been developed over time, including the bacterivore maturity index (BaMI) or fungivore maturity index (FuMI) (Ferris et al.,

1996a; Bongers et al., 1997) and the maturity index cp 2-5 (MI25) (Bongers and Korthals, 1993) or total maturity index cp 2-5 ( $\Sigma$ MI25) (Yeates, 1994). Wasilewska (1998) showed that the BaMI decreased in nutrient rich conditions created by insect or sheep excrement. Higher values of the BaMI have been associated with steady decomposition rates and a stable environment (Wasilewska, 2004). No treatment effects were detected by the FuMI in an organic tomato study with vetch organic matter amendment (Ferris et al., 1996a). The MI25 and  $\Sigma$ MI25 exclude the variability created by short-term opportunistic cp-1 bacterivores, providing better measures of stability across scales (Neher and Campbell, 1996). The  $\Sigma$ MI25 was used to effectively detect differences in both tillage and fertilizer treatments in a Japanese agricultural study, with higher values reflecting no-till treatment and lower values reflecting conventional fertilizer treatment (Okada and Harada, 2007).

The development of the enrichment index (EI), structure index (SI), and channel index (CI) has enabled further interpretation of ecosystem status (Ferris et al., 2001). These indices have different weightings for cp groups than the maturity indices. Weightings in the EI reflect observed bacterivore and fungivore responses (nematode abundance and biomass) after enrichment with organic matter (Ferris et al., 2001), and for the SI, represent the linear increase in diversity and connectance associated with each increase in trophic level (Table 4.1). Together the EI and SI represent independent trajectories of nematode community dynamics. Ferris et al. (2001) proposed graphing values together in a box plot, with quadrants representing a range from stressed and disturbed (D) to enriched and stable (B). High EI values have been observed after amendment with low C/N ratio organic matter, representing opportunistic bacterivore



nematode activity, whereas high CI values have been observed after amendment with high C/N ratio material, in forests, and in dry or acidic conditions, representing fungivore activity (Ferris et al., 2001; Ferris and Matute, 2003; Neher et al., 2005). High SI values may be found after enrichment of the food web, after addition of high carbon sources, or in undisturbed environments, representing an abundance of higher trophic groups and greater niche partitioning (Ferris et al., 2001; Forge et al., 2002; Okada and Harada, 2007).

Nematodes provide a relatively simple way to assess the soil biological condition because they occupy every level of the food web and are easy to extract from the soil. Since nematode community dynamics reflect combined soil chemical, physical, and biological properties over time, nematode community analysis offers insight into how particular agricultural tools, such as cover crops, may be managed to optimize their impact. The objective of this study was to determine the effects of brassicaceous and rye cover crops on the nematode community, via analysis of nematode genera, trophic group and community indices.

## **2. Materials and methods**

### *2.1. Experiment 1*

This field trial was conducted at the University of Maryland Lower Eastern Shore Research and Education Center (LESREC) in Salisbury, MD (N38°22', W75°39'). The soil transitioned from a Hammonton series (coarse-loamy, siliceous, semiactive, mesic, aquatic Hapludult) to a Galestown series (siliceous, mesic, psammentic Hapludult) from

east to west across the field. The depth to subsoil clay (argillic horizon) in the eastern end was 20-60 cm closer to the soil surface than in the western end. Average surface soil properties (0-15 cm) were loamy sand texture, pH 6.8, and organic matter 9.7 mg/g (n=4). Sand and clay contents ranged from 83% and 5% at the eastern end to 90% and 3% on the western end. Precipitation and temperature at LESREC during the study are shown in Figures 4.1 and 4.2. Sprinkler irrigation was used to supplement rainfall at this site (Fig. 4.1).

Experiment 1 was initiated in August 2003 and data collection was completed in fall 2004. A baseline survey of nematode populations and soil parameters was conducted prior to establishment of experimental plots in a randomized complete block design with two blocks located in the eastern and two blocks in the western end of the field. Prior to the experiment, the field was cropped with a soybean (*Glycine max*)-corn (*Zea mays*)-wheat (*Triticum aestivum*) rotation, using conventional tillage. Plots were 3 x 9 m with all planting and tillage operations conducted parallel to (not across) the plot boundaries. The treatments evaluated in this experiment included five brassicaceous cover crops--mustard blend (*Sinapis alba* and *Brassica juncea*) 'Caliente', rapeseed (*B. napus*) 'Essex' and 'Humus', forage radish (*Raphanus sativus*) 'Dichon', and oilseed radish 'Adagio'--and a weedy control.

Cover crop seeds were broadcast by hand into bare tilled soil on 25 August 2003 and plots were then cultipacked. Seeding rates were 4.5 kg/ha mustard blend, 9 kg/ha rapeseed, and 14.6 kg/ha radishes. Cover crops were fertilized with 90 kg/ha N as ammonium sulfate and ammonium nitrate on 15 September 2003, to assure adequate

nitrogen and sulfur nutrition for vigorous cover crop growth. A second application of 45 kg N/ha as ammonium sulfate was applied on 22 October.

Cover crop biomass was collected from 0.25 m<sup>2</sup> quadrats on 18 October 2003 and 28 April 2004. Winter-surviving cover crops were killed by incorporation when all plots were disked three times and cultipacked on 28 April 2004. A soybean cyst susceptible, glyphosate tolerant soybean, cultivar 'NK/Syngenta S39Q4', was planted in 38 cm rows on 12 May 2004 at a seeding rate of 101 kg/ha. No further cultivation was performed after cover crop incorporation. To permit data collection on weed establishment for complementary studies, application of herbicide (N-(phosphonomethyl)glycine) at a rate of 0.96 L/ha active ingredient was delayed until 15 June 2004. The soybeans were sidedressed with an 8-11-30 (N/P/K) fertilizer at a rate of 36 kg N/ha, 22 kg P/ha, and 112 kg K/ha on 29 June 2004. On 18 October 2004 soybeans were combine-harvested and sub-samples were collected for laboratory for determination of moisture content.

## *2.2. Experiment 2*

Experiment 2 at LESREC was located in the unused middle portion of the same field used for Exp. 1. Exp. 2 was also a randomized complete block design with plot size 3 x 9 m. Prior to planting this area had been kept in fallow with repeated disking since fall 2003. Experiment 2 included six cover crop treatments: mustard blend 'Caliente', rapeseed 'Essex', forage radish 'Dichon', oilseed radish 'Adagio', cereal rye 'Wheeler', and a weedy control. On 27 August 2004, cover crops were broadcast seeded (same rates as in Exp. 1, and 126 kg/ha rye) into tilled soil and then cultipacked. A total of 100 kg N/ha as ammonium nitrate was broadcast by hand on 1 September and 22 September

2004. Cover crop biomass was collected from 0.25 m<sup>2</sup> quadrats on 8 November 2004 for rapeseed, forage radish, and rye treatments and 15 November 2004 for oilseed and mustard treatments. On 13 and 14 April 2005, the plant biomass was collected for winter-surviving cover crops and weeds (in the controls only). All plots were then rotary mowed, leaving a plant height of 7.6 cm above the soil surface. All plots were tilled to incorporate plant biomass by one pass of a chisel plow (15 cm deep) followed by 2 passes of a disk harrow with solid wheel cultipacker. On 9 May 2005, plots were again disked twice, fertilized with 12 kg P/ha, 84 kg K/ha, 28 kg S/ha, 1 kg B/ha, and sown with glyphosate tolerant corn 'Pioneer 34B62' in 76 cm rows at a rate of 64,000 seeds/ha. On 10 June 2004, herbicide (N-(phosphonomethyl)glycine) was applied at 0.62 L/ha active ingredient. Nitrogen (34-0-0) was applied at a rate of 67 kg N/ha on both 13 June and 24 June 2005. In response to spider mite infestation, the pesticide cyhalothrin, lambda ((RS)-alpha-cyano-3-phenoxybenzyl 3-(2-chloro-3,3,3-trifluoropropenyl)-2,2,-dimethylcyclopropanecarboxylate) was sprayed at a rate of 0.03 L/ha active ingredient on 15 July 2004. Corn was combine harvested on 26 September 2004.

### *2.3. Experiment 3*

Experiment 3 was established at the Central Maryland Research and Education Center (CMREC), Laurel, MD (N39°1', W76°51'). The soils transitioned from a Rosedale series (loamy, siliceous, semiactive, mesic Arenic Hapludult) at the northern end to an Evesboro series (mesic, coated-lamellic Quartzipsamment) at the southern end of the field. The significance of this transition was a difference in subsoil texture with a sandy loam or finer texture beginning at 60-80 cm and redoximorphic features beginning

80-100 cm deep in the northern half of the field. This suggests more subsoil moisture in northern half of the field. Surface soil texture was a loamy sand throughout the field ( $85.9 \pm 1.2$  % sand,  $9.8 \pm 0.9$  % silt,  $4.4 \pm 0.3$  % clay; n=4) with pH 6.5 (June 2003) and organic matter 16.9 mg/g. The precipitation and temperature during the study are shown in Figures 4.1 and 4.2.

The experiment was initiated in August 2004 and completed in fall 2005 as a randomized complete block design. The field was no-till managed for five years prior to the experiment and remained in no-till management during the experiment. The land was fallow the previous winter and cropped to soybean prior to cover crop planting.

Soybeans in early pod fill (growth stage R6) were mowed on 18 August 2004 to provide an organic source of nitrogen (the residue contained 208 kg N/ha) for fall planted cover crops. Cover crops were no-till drilled on 25 August 2004 at 16.5 kg/ha radish seed (forage 'Dichon' and oilseed 'Colonel'), 8 kg/ha rapeseed 'Essex' seed, and 126 kg/ha rye 'Wheeler' seed. Plot size and orientation of operations was the same as in the LESREC experiments.

Cover crop plant biomass (dry matter) was determined from two 0.25 m<sup>2</sup> quadrats per plot on 30 October 2004 for all treatments and on 23 April 2005 for winter-surviving cover crops (rapeseed and rye). The cover crops were then killed with herbicide (N-(phosphonomethyl) glycine) at 2.3 L/ha active ingredient on 27 April 2005. Lime was spread on 5 May 2005 at a rate of 1100 kg/ha based on soil test recommendation. Corn (Pioneer '34B62') was planted on 10 May 2005 in 76 cm wide rows and a second application of herbicide was applied on 4 June at a rate of 1.7 L/ha active ingredient. Corn was fertilized with 146 kg/ha N using 30% urea-nitrate dribbled between the rows

on 15 June 2005. Corn silage yield was determined on 12 September 2005 by cutting all corn plants at 5 to 10 cm above ground level from two center rows of corn, 3 m in length, in each plot. This material was weighed in the field and a sub-sample was dried for several days at 65°C for moisture determination.

#### *2.4. Cover crop biomass determination*

Cover crop biomass was determined by harvesting plant material from an area of 0.25 m<sup>2</sup> on each end of the plot. Samples were harvested at least 30 cm from the plot borders to avoid an edge effect. Under favorable moisture conditions, the fleshy roots were also harvested by gently pulling them out of the soil. When biomass samples were collected during dry conditions and pulling roots was not possible, only the shoots were collected. Roots were washed either in the field or lab to remove adhering soil. Plant matter was weighed fresh if sub-samples were collected. Samples were placed in cloth bags and oven dried for several days at 65 °C and weighed. To determine the quality of plant residues associated with selected treatments, samples were ground and analyzed for total N content by a high temperature combustion method (CHN 2000 analyzer; LECO, St. Joseph, MI).

#### *2.5. Soil sampling and analysis*

Soil samples to a depth of 15 cm were collected in April (from selected treatments), June, and September 2004 for Exp. 1; June and August 2005 for Exp. 2; and November 2004, June and August 2005 for Exp. 3. The cover crops were growing when soil samples were taken in April 2004 (for rapeseed 'Essex') and November 2004 (for

forage and oilseed radish, rapeseed, and the weedy control). All soil samples were taken approximately 60 cm or more distance from the plot borders and within 8 cm from the stem of cover crop or cash crop plants. Twelve 2.3 cm diameter subsample cores were collected and combined from each plot. Samples were transported to the laboratory in coolers and kept at 6 °C for 1-7 days before nematode extraction.

To determine bulk density for each sample, the entire composite soil sample was weighed and field water content determined on a small subsample. In a complementary study, samples from September 2004 Exp. 1 were separated into very coarse (1.0-2.0 mm), coarse (0.5-1.0 mm), medium (250-500 µm), fine (106-250 µm), and very fine (53-106 µm) size sand fractions (modified from Kilmer and Alexander, 1949).

#### *2.6. Nematode extraction and identification*

Before opening the plastic bags, in which soil samples were sealed in the field, the soil inside was gently crumbled and mixed. Nematodes were extracted with the modified Baermann funnel technique (Christie and Perry, 1951). A volume of approximately 300 cm<sup>3</sup> of soil was weighed and submerged in approximately 1.6 L of tap water and stirred. Samples were allowed to settle for 135 seconds before the slurry was decanted into a 20- (850 µm) and 325-mesh (45 µm) stack of sieves. Nematodes retained on the 325-mesh sieve were washed onto a Baermann funnel. After 48 hours, nematodes were drained from the funnels into 20-ml glass vials. Samples were stored at 4°C for 12 to 72 hours before removing 15 ml of supernatant water. Five ml of 10% formalin (1 ml glycerol, 28 ml formaldehyde, 72 ml distilled water) was added to the remaining 5 ml of sample at 55-65°C (Grewal et al., 1990). Alternatively, 4 ml of 10% formalin and 1 ml of

streptomycin (5g 100 ml<sup>-1</sup> water) (K.-H. Wang, personal communication, 2004) were added to a 5 ml sample. Preserved samples were stored at 4 °C.

Nematode community identification was primarily conducted at 400-1000x magnification with differential interference contrast microscopy (DIC) optics (Olympus BX51 microscope; Olympus America, Inc., Center Valley, PA). Slides were prepared by sampling an aliquot size estimated to have at least  $150 \pm 15$  free-living nematodes (not including dauer larvae); additional aliquots were taken if necessary. Each aliquot was centrifuged at 1700 rpm for 3 min, allowed to settle, and the supernatant removed with a pipette. The remaining liquid was removed with a pipette and placed on a slide; slides were sealed with clear nail polish. Nematodes were identified to genus level when possible (Bongers, 1988). Total numbers of nematodes/m<sup>2</sup> was calculated by using data on soil bulk density, soil water content, volume of soil sampled in the field and lab (for nematode extraction), and the proportional volume of nematodes counted.

Dauer larvae (Fuchs, 1915) were identified by the presence of an obstruction in the buccal cavity—either a mass of cuticle in a “plug”, lip-like plugs, or dense cuticle throughout the buccal cavity (I. Zasada, personal communication, 2003). Often the specimens appeared to be molting from this state, which may have been the result of fixation though it was not apparent in non-dauer specimens. The dauer were relatively small in size (~430 µm long, ~25 µm wide), and round bacteria in the body, a characteristic common to the entomopathogenic dauer larvae, were not observed.



### 2.7. Nematode indices

Formulas used to calculate community ecology indices are shown in Table 4.1. Dauer larvae were not included in any of the index calculations, to limit indices to active feeding populations. Dauer formation is known to extend the life span of *Caenorhabditis elegans* 8-16 weeks compared to the average 2-week life span (Riddle and Albert, 1997). Therefore, in this study, it cannot be determined whether populations of dauer larvae are indicators of present or historical enrichment conditions, nor can it be discerned if dauer populations are daily fluctuating with increases in dauer formation or recovery as observed by Zelenev et al. (2004). Influence of other factors apart from food resources, including abiotic factors (Golden and Riddle, 1984b), provides additional reason to exclude them from calculation of the EI.

Consistent with Bongers et al. (1997), Tylenchidae plant associates were not included in the FuMI or BaMI; half the Tylenchidae abundances were grouped as fungivores for calculation of the EI, CI, and SI (H. Ferris, personal communication, 2007).

### 2.8. Statistical analysis

The nematode response variables (genera/family abundance, trophic group abundance, or community indices) collected from the three randomized complete block design experiments, with either six or five treatment levels each, were analyzed with treatments as explanatory variables and block as a random factor, using SAS 9.1 (SAS Institute Inc., Cary, NC, USA) software. Data were transformed ( $\ln(x + 1000)$  or  $\sqrt{x + 1000}$ ) as needed and analysis of variance (ANOVA) was performed using the SAS

MIXED procedure or the GLIMMIX procedure, with either a Poisson or negative binomial distribution and log or logit function, respectively. Pairwise multiple mean comparisons of the response variables were made after significant overall F-test using the Tukey (HSD) method. Variables presented across time in figures were analyzed as a repeated measures ANOVA, using the SAS MIXED procedure with REPEATED option and a covariance structure that best modeled the nature of the temporal correlations. The interaction term was dropped from the model on condition that  $P > 0.60$  and normality or homogeneity of variance were not compromised. In cases of significant interaction with time, data were analyzed as a split-plot in time (two dates) or separately by date. Variance grouping using the REPEATED statement of the MIXED procedure was used when the residual variances were significantly heterogeneous as indicated by the Null Model Likelihood Ratio Test. Analysis of covariance (MIXED procedure) with covariates initial *Coslenchus* populations or soil moisture was performed for *Coslenchus* abundance and the EI, respectively, for Exp. 1. The SAS CORR procedure was used to perform correlation analysis between nematode and soil parameters. Contrasts were performed on community indices comparing winter-terminated cover crops to spring-terminated cover crops. The weedy control was not included in the contrasts because of uncertainty and variation regarding the date of kill for various weed species. Canonical Discriminate Analysis (CDA) was performed to further elucidate whether the total nematode community responded to timing of kill or type of cover crop. CDA was performed, using the SAS CANDISC procedure, on data from Exps. 1 and 2 (LESREC), where the winter-killing mustard treatment was included. Data from the June sample dates were grouped into 16 categories of c-p groups by trophic classification and  $\ln(x +$

1000) or  $\sqrt{x + 1000}$  transformed prior to analysis. Any variable that indicated an abnormal value after transformation was removed from CDA, which is highly sensitive to outliers.

### 3. Results

Nematode genera identified were similar among the three experiments and are listed in Table 4.2. Total nematode abundance ranged between 1.9 and 2.7 billion/m<sup>2</sup> in Exp. 1, 1.5 and 3.2 billion/m<sup>2</sup> in Exp. 2, and 1.3 and 1.8 billion/m<sup>2</sup> in Exp. 3. Bacterivore *Alaimus*<sup>cp-4</sup> and fungivore *Leptonchus*<sup>cp-4</sup> were more prevalent in Exps. 1 and 2 than Exp. 3. Generally trophic group populations were highest in June compared to the other dates, however, in Exp. 3 bacterivore populations were highest in November ( $P < 0.001$ ). Plant associates were highest in April ( $P < 0.05$ ) in Exp. 1. The dominant genera are characterized by site in Appendix I. Tables 4.3, 4.4, and 4.5 present abundances, when cover crop treatments affected genera, families, or trophic groups on at least one sampling date within an experimental year. There were no correlations among summer crop yield and nematode community indices across experiments, and there were no cover crop effects on soybean or corn grain yield. Cover crop N contents are presented in Table 4.6, for those cover crops where data were available. Cover crop biomass averaged between 3,000 and 5,200 kg/ha across experiments, with largest biomass values obtained in Exp. 1 and in the rapeseed treatment across sites (6,300 kg shoots + roots/ha).

Canonical discriminant analysis, using normalized cp-trophic group abundances in June from Exps. 1 and 2, separated cover crop treatments (Wilks Lambda  $P = 0.0001$ )

(Fig. 4.3). Only the first canonical variable (CANVAR1) was significant ( $P = 0.0001$ ), and it discriminated the radishes from the other treatments (rapeseed 'Essex', mustard, and the control). The importance of the response variables in the construction of CANVAR 1 can be shown by the loadings of the response variables on the function (Table 4.7). Such loadings are the correlation coefficient between the responses and the function. The highest loadings were negative and were for cp-4 plant-parasitic nematodes and dauer larvae. Still significant, though not as high, were the positive loadings for cp-2 bacterivores, fungivores, and plant associates.

### *3.1. Bacterivore nematode activity*

Across all three experiments, dauer larvae were high in forage and oilseed radish plots (Fig. 4.4). Across all dates and seasons (except in November in Exp. 3 when and where no treatment effect was detected), dauer larvae populations in the forage radish plots ranged from 3.5 to 15.7 times higher than the controls. Dauer larvae abundance in oilseed radish plots was 2.5 to 9.9 times higher than in the controls in April or June, across experiments. In August, dauer larvae populations in oilseed radish plots were 7.1 times higher than the control in Exp. 3. Dauer larvae abundance in rye plots was 3.3 times greater than the controls in Exp. 3 across June and August, and 3.7 times greater than the controls in August in Exp. 2. Dauer larvae abundance in rapeseed 'Essex' was different from the controls (on average 3 times higher) only in Exp. 2.

In June 2005, six months after freeze-kill of the radishes, EI values in radish plots were 1.2 times higher than the controls in Exp. 2 and 1.6 times higher in forage radish

plots than the controls in Exp. 3 (Fig. 4.5). Across time, cover crop plots had higher EI values in Exp. 3 than the control.

Bacterivore nematode activity was strongly associated with soil properties in Exp. 1. Effects on the EI were detected only with use of soil moisture as a covariate (Fig. 4.5), and the EI was positively correlated with percent fine sand (of the total sand fraction) in April (Fig. 4.6a.). In June, dauer larvae in radish plots were strongly negatively correlated with percent sand (Fig. 4.6b).

### 3.2. *Fungivore nematode activity*

Contrasts showed that spring-terminated cover crops had higher fungivore abundance, *Coslenchus* abundance, and CI values than winter-terminated cover crops (Table 4.8). Fungivore abundance in rapeseed ‘Essex’ plots was on average 2.5 times higher than the control plots in Exp. 1, across time (Fig. 4.7); abundance of cp-2 fungivores, primarily *Aphelenchoides*, contributed to this effect (Table 4.3), and was higher in rapeseed ‘Essex’ across dates compared to all other treatments ( $P < 0.03$ ). In Exp. 2, total fungivore abundance was 4.0 to 9.8 times greater in rye than other treatments (except rapeseed ‘Essex’) in June ( $P < 0.10$ ) and 2.6 to 3.7 times greater in rye than mustard ( $P < 0.09$ ), forage radish ( $P < 0.01$ ) or the control ( $P < 0.05$ ) in August (Fig. 4.7). Differences in Exp. 2 were also primarily the effect of *Aphelenchoides* (Table 4.4). In Exp. 3, abundance of fungivores was on average 1.5 times higher in rapeseed ‘Essex’ plots than the control plots across time (Fig. 4.7). Rye had 2.3 to 2.6 times more total fungivores than forage or oilseed radish in August ( $P < 0.04$ ), but was not different from

the control across dates. *Diphtherophora* was the dominant fungivore in rye plots in Exp. 3 (Table 4.5).

Rapeseed and rye dramatically increased populations of the plant associate (presumed facultative root hair/hyphal feeder) *Coslenchus* compared to the control (Fig. 4.8) and winter-killed cover crops (Table 4.8). In Exp. 1, rapeseed ‘Essex’ had 13.2 times more *Coslenchus* than the other treatments across time, including April when rapeseed was growing. However, analysis with initial populations as a covariate revealed only greater abundance of *Coslenchus* in rapeseed ‘Essex’ compared to oilseed radish in April ( $P < 0.04$ ). In Exps. 2 and 3, together rapeseed and rye had 5.4 and 8.7 times more *Coslenchus* than all other treatments, respectively, across June and August.

Across experiments, the CI, which includes half of the plant associates as cp-2 fungal feeders, was higher in rapeseed ‘Essex’ or rye plots compared to radish plots and in some cases, higher than in the control plots (Fig. 4.9). In Exp. 1, CI values were on average 2.3 times higher in rapeseed ‘Essex’ plots than the radish and control plots across time, and were on average 3 times higher in rapeseed ‘Essex’ plots compared to radish plots in Exp. 2 in June. In Exp. 3, CI values were on average 2.1 times higher in rapeseed ‘Essex’ plots compared to radish plots across June and August. The CI was on average 3.3 times higher in rye plots than in the radish plots in Exp. 2 in August, and was on average 2.2 times higher than radish plots across June and August in Exp. 3.

### 3.3. Nematode community succession and structure

Contrasts between winter and spring-terminated cover crops revealed higher maturity indices (BaMI, FuMI,  $\Sigma$ MI25) or SI values in spring and summer across

experiments in plots that had winter-terminated cover crops (Table 4.9). The BaMI and FuMI did not show consistent trends across experiments for a particular cover crop treatment (Appendix V). Cover crops only affected the MI25 in the 2005 experiments. In Exp. 2, forage (3.12;  $P < .07$ ) and oilseed (3.41;  $P < 0.005$ ) radishes were higher than rye (2.99) across time, and in Exp. 3 in June, forage (3.39;  $P < 0.03$ ) and oilseed (3.33;  $P < 0.08$ ) radish were higher than rapeseed 'Essex' (3.01). The  $\Sigma$ MI25 was low across experiments in rapeseed 'Essex' and rye compared to the radishes (Fig. 4.10). On average, across dates in Exp. 1, the  $\Sigma$ MI25 was 5.2% higher in forage radish than in control plots. In Exp. 3 in June, the  $\Sigma$ MI25 was 7.2% higher in forage radish plots than in controls. The SI had a similar trend as the  $\Sigma$ MI25, but fewer differences among treatments (Fig. 4.11). The SI was 11% higher in forage radish plots than rapeseed 'Essex' plots across dates ( $P < 0.06$ ) in Exp. 1, and SI values in the forage radish, oilseed radish, and control plots were 1.7 to 1.8 times higher than in rye plots ( $P < 0.05$ ) in June in Exp. 2. In Exp. 3, SI values in forage and oilseed radish plots were 25 to 26% higher than in rapeseed 'Essex' plots ( $P < 0.01$ ) and 13 to 14% higher than in rye plots ( $P < 0.06$ ) across June and August. The SI in control plots was 19% higher than in rapeseed 'Essex' plots across June and August ( $P < 0.05$ ). Nematode genera with cp ranks 3-5, which contributed to higher SI values in winter-killed cover crop plots in one or more experiment, included bacterivores (*Cylindrolaimus*), fungivores (Leptonchidae), omnivores (*Aporcelaimellus*), and predators (*Mylonchulus*) (Tables 4.3, 4.4, and 4.5). Rapeseed and rye also had high abundances of cp-4-5 nematodes (*Ecumenicus*, *Mylonchulus*, *Alaimus*, *Mesodorylaimus*), but because abundances of lower ranked nematodes were also high, this was not evident in the SI.

#### 4. Discussion

Cover crops had long lasting effects on the nematode community, however nematode response to cover crops was almost never an effect of cover cropping in general, compared to the control, but rather appeared to be a response to winter or spring-termination of cover crops or the type of cover crop. With an average weed biomass across sites and season of 1769 kg/ha, the control often had similar values as at least one other cover crop treatment. Presumably a significant portion of weed biomass was killed in both winter and spring. Multiple fertilizer applications on corn, or nodulation in the case of soybean, were necessary to avoid severe plant nitrogen deficiency, but may have reduced cash crop dependency on biological fertility. This reduced dependency may explain the lack of correlation between cash crop yields and nematode indices.

Cover crops had a distinct impact on the nematode community composition, as evident in the canonical discriminant analysis (Fig. 4.3; Table 4.7). Dauer larvae and cp-4 plant-parasitic nematodes (*Trichodorus*, *Paratrichodorus*, and *Longidorella*) contributed most to cover crop means separation, though cp-2 bacterivores, fungivores, and plant associates also contributed. The CDA suggests that the radishes had impacts on the nematode community that were distinct from mustard, which was also a winter-killing cover crop. Therefore, cover crop type, probably defined by root exudate and/or tissue decomposition chemistry, appears to have a role in nematode community response. Several studies have found plant identity effects on nematode communities (De Deyn et al., 2004; Wardle et al., 2006) Van Diepeningen et al. (2006) discriminated between brassicaceous (unidentified species) cover crops and legumes and grains, in Dutch



agricultural fields, with bacterivore genera and the cp-4 predator *Mylonchulus*. That mustard, rapeseed, and weeds were not significantly discriminated from one another suggests similarity among their resource quality, in contrast to the radishes.

#### *4.1. Bacterivore nematode activity*

The greater abundance of dauer larvae in radish plots compared to rapeseed or rye plots (Fig. 4.4) may have been related to the higher N contents in radish tissues compared to rapeseed and rye in this study (Table 4.6). The nitrogen data in Table 4.6 and a complementary N uptake research on the same plots used in this study showed that radishes had lower C/N ratios ( $C/N \approx 10$ ) and mineralized N faster than other cover crops ( $C/N \approx 24$ ) in spring (Kremen, 2006). High dauer populations have been reported in several studies after the addition of low C/N ratio amendments. Dauer comprised 80% of nematode populations (in fine textured soil types) after only two weeks of enrichment with banana slices in a simple laboratory study (Ferris and Bongers, 2006). Large populations of dauer larvae were observed after vetch root burial ( $C/N=8$ ), in contrast to rye root burial ( $C/N=22$ ) in both field and pot studies (Georgieva et al., 2005a, 2005b). Dauer larvae are also prolific in cow dung pats, where they phoretically disperse to new environments via beetles (Sudhaus et al., 1988).

The specific mechanism that induces dauer formation appears to be a low ratio between cues from bacteria (yeast-like carbohydrate) (Golden and Riddle, 1984b) and a dauer pheromone (pyran ring-heptanoic acid complex) (Jeong et al., 2005). It is well known that bacterivore nematode populations increase shortly after bacterial populations surge in response to nutrient enrichment (Anderson et al., 1983; Ferris et al., 1996b,

1998; Zelenev et al., 2004), and therefore bacterivore nematode overgrazing is the likely cause of dauer formation (Georgieva et al., 2005b; Zelenev et al., 2004) during decomposition of organic matter with high N contents. However, other factors may also induce or influence dauer formation. Root tip exudates of both radish and corn, but not mustard, were found to induce a period of quiescence for *C. elegans*, lasting 5 days (Hubbard, et al. 2005). In a laboratory study with *C. elegans*, all the nematodes formed dauer larvae at 25 °C, whereas at 17.5 °C only 0-10% formed dauer larvae (Golden and Riddle, 1984a). There is no information on the influence of cold temperatures on dauer formation. Radishes decomposed in a freezing and thawing environment in winter and early spring, and it is unknown whether this influenced dauer formation. Magid et al. (2004) observed complete disintegration of radish leaf tissue after 35 days at 9 °C in a laboratory study, during which time they observed a rapid increase in amoebae and bacterivore nematode activity and then a sudden drop in abundance, which they attributed to lack of oxygen.

Lower dauer formation in rapeseed and rye may have been due to a shorter period of intense bacteria-mediated decomposition. As the microbial community mediates decomposition of more recalcitrant forms of carbon in rye plant tissue, fungi and fungivores become more active (Lundquist et al., 1999). Rye roots added to the soil in a litterbag pot study, with higher C/N ratio (22) than vetch roots (8), lower lignin content, and higher non soluble C, had 16-38 times higher large-diameter-fungal biomass over the 12 week study (Georgieva et al., 2005a). In a complementary field study, six weeks after addition of rye root litterbags to the soil, fungi were the dominant microbe in rye litterbag soil (Georgieva et al., 2005b). Allelopathic chemicals, in both rye and rapeseed, known

to suppress plant-parasitic nematodes and soil pathogens (McBride et al., 1999, 2000; Zasada et al., 2005), may have been an additional limiting influence on dauer abundance (and their bacteria prey).

Enriched conditions, as indicated by the EI, in radish plots in June may have been the result of spring tillage, which is known to mineralize microbial biomass (Kristensen et al., 2003), or growth and turnover of roots from summer crops (Ferris and Matute, 2003). Priming of the food web earlier in the season (late winter-early spring) may also account for the higher EI values in June. For an organic tomato system in California, Ferris et al. (1996a) concluded that activation of the bacterivore food web earlier in the season would synchronize tomato nutrient demands during fruit set with the one month lag period between organic matter amendment and bacterivore response. In a subsequent study, Ferris et al. (2004) observed higher summer EI values in tomato plots treated previously with winter cover crops and fall irrigation. Thus, early decomposition of radishes in this study and higher rainfall in 2005 (2.2 times more precipitation during the period between April tillage and June soil sampling compared to 2004; Figs. 4.1, 4.2), may explain the high EI values in the 2005 experiments in June (Fig. 4.5).

Evidence of enrichment through organic matter addition was particularly pronounced in Exp. 2 in rye plots (Table 4.4). Opportunist cp-1 bacterivores were more abundant in rye plots than other treatments, but because of equally high abundances of cp-2 fungivores and cp-2 bacterivores, the EI did not reflect these differences. It is not clear why this response was observed with rye. Total N applied as shoot biomass was not different between rapeseed and rye in Exp. 2. Several extreme rainfall events in 2005 (Fig. 4.1) may have contributed to the formation of an active decomposer community in

rye plots 6+ weeks after incorporation. In a grassland study, Murray et al. (2006) observed a stronger influence of soil moisture on the nematode community than increased primary productivity of plants.

Differences in precipitation between 2004 and 2005 at LESREC probably also account for the stronger association with soil properties in Exp. 1. In April, in Exp. 1, there was no precipitation for nearly a week prior to sampling, and treatment effects on the EI were observed only with the use of moisture as a covariate, which was greater in the bare radish plots. The positive correlation between the EI and fine sand grain fraction (Fig 4.6a) in April, suggests that in particularly sandy soils, sand grain sizes, rather than simply percentages of sand, silt, and clay, may have a strong influence on nematode communities and their prey during droughty periods. Association of dauer larvae in radish plots with sand content in June (Fig. 4.6b), is probably related to soil moisture (Chen and Glazer, 2004), habitable pore space (Elliot et al., 1980), and/or association of fine textured minerals with bacteria (Rønn et al., 2001). There are only a few studies describing the effect of soil texture on dauer formation (Ferris and Bongers, 2006; van Diepeningen et al., 2006).

#### *4.2. Fungivore nematode activity*

The fungivore nematode community was considerably more active in spring-terminated cover crops compared to winter-terminated cover crops (Table 4.8), and this may have been due to higher C/N ratios (Table 4.6) resulting from a longer growing period and/or winter stress. Several studies have shown that organic matter additions with higher C/N ratios stimulate nematode fungivore activity (Forge et al., 2003;

Georgieva et al., 2005) and the CI has been shown to be a good indicator of a shift towards proportionally greater fungivore activity (Ferris et al., 2001; Ferris and Matute, 2003). The high abundances of fungivores in rapeseed ‘Essex’ (Fig. 4.7), despite evidence of rapeseed being a suppressor of fungal pathogens (Smolinska et al., 2003) and a poor host for mycorrhizae (Glenn et al., 1988), warrants further research on the decomposition food web of rapeseed. Rapeseed ‘Humus’ was only present in one experiment, but lack of differentiation from the control, in contrast to rapeseed ‘Essex’, with regard to fungivore abundance (Fig. 4.7), *Coslenchus* abundance (Fig 4.8), CI values (Fig. 4.9), may suggest that cover crop biomass quality or decomposition chemistry differed between the two cultivars. The timing of bloom differed between rapeseed ‘Humus’ and rapeseed ‘Essex’, and soil biology may be sensitive to slight differences in chemical composition (Gardiner et al., 1999).

The uncertainty surrounding trophic classification of *Coslenchus* sp. and other Tylenchidae (Bongers and Bongers, 1998; Yeates, 1987) is a problem magnified in this study. Large populations of *Coslenchus* were observed in rapeseed and rye (Fig. 4.8), and inclusion of half their abundance as cp-2 fungivores resulted in the detection of more treatment differences. High initial populations of *Coslenchus* were primarily found in rapeseed plots in Exp. 1, but high abundances of *Coslenchus* in rapeseed and rye in the other two experiments suggests that an attribute of either the living or decaying rhizosphere or tissue-amended soil, sustained these populations. Ilmarinen et al. (2005) reported that *Coslenchus* populations paralleled root biomass trends as plants were defoliated at different times during the growing season, while arbuscular mycorrhizal population trends were unaffected by defoliation. Other members of the Tylenchidae

family also correlated positively with root biomass in a grassland study (Viketoft et al., 2005). In this study, populations were abundant during soybean and corn growth in summer, and not high during rapeseed growth in November in Exp. 3 (Fig. 4.8). More frequent sampling during cover crop growth and across experiments would have helped clarify whether the living roots of cover crops were influential in hosting high *Coslenchus* populations.

Increasing indications of fungal feeding behavior in Tylenchidae nematodes (Häněl, 2003; Magnusson, 1983; McSorley and Frederick, 1999; Okada et al., 2005) suggests that *Coslenchus* should be targeted for further study. Yeates et al. (1993) classified *Coslenchus* and Tylenchidae nematodes as epidermal cell/root hair feeders, but facultative root hair-fungal hyphae may be more accurate than categorization into one group. It remains to be understood how to appropriately place them in index calculations based on ecological behavior. This study suggests that like *Aphelenchoides* (Tables 4.3 and 4.4) (Porazinska et al., 1999; Wang et al., 2004), *Coslenchus* also can respond like an opportunist r-selected organism. Similarly, McSorley and Frederick (1999) observed rapid increases of another Tylenchidae nematode, *Filenchus*, after organic matter addition.

#### 4.3. Nematode community succession and structure

Winter-terminated cover crops had higher BaMI, FuMI,  $\Sigma$ MI25, and SI values relative to spring-terminated cover crops (Table 4.9), despite the other disturbances which followed their addition to the soil, including tillage in April (Exps. 1 and 2), tillage and fertilization (P, K, B, S) in May at planting (Exp. 2), herbicide spray in April and

early June (Exp. 3), and lime application at planting in May (Exp. 3). Exposure to inorganic nitrogen fertilizers in a lab study, decreased abundance of cp-4 and cp-5 nematodes (Tenuta and Ferris, 2004), but high BaMI, FuMI,  $\Sigma$ MI25, and SI values in winter-killed cover crops suggested that cover crop effects were stronger than the potentially disturbing influence of nitrogen fertilization. Fewer effects on the BaMI or FuMI at CMREC may be the result of no-till management practices, lime application in spring, or fertilization with organic matter in the fall. Low soil pH has been shown to increase fungivore abundance, though often attributed to indirect effects on soil moisture or food resources (Korthals et al., 1996; Murray et al., 2006).

Fiscus and Neher (2002) showed that direct and indirect effects of disturbance can have different impacts on the same genera. While nematode response to direct and indirect effects cannot be distinguished in this study, it is likely that winter-terminated cover crops had more indirect effects on nematode communities, particularly in summer and fall, while spring-terminated cover crops may have had some direct effects, especially in June. Plant-parasitic nematodes, for example, may have been directly affected by spring-terminated covers. Inclusion of plant-parasitic nematodes in the  $\Sigma$ MI25 showed more treatment effects, compared to the MI25, which excludes all plant nematodes, or compared to the SI, which includes half of the plant associates (Figs. 4.10 and 11; MI25 not shown). Bongers (1990) noted that when a nematode community had a lower MI due to enrichment, generally the density (abundance per volume of soil) of nematodes was higher. In this study, rapeseed 'Essex' or rye treatments had greater abundances of nematodes in June 2005 (Exps. 2 and 3) than control plots (Tables 4.4 and 4.5). Inclusion of plant parasites in the  $\Sigma$ MI25 contributed to detection of more treatment

differences because on some dates (both in June or August) percentages of plant parasites (excluding plant associates) were significantly lower in rapeseed 'Essex' or rye compared to the control plots or a radish plot (data not shown). Inclusion of the total plant associate abundance also contributed to greater detection of treatment effects, and may account for the similarities between the trends of the  $\Sigma MI_{25}$  and the SI. These results may suggest that cover crop termination in spring has a greater influence in disturbing plant-parasitic nematode community structure, whether through indirect or direct effects, than winter-killed cover crops which may have little opportunity to influence plant-parasitic nematodes through indirect effects in the short-term.

Overall, nematode communities had surprisingly abundant and diverse populations of cp 3-5 nematodes in this study, despite cultivation and numerous agronomic disturbances. According to Ferris et al. (2001) SI values greater than 50 indicate a stable community. Structure index values were rarely below 50 on any sampling date in this study. One possible explanation may be the abundant habitable pore space (Elliot and Coleman, 1980) in the loamy sand surface soil texture of the experimental sites. In a grassland nematode community comparison, Yeates and Bongers (1999) show that sandy soils had higher MI values, omnivorous nematode abundance, and fungivore abundance. These observations suggest that absolute values of nematode indices cannot be compared without consideration of soil texture.

It is possible also that high index values observed in this study were the result of uncertainties with regard to assignment of some genera into feeding groups.

*Mylonchulus* is in the Mononchidae family, and like *Mononchus*, probably feeds on bacteria as a juvenile (Yeates, 1987). *Tylencholaimus* (included in Leptonchidae) has



been considered a facultative root hair/fungal feeder (Sohlenius, 1977), and *Aporcelaimus*, related to *Aporcelaimellus*, has been observed to rapidly recolonize fumigated soils (contrary to K-selected behavior) (Yeates and van der Meulen, 1996), which may be an effect of feeding on algae, common to other Dorylaimidae (Ettema and Bongers, 1993). Observation of algae in the gut, indicated by green pigmentation, of omnivore and predator nematodes was common in this study.

## **5. Conclusion**

Fall planted cover crops altered nematode communities and these effects lasted six to nine months after cover crop termination. Radishes and mustard winter-killed, while rapeseed cultivars and rye were terminated in spring; weeds were probably terminated in both seasons. Nematode community composition in summer and fall after cover crop termination appeared to reflect the timing and identity of the organic material additions, though the effects could not be isolated in this study. Response variables measured in control plots tended to be similar to either winter or spring killed cover crops and rarely opposite in trend from cover crops as a group.

Decomposition of N rich radishes stimulated dauer formation, which were present in high numbers even in summer and fall. High EI values in radish plots in summer of the 2005 experiments may have been partly a result of dauer larvae recovering from dormancy. Further research, in the laboratory and the field, is needed to understand how dauer larvae influence N-mineralization, especially when they recover from dormancy, potentially months later. Dauer larvae may also serve as a food source for nematodes or

other organisms of higher trophic levels. This potentially would transfer carbon more efficiently (given that nematodes in the dauer state are rich in lipids), and according to Ferris and Bongers (2006) higher sustained populations of upper trophic levels increases opportunity for plant-parasitic nematode control through top-down predation.

Rapeseed and rye increased fungivore activity as indicated by higher abundances of fungivores, high CI values, and possibly indicated by high populations of *Coslenchus*. Further studies on Tylenchidae, and especially *Coslenchus*, feeding preferences and responses to organic matter amendment are needed to determine the ecological and management implications of these population increases. This is also particularly important with regard to understanding how Tylenchidae should be placed in community indices. Allocation of half the abundance of plant associates as fungivores may have overestimated treatment effects determined by index values.

By summer or fall, community succession was greater following winter-killed cover crops than following spring killed cover crops, as indicated by higher FuMI, BaMI,  $\Sigma$ MI25 or SI values in contrasts. Lower MI values in these experiments were indicative of a highly active decomposer community and therefore may be more preferable in agronomic systems. However, greater community resilience and diversity may also be important for top-down regulation of the food web. Future studies should investigate the potential for both sustained active bacterivore and fungivore decomposer communities, and simultaneously basal and structured food webs, by combining forage radish with rye or rapeseed 'Essex' into a single cover crop treatment. Future research should also include a fine-rooted, high carbon biomass cover crop, such as winter-killing oats, to help

elucidate whether timing of cover crop termination or cover crop chemistry is more dominant in shaping the soil food web under similar environmental conditions.

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**Table 4.2.** Free-living nematode community index calculations.

<b>Index</b>	<b>Calculation<sup>a</sup></b>
BaMI <sup>b</sup>	cp-1(1) + cp-2(2) + cp-3(3) + cp-4(4)
FuMI <sup>c</sup>	cp-2(2) + cp-3(3) + cp-4(4)
ΣMI25 <sup>d</sup>	cp-2(2) + cp-3(3) + cp-4(4) + cp-5(5)
MI25 <sup>e</sup>	cp-2(2) + cp-3(3) + cp-4(4) + cp-5(5)
basal component (b)	(cp-2 bacterivores + cp-2 fungivores)*0.8
enrichment component (e)	(cp-1 bacterivores*3.2) + (cp-2 fungivores*0.8)
structure component (s)	cp-3(1.8) + cp-4(3.2) + cp-5(5.0)
EI <sup>bf</sup>	(e/(e+b))*100
CI <sup>bf</sup>	((cp-2 fungivores*0.8)/e)*100
SI <sup>f</sup>	(s/(s+b))*100

<sup>a</sup> Indices calculated using proportions for maturity indices (Bongers, 1990) and abundances for calculation of b, e, s, which are used in proportions for calculation of EI, CI, and SI (Ferris et al., 2001).

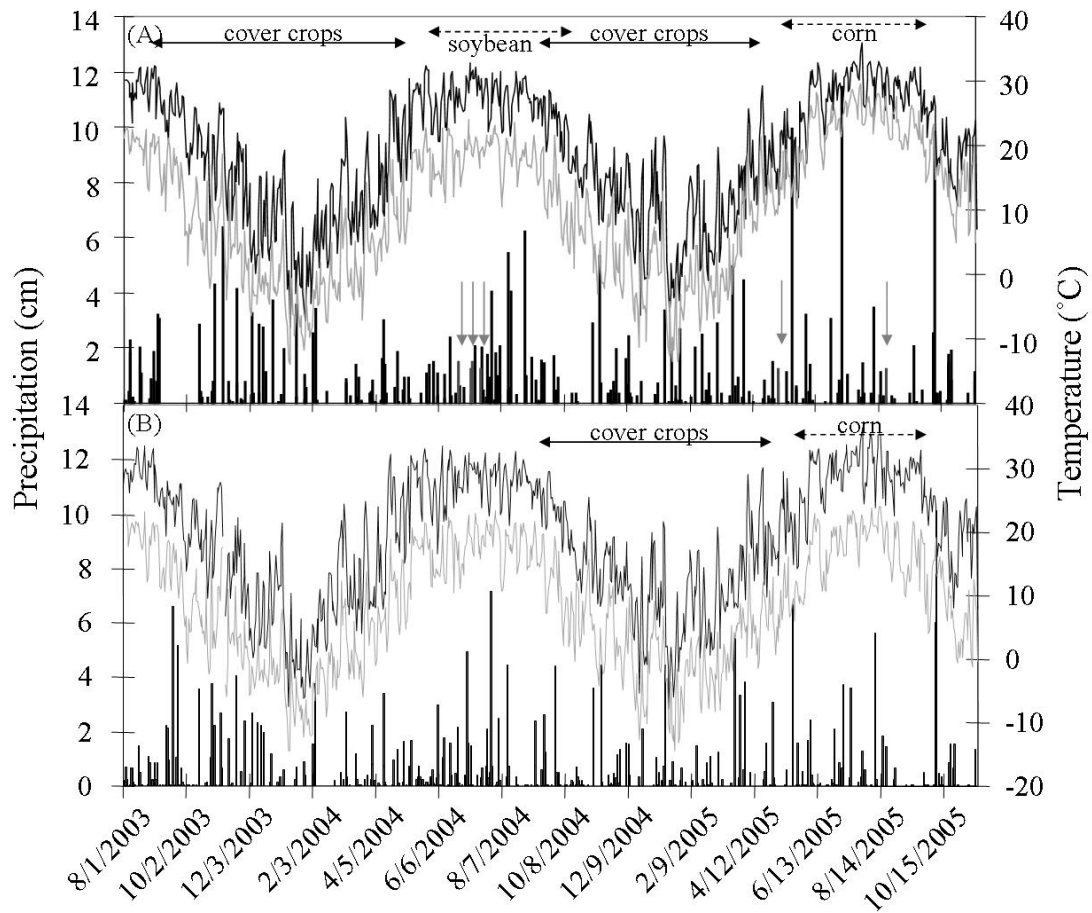
<sup>b</sup> Dauer larvae were not included as cp-1 bacterivores for these calculations.

<sup>c</sup> Plant associates were not included in calculation of this index.

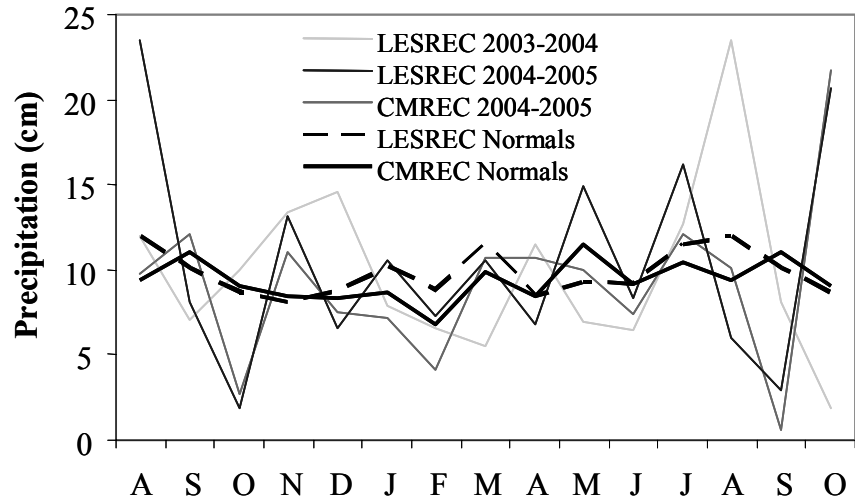
<sup>d</sup> Total maturity index including plant parasites, plant associates, and free-living nematodes ranked cp 2-5 (Yeates, 1994).

<sup>e</sup> Includes only free-living nematodes (Bongers and Korthals, 1993).

<sup>f</sup> half of plant associate abundance was assigned to the fungivore trophic group (H. Ferris, personal communication, 2007).



**Figure 4.1.** Daily precipitation and daily average high and low temperatures for 2003-2005 at A) LESREC and B) CMREC. Solid horizontal arrows indicate duration of cover crop growth and dashed lines represent cash crop growth. Vertical arrows indicate irrigation events (available at LESREC only).



**Figure 4.2.** Average monthly rainfall during experimental years by site compared with monthly normals from 1971-2000 (Maryland State Climatologist Office, 2007).

**Table 4.2.** Nematode genera found across all dates from two sites in Maryland, grouped within respective trophic classifications (Yeates et al., 1993) and assigned superscript numbers signifying colonizer-persister ranks (Bongers and Bongers, 1998) used for index calculations in this study.

<b>Bacterivores</b>	<b>Fungivores</b>	<b>Omnivores</b>	<b>Predators</b>
<i>Acrobeles</i> <sup>2</sup>	<i>Aphelenchoides</i> <sup>2</sup>	<i>Aporcelaimellus</i> <sup>5</sup>	<i>Anatonchus</i> <sup>4</sup>
<i>Acrobeloides</i> <sup>2a</sup>	<i>Aphelenchus</i> <sup>2</sup>	Dorylaimidae <sup>4</sup>	<i>Clarkus</i> <sup>4</sup>
<i>Alaimus</i> <sup>4</sup>	<i>Diphtherophora</i> <sup>3</sup>	<i>Ecumenicus</i> <sup>4</sup>	<i>Discolaimus</i> <sup>5</sup>
<i>Amphidelus</i> <sup>4</sup>	Leptonchidae <sup>4c</sup>	<i>Lordellonema</i> <sup>4</sup>	<i>Mylonchulus</i> <sup>4</sup>
<i>Anaplectus</i> <sup>2</sup>	<i>Leptonchus</i> <sup>4</sup>	<i>Mesodorylaimus</i> <sup>4</sup>	<i>Nygolaimus</i> <sup>5</sup>
<i>Bastiana</i> <sup>3</sup>	<i>Tylolaimophorous</i> <sup>3</sup>	<i>Microdorylaimus</i> <sup>4</sup>	<i>Paractinolaimus</i> <sup>5</sup>
<i>Bunonema</i> <sup>1</sup>			<i>Paraxonchium</i> <sup>5</sup>
<i>Ceratoplectus</i> <sup>2</sup>			Predator ( <i>Trischistoma</i> ) <sup>3f</sup>
<i>Cervidellus</i> <sup>2</sup>			Qudsianematidae <sup>4g</sup>
<i>Cruznama</i> <sup>1</sup>			<i>Seinura</i> <sup>2</sup>
<i>Cylindrolaimus</i> <sup>2</sup>			<i>Thonus</i> <sup>4</sup>
dauer larvae (Rhabditidae) <sup>b</sup>			
<i>Diploscapter</i> <sup>1</sup>	<b>Plant Associates</b>	<b>Algivores</b>	<b>Plant Parasites</b>
<i>Drilocephalobus</i> <sup>2</sup>	<i>Boleodorus</i> <sup>2</sup>	<i>Achromadora</i> <sup>3</sup>	<i>Helicotylenchus</i> <sup>3</sup>
<i>Eumonhystera</i> <sup>2</sup>	<i>Coslenchus</i> <sup>2</sup>		<i>Heterodera</i> <sup>3</sup>
<i>Mesorhabditis</i> <sup>1</sup>	<i>Ditylenchus</i> <sup>2</sup>		<i>Hoplolaimus</i> <sup>3</sup>
<i>Odontolaimus</i> <sup>3</sup>	<i>Filenchus</i> <sup>2</sup>		<i>Longidorella</i> <sup>4</sup>
Panagrolaimidae <sup>1c</sup>	<i>Laimaphelenchus</i> <sup>2</sup>		<i>Paratrichodorus</i> <sup>4</sup>
<i>Plectus</i> <sup>2</sup>	<i>Miculenchus</i> <sup>2</sup>		<i>Pratylenchus</i> <sup>3</sup>
<i>Prismatolaimus</i> <sup>3</sup>	<i>Psilenchus</i> <sup>2</sup>		<i>Quinisulcius</i> <sup>2</sup>
<i>Pristionchus</i> <sup>1</sup>	Tylenchidae <sup>2</sup>		<i>Trichodorus</i> <sup>4</sup>
<i>Prodontorhabditis</i> <sup>1d</sup>			<i>Tylenchorhynchus</i> <sup>2</sup>
Rhabditidae <sup>1</sup>			<i>Xiphinema</i> <sup>5</sup>
<i>Rhabditis</i> <sup>1</sup>			
<i>Teratocephalus</i> <sup>3</sup>			
<i>Tylocephalus</i> <sup>2</sup>			
<i>Wilsonema</i> <sup>2</sup>			
<i>Zeldia</i> <sup>2</sup>			

<sup>a</sup> *Acrobeloides* was the dominant genera, but this group may include some similar genera like *Cephalobus*.

<sup>b</sup> Rhabditidae dauer larvae were not used in index calculations.

<sup>c</sup> Panagrolaimidae were primarily *Panagrolaimus* or *Panagrobelus*.

<sup>d</sup> *Prodontorhabditis* abundance also included *Protorhabditis*, due to name recording errors.

<sup>e</sup> Leptonchidae included *Tylencholaimus* and *Tylencholaimellus*.

<sup>f</sup> Predator included *Tobrilus* and *Trischistoma*, though predominantly the latter.

<sup>g</sup> Qudsianematidae was used to represent an unknown nematode genera resembling *Labronema*.

**Table 4.3.** Abundances of nematode genera, family, or trophic groups that were affected by treatments on at least one of the three sampling dates in Experiment 1.

Nematode group or genera <sup>a</sup>	21 April 2004										11 June 2004										19 September 2004														
	Rape			Forage			Oilseed			Cntrl	Rape			Forage			Oilseed			Cntrl	Rape			Forage			Oilseed			Cntrl					
	Essex	Radish	Humus	Essex	Radish	Humus	Must	Essex	Radish		Humus	Must	Essex	Radish	Humus	Must	Essex	Radish	Humus		Must	Essex	Radish	Humus	Must	Essex	Radish	Humus	Must						
----- nematodes 10 <sup>3</sup> /m <sup>2</sup> -----																																			
<b>Bacterivores</b>																																			
<i>Cylindrolaimus</i> <sup>2</sup>	38.4 ab <sup>b</sup>	64.3 a	88.3 a	20.6 b	16.0	11.9	7.6	28.5	17.6	13.4	10.8	12.6	12.7	26.0	15.4	15.4	15.4	15.4	15.4	15.4	15.4	15.4	15.4	15.4	15.4	15.4	15.4	15.4	15.4	15.4	15.4	15.4	15.4	15.4	15.4
Dauer larvae	48.8 c	1096.7 a	338.4 b	70.0 c	254.3 c	328.8 bc	341.8 bc	752.7 ab	868.8 a	146.4 c	116.7 ab	182.1 ab	118.5 ab	330.2 a	237.3 ab	84.4 b	84.4 b	84.4 b	84.4 b	84.4 b	84.4 b	84.4 b	84.4 b	84.4 b	84.4 b	84.4 b	84.4 b	84.4 b	84.4 b	84.4 b	84.4 b	84.4 b	84.4 b	84.4 b	84.4 b
Panagrolaimidae <sup>1</sup>	227.8	137.3	137.5	170.9	143.4	252.6	239.1	204.5	323.3	298.2	65.8 b	99.5 ab	165.1 a	90.3 ab	111.7 ab	86.8 ab	86.8 ab	86.8 ab	86.8 ab	86.8 ab	86.8 ab	86.8 ab	86.8 ab	86.8 ab	86.8 ab	86.8 ab	86.8 ab	86.8 ab	86.8 ab	86.8 ab	86.8 ab	86.8 ab	86.8 ab	86.8 ab	86.8 ab
<b>Fungivores</b>																																			
<i>Aphelenchooides</i> <sup>2</sup>	59.8	20.5	15.0	42.9	81.1 b	244.6 a	108.6 ab	101.7 ab	59.3 b	95.8 ab	46.9 ab	128.9 a	28.8 b	38.8 ab	56.8 ab	27.9 b	27.9 b	27.9 b	27.9 b	27.9 b	27.9 b	27.9 b	27.9 b	27.9 b	27.9 b	27.9 b	27.9 b	27.9 b	27.9 b	27.9 b	27.9 b	27.9 b	27.9 b	27.9 b	27.9 b
<i>Leptonchus</i> <sup>4</sup>	101.8 a	98.7 a	56.4 ab	37.2 b	154.1	183.9	162.2	99.7	107.8	107.5	16.5	26.8	28.5	12.2	24.7	33.3	33.3	33.3	33.3	33.3	33.3	33.3	33.3	33.3	33.3	33.3	33.3	33.3	33.3	33.3	33.3	33.3	33.3	33.3	33.3
<b>Total</b>	262.7	242.2	151.7	200.3	435.9 ab	851.9 a	662.8 ab	370.8 ab	308.5 b	383.0 ab	181.2	241.8	124.1	112.1	123.2	130.5	130.5	130.5	130.5	130.5	130.5	130.5	130.5	130.5	130.5	130.5	130.5	130.5	130.5	130.5	130.5	130.5	130.5	130.5	130.5
<b>Plant Associates</b>																																			
<i>Coslenchus</i> <sup>2</sup>	368.6 a	29.3 b	29.9 b	23.9 b	34.8 ab	242.1 a	228.4 ab	8.9 b	40.1 ab	17.8 b	20.4	188.2	85.1	5.9	10.0	16.3	16.3	16.3	16.3	16.3	16.3	16.3	16.3	16.3	16.3	16.3	16.3	16.3	16.3	16.3	16.3	16.3	16.3	16.3	16.3
Tylenchidae <sup>2</sup>	127.3 a	55.0 b	75.4 ab	84.3 ab	20.5	28.2	4.8	14.4	18.4	13.9	2.1	0.0	1.7	3.9	0.0	9.8	9.8	9.8	9.8	9.8	9.8	9.8	9.8	9.8	9.8	9.8	9.8	9.8	9.8	9.8	9.8	9.8	9.8	9.8	9.8
<b>Total</b>	519.8 a	104.7 b	124.3 b	131.2 b	80.5	321.7	264.8	98.0	96.1	89.9	56.0 b	202.4 a	121.0 ab	32.5 b	20.5 b	79.9 b	79.9 b	79.9 b	79.9 b	79.9 b	79.9 b	79.9 b	79.9 b	79.9 b	79.9 b	79.9 b	79.9 b	79.9 b	79.9 b	79.9 b	79.9 b	79.9 b	79.9 b	79.9 b	
<b>Omnivores</b>																																			
<i>Ecumenicus</i> <sup>4</sup>	23.5	34.4	10.8	27.7	97.6	59.4	60.0	112.8	62.9	84.5	2.9 ab	7.1 ab	15.7 a	0.0 b	0.0 b	9.3 ab	9.3 ab	9.3 ab	9.3 ab	9.3 ab	9.3 ab	9.3 ab	9.3 ab	9.3 ab	9.3 ab	9.3 ab	9.3 ab	9.3 ab	9.3 ab	9.3 ab	9.3 ab	9.3 ab	9.3 ab	9.3 ab	9.3 ab
<b>Predators</b>																																			
<i>Thonus</i> <sup>4</sup>	4.1 b	3.3 b	12.9 a	10.3 ab	20.6	3.4	0.0	0.0	0.0	0.0	3.9	0.0	0.0	0.0	0.0	3.1	3.1	3.1	3.1	3.1	3.1	3.1	3.1	3.1	3.1	3.1	3.1	3.1	3.1	3.1	3.1	3.1	3.1	3.1	3.1

<sup>a</sup> Colonizer-persister score according to Bongers and Bongers (1998).

<sup>b</sup> Means with the same letter are not significantly different within a single date and row at  $P \leq 0.10$  (HSD).

**Table 4.4.** Abundances of nematode genera, family, or trophic groups that were affected by treatments on at least one of the two sampling dates in Experiment 2.

Nematode group or genera <sup>a</sup>	4 June 2005						20 August 2005											
	Must	Rape		Forage		Oilseed	Cntrl	Rye	nematodes 10 <sup>3</sup> /m <sup>2</sup>	Must	Rape		Forage		Oilseed	Cntrl	Rye	
		Essex	Radish	Radish	Oilseed						Essex	Radish	Radish	Oilseed				
<b>Bacterivores</b>																		
<i>Acrobelus</i> <sup>2</sup>	21.8 <sup>b</sup>	149.4	20.7	22.1	14.5	19.9	19.4 ab	19.4 ab	3.1 b	32.7 a	8.4 ab	8.4 ab	13.1 ab	6.3 b				
<i>Acrobeloides</i> <sup>2</sup>	507.2 b	364.9 b	350.6 b	331.6 b	466.7 b	1149.2 a	47.2	47.2	47.5	62.3	44.4	44.4	61.4	57.1				
<i>Ceratoplectus</i> <sup>2</sup>	0.0	0.0	6.3	3.4	9.3	8.1	9.9 ab	9.9 ab	3.2 ab	8.5 ab	11.5 a	11.5 a	2.0 ab	0.0 b				
Dauer larvae	328.4 c	928.6 ab	1370.5 a	981.5 a	390.6 bc	840.3 abc	196.6 bc	196.6 bc	493.6 ab	585.3 a	266.4 abc	266.4 abc	97.5 c	356.6 ab				
Panagrolaimidae <sup>1</sup>	87.5 b	86.4 b	201.7 b	143.0 b	95.0 b	639.2 a	36.6	36.6	52.9	55.2	41.1	41.1	35.7	62.1				
<i>Prodonatorhabditis</i> <sup>1</sup>	1.9	9.9	1.6	6.0	2.0	4.1	0.8 b	0.8 b	7.7 ab	0.9 b	2.4 ab	2.4 ab	2.3 ab	14.9 a				
<b>Total</b>	1261.3 b	1930.7 b	2255.2 b	1742.2 b	1233.2 b	3388.6 a	559.6 ab	559.6 ab	943.0 ab	962.7 ab	575.8 ab	575.8 ab	392.5 b	795.6 a				
<b>Total</b> (without dauer)	932.8 bc	1002.1 bc	884.6 b	760.7 bc	842.6 c	2548.3 a	363.0	363.0	449.4	377.4	309.4	309.4	295.0	439.0				
<b>Fungivores</b>																		
<i>Aphelenchooides</i> <sup>2</sup>	151.9 bc	260.0 b	122.3 bc	58.7 c	130.7 bc	1189.6 a	27.5 b	27.5 b	69.9 ab	25.0 b	19.2 b	19.2 b	24.1 b	167.8 a				
<i>Diphtherophora</i> <sup>3</sup>	19.6	23.5	11.7	11.7	30.4	55.2 a	11.5 c	11.5 c	18.3 bc	31.1 ab	40.9 a	40.9 a	35.5 ab	45.3 a				
Leptonchidae <sup>4</sup>	9.6	7.6	11.5	12.4	0.0	3.6	8.9 ab	8.9 ab	0.9 b	0.8 b	15.4 a	15.4 a	5.3 ab	6.3 ab				
<i>Leptonchus</i> <sup>4</sup>	33.6 ab	17.1 b	40.9 ab	15.6 b	30.5 ab	66.1 a	37.4 ab	37.4 ab	44.0 ab	15.12 b	40.5 ab	40.5 ab	14.4 b	63.5 a				
<b>Total</b>	338.3 bc	404.1 ab	211.3 bc	138.0 c	298.9 bc	1356.3 a	111.3 b	111.3 b	156.1 ab	77.6 b	122.8 ab	122.8 ab	103.7 b	289.2 a				
<b>Plant Associates</b>																		
<i>Coslenchus</i> <sup>2</sup>	224.0 bc	590.7 ab	24.7 d	71.9 cd	146.2 c	713.8 a	70.8 b	70.8 b	238.5 ab	25.8 b	36.8 b	36.8 b	125.0 b	403.8 a				
<b>Total</b>	276.2 ab	671.1 a	98.1 b	150.0 b	208.8 ab	773.2 a	120.9 bcd	120.9 bcd	260.3 ab	42.4 d	49.7 cd	49.7 cd	140.0 abc	443.3 a				
<b>Predators</b>																		
<i>Mylonchulus</i> <sup>4</sup>	17.7 ab	23.3 ab	4.1 c	35.3 a	16.5 ab	8.0 bc	6.4	6.4	14.6	10.7	12.3	12.3	17.8	10.1				
<i>Nygolaimus</i> <sup>5</sup>	25.4	40.8	21.3	18.9	23.9	62.9	31.1	31.1	36.2	11.3	20.5	20.5	14.3	21.3				
<b>Plant Parasites</b>																		
<b>Total</b>	135.1 d	143.7 c	154.6 b	66.3 f	95.7 e	322.8 a	526.5 a	526.5 a	404.9 ab	386.2 ab	385.8 ab	385.8 ab	350.8 ab	124.5 b				
<b>Total</b> (without dauer)	2245.3 b	3404.7 b	2946.2 b	2359.8 b	2221.2 b	6153.5 a	1495.5 ab	1495.5 ab	1939.9 ab	1604.5 ab	1315.2 ab	1315.2 ab	1124.2 b	1797.2 a				
<b>Total</b> (without dauer)	1916.9 b	2476.1 b	1575.6 b	1378.2 b	1830.6 b	5313.2 a	1298.9 ab	1298.9 ab	1446.2 ab	1019.2 ab	1048.9 ab	1048.9 ab	1026.7 b	1440.6 a				

<sup>a</sup> Colonizer-persister score according to Bongers and Bongers (1998).

<sup>b</sup> Means with the same letter are not significantly different within a single date and row at  $P \leq 0.10$  (HSD).

**Table 4.5.** Abundances of nematode genera, family, or trophic groups that were affected by treatments on at least one of the three sampling dates at CMREC.

Nematode group or genera <sup>a</sup>	3 November 2004				11 June 2005				17 August 2005				
	Rape Essex	Forage Radish	Oilseed Radish	Cntrl	Rape Essex	Forage Radish	Oilseed Radish	Cntrl	Rape Essex	Forage Radish	Oilseed Radish	Cntrl	Rye
<b>Bacterivores</b>													
<i>Alaimus</i> <sup>4</sup>	29.2 <sup>b</sup>	26.5	22.3	49.9	12.8 ab	4.1 b	13.1 ab	22.3 ab	15.4	19.8	10.4	18.5	14.3
<i>Acroboloides</i> <sup>2</sup>	128.0	65.6	123.4	98.2	68.0 a	17.5 b	47.9 ab	29.7 ab	40.5	39.0	23.2	40.5	44.5
Dauer larvae	113.3	80.0	98.7	76.3	66.0 c	1199.6 a	893.6 a	90.1 bc	73.2 b	702.3 a	675.6 a	95.1 b	136.1 b
<b>Total</b> (without dauer)	585.0	468.5	501.5	626.7	445.5	246.7	424.3	392.0	336.9 a	244.8 ab	178.7 b	289.8 ab	347.1 a
<b>Fungivores</b>													
<i>Aphelenchoides</i> <sup>2</sup>	27.8 ab	28.2 ab	50.9 a	14.2 b	12.3	10.7	8.1	8.2	20.8	20.6	12.8	11.3	25.3
<i>Aphelenchus</i> <sup>2</sup>	34.7	31.1	24.0	31.1	50.8 a	26.0 a	15.2 ab	30.5 ab	36.1	10.5	8.6	21.3	5.2
<i>Diphtherophora</i> <sup>3</sup>	59.0	29.0	41.3	39.9	40.8	27.1	24.6	29.8	71.6 abc	41.0 c	55.4 bc	85.0 ab	164.7 a
Leptonchidae <sup>3</sup>	21.6	9.1	2.2	7.3	20.0 a	6.8 ab	16.4 ab	9.2 ab	26.3 a	3.1 ab	10.1 ab	6.7 ab	0.0 b
<b>Total</b>	145.7	99.3	122.3	92.6	125.3	70.5	65.3	77.7	154.6 ab	75.1 b	86.9 b	125.2 ab	197.2 a
<b>Plant Associates</b>													
<i>Coslenchus</i> <sup>2</sup>	43.3 b	41.6 b	37.3 b	89.9 a	575.5 a	18.8 c	77.2 b	87.2 b	482.9 a	48.3 b	53.6 b	72.9 b	545.1 a
<b>Total</b>	61.0	58.3	57.9	120.4	598.3 a	21.4 c	113.7 b	104.1 b	500.2 a	59.8 b	84.3 b	106.2 b	567.6 a
<b>Omnivores</b>													
<i>Aporcelaimellus</i> <sup>5</sup>	32.5	20.5	34.0	25.8	39.7 ab	33.2 b	78.8 a	68.6 ab	29.8	33.8	30.3	31.4	21.4
<i>Mesodorylaimus</i> <sup>4</sup>	21.6	17.6	7.9	22.6	38.8	43.0	53.6	68.5	49.3 ab	26.1 b	44.9 ab	38.8 b	98.2 a
<b>Predators</b>													
<i>Mylonchulus</i> <sup>4</sup>	61.4 a	24.4 ab	13.4 b	35.9 ab	41.4	22.5	11.2	61.2	21.7	35.2	10.3	14.0	32.0
<b>Overall Totals</b> (without dauer)	1295.5	1026.9	1056.1	1288.6	1608.5 a	794.1 b	1145.8 ab	1140.3 ab	1855.3	1210.4	1119.0	1340.1	1803.3

<sup>a</sup> colonizer-persister score according to Bongers and Bongers (1998).

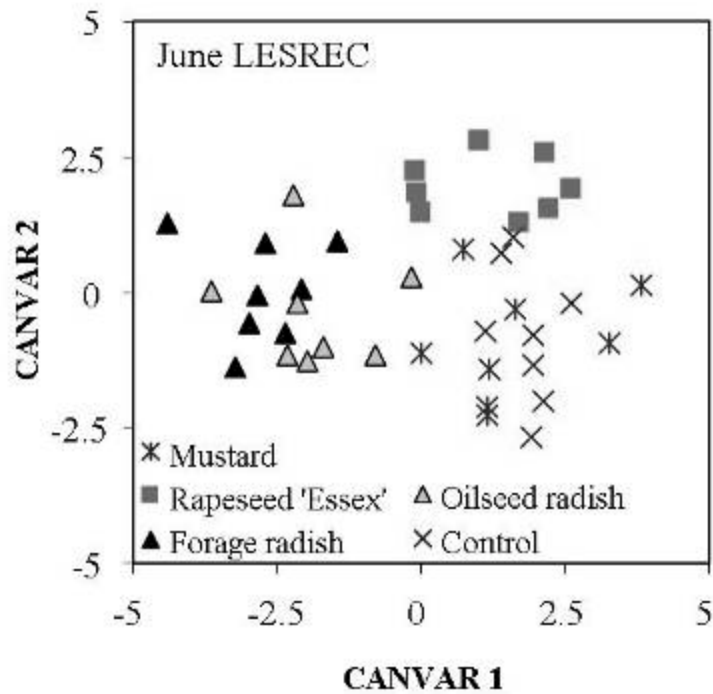
<sup>b</sup> Means with the same letter are not significantly different within a single date and row at  $P \leq 0.10$  (HSD).



**Table 4.6.** Percent N in cover crop dry matter before cover crop termination. Data from three experiments at two sites in Maryland. Data were not available for all treatments.

Site	Harvest Date <sup>a</sup>	Cover crop	Plant Part (root/shoot)	% N
<b>Experiment 1</b>				
	25-Apr-04	Rapeseed E	R	0.89
		Rapeseed E	S	1.87
		Rapeseed H	R	0.91
		Rapeseed H	S	1.61
		Weeds	S	1.65
<b>Experiment 2</b>				
	8-Nov-04	Forage	R	2.00
		Forage	S	4.44
	13-Apr-05	Rapeseed E	S	2.89
		Rye	S	2.24
<b>Experiment 3</b>				
	30-Oct-04	Forage	R	3.12
		Forage	S	3.94
		Oilseed	R	2.86
		Oilseed	S	3.94
	23-Apr-05	Rapeseed E	R	1.42
		Rapeseed E	S	2.66
		Rye	S	1.61

<sup>a</sup> Planting dates of cover crops for Exp. 1, Exp. 2, and Exp. 3 were 25, 27, and 25 August respectively. Winter-kill date for radishes was early December in 2004 and late December to early January for 2005. Spring cover crops were terminated on the cover crop harvest date in Exps. 1 and 2 and in Exp. 3 were herbicide-sprayed on 27 April 2005.

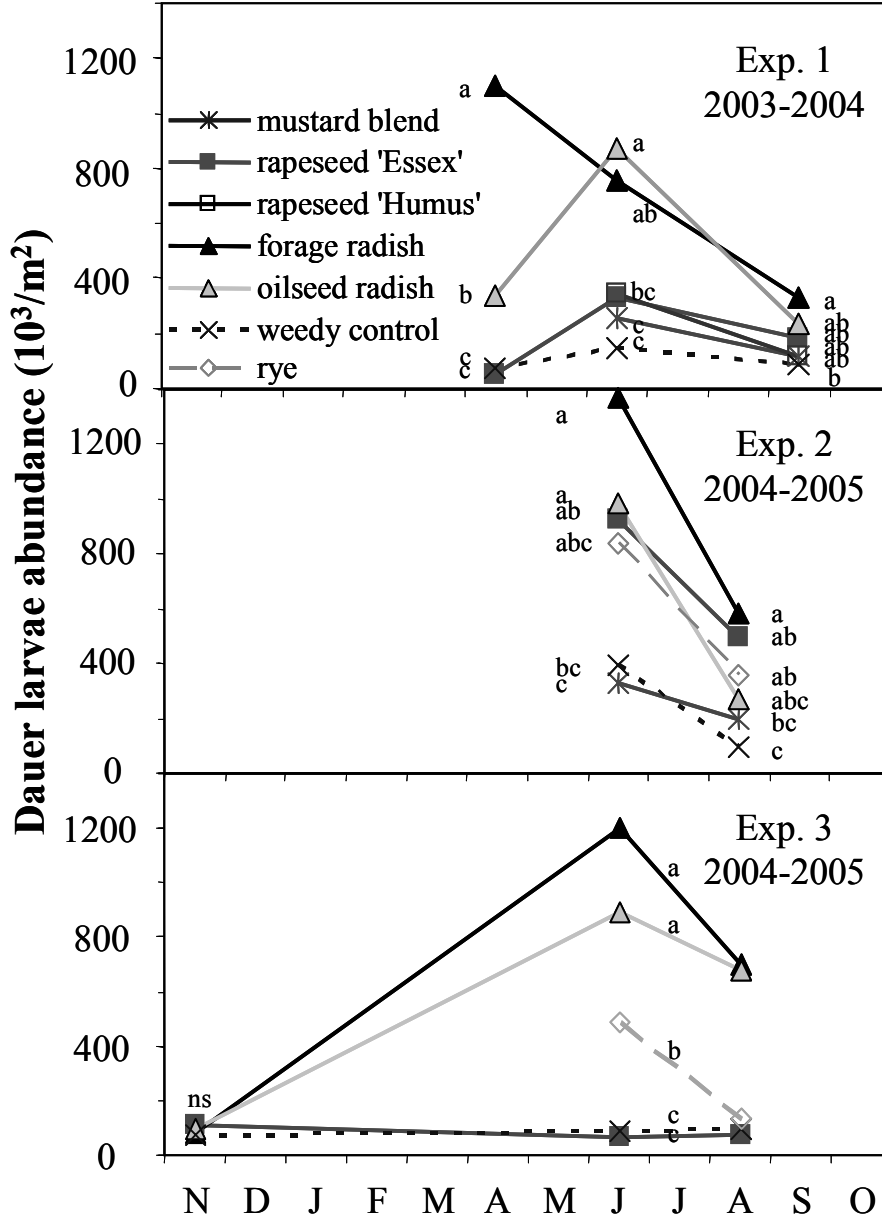


**Figure 4.3.** Results of canonical discriminant analysis of cover crop treatments using abundances of nematodes in cp-trophic groups from Exps. 1 and 2 sampled in June. Canonical variables (CANVARs) are linear functions derived by assigning coefficients to each trophic group variable such that the CANVAR will maximally discriminate between cover crop means. CANVAR 1 and 2 represented 71% and 20% of the variation, respectively, and CANVAR1 significantly discriminated between cover crop treatments ( $P < 0.01$ ).

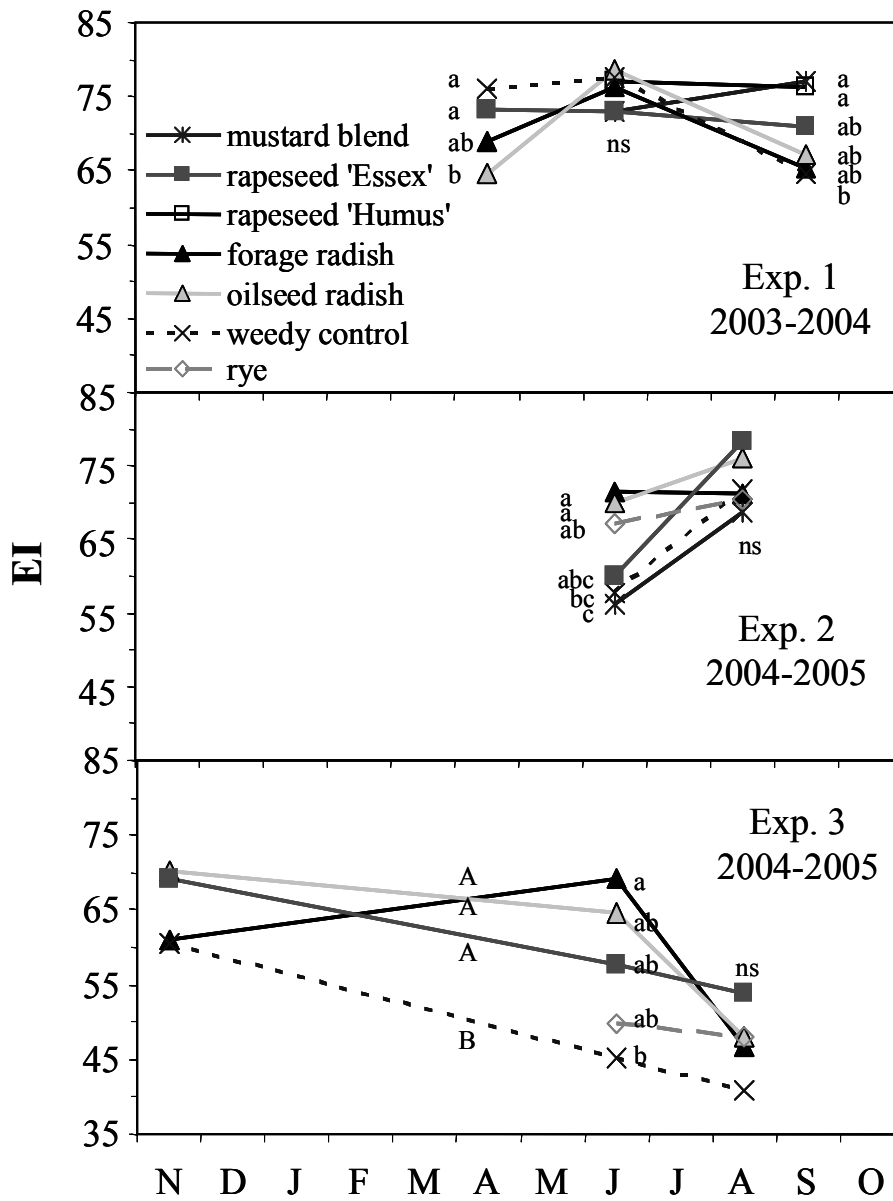
**Table 4.7.** Correlation coefficients (loadings) of trophic group variables with canonical variables (CANVARs) 1 and 2, depicted in Fig. 4.3. High loadings of nematode parameters on CANVARs indicate those variables which contributed the most to the CANVAR's discrimination between treatments.

Trophic group and cp rank	Total Canonical Structure	
	CANVAR 1	CANVAR 2
Dauer larvae	-0.72 <sup>****</sup>	0.36 <sup>*</sup>
Bacterivores cp-1	-0.16	0.34 <sup>*</sup>
Bacterivores cp-2	0.28 <sup>†</sup>	0.18
Bacterivores cp-4	-0.16	-0.15
Fungivores cp-2	0.39 <sup>*</sup>	0.59 <sup>****</sup>
Fungivores cp-3	0.03	0.24
Fungivores cp-4	0.10	-0.06
Predators cp-5	-0.20	-0.07
Omnivores cp-4	0.06	-0.13
Omnivores cp-5	-0.07	-0.13
Plant Associates cp-2	0.33 <sup>*</sup>	0.58 <sup>****</sup>
Plant Parasites cp-3	-0.12	-0.29 <sup>†</sup>
Plant Parasites cp-4	-0.74 <sup>****</sup>	0.33 <sup>*</sup>

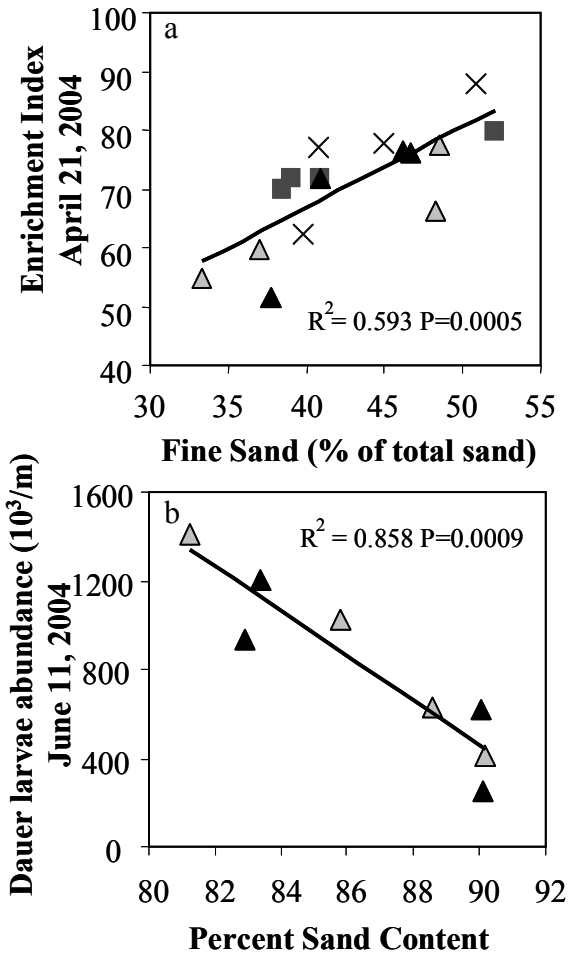
†, \*, \*\*, \*\*\*, \*\*\*\*  $P \leq 0.10, P \leq 0.05, P \leq 0.01, P \leq 0.001, P \leq 0.0001$



**Figure 4.4.** Daur larvae populations over time at two sites in Maryland after cover crop treatments sown in fall (August) and terminated in December/January (radishes and mustard) or mid-late April (rapeseed and rye). Capital letters represent means across three dates, and lower case letters represent means on a single date or across two dates. Means with the same letter are not significantly different at  $P \leq 0.10$  (HSD) ( $n=4$ ).



**Figure 4.5.** Enrichment index (EI) over time at two sites in Maryland after cover crop treatments were sown in fall (August) and terminated in December/January (radishes and mustard) or mid-late April (rapeseed and rye). Capital letters represent means across three dates, and lower case letters represent means on a given date. Means with the same letter are not significantly different at  $P \leq 0.10$  (HSD). Soil moisture was used as a covariate at LESREC Exp. 1 ( $n=4$ ).



**Figure 4.6.** Correlation between the enrichment index (EI) or dauer larvae abundance with soil textural properties at LESREC. Data were collected from plots planted to cover crops in August 2003, which winter freeze-killed (radishes) or were terminated by incorporation in April 2004 (rapeseed and weeds): rapeseed ‘Essex’ (squares), forage radish (black triangles), oilseed radish (gray triangles), and no cover crop (X).

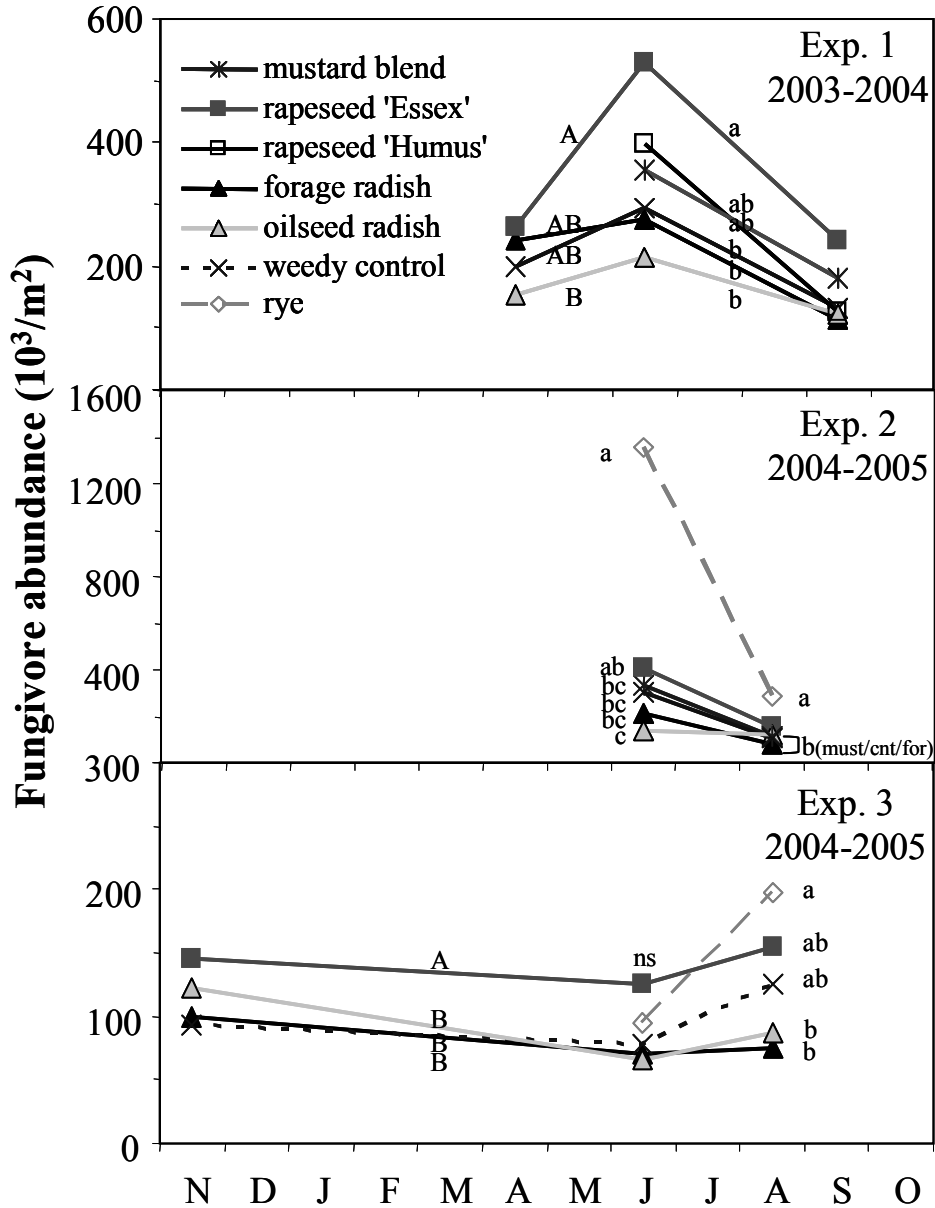
**Table 4.8.** Contrasts between winter-susceptible (radishes and mustard) and winter-hardy (rapeseed and rye) cover crops for fungivore abundances, *Coslenchus*, and the channel index (CI). Contrasts were conducted for each date or set of dates graphed in Figures 4.7, 4.8, and 4.9.

Parameter	Site	Date	Covers Contrasted	Winter Terminated	Spring Terminated
<b>Fungivore Abundance<sup>a</sup> (10<sup>3</sup>/m<sup>2</sup>)</b>					
Exp. 1	April-Sept June-Sept	radishes v. rapeseed 'Essex'		186.5	344.9*
		radishes and mustard v. rapeseeds 'Essex'/'Humus'		210.3	323.5**
	June August	radishes and mustard v. rapeseed 'Essex'/rye radishes and mustard v. rapeseed 'Essex'/rye		229.2 103.9	880.2**** 222.7***
Exp. 2	Nov-Aug June	radishes v. rapeseed 'Essex'		86.6	141.9***
	August	radishes v. rapeseed 'Essex'/rye radishes v. rapeseed 'Essex'/rye		67.9 81.0	110.5† 175.9**
<b><i>Coslenchus</i> sp. (10<sup>3</sup>/m<sup>2</sup>)</b>					
Exp. 1	April-Sept June September	radishes v. rapeseed 'Essex'		20.7	266.3****
		radishes and mustard v. rapeseeds 'Essex'/'Humus'		28.0	235.2*
	June August	radishes and mustard v. rapeseeds 'Essex'/'Humus'		12.1	136.6***
Exp. 2	June August	radishes and mustard v. rapeseed 'Essex'/rye radishes and mustard v. rapeseed 'Essex'/rye		106.9 44.5	652.2**** 321.2****
	November June August	radishes v. rapeseed 'Essex'		39.5	43.3
Exp. 3	June August	radishes v. rapeseed 'Essex'		48.0	521.1****
		radishes v. rapeseed 'Essex'/rye		50.9	514.0****
	November June-Aug	radishes v. rapeseed 'Essex'		14.8	9.9*
<b>Channel Index<sup>b</sup></b>					
Exp. 1	April-Sept June-Sept	radishes v. rapeseed 'Essex'		7.6	18.0****
		radishes and mustard v. rapeseeds 'Essex'/'Humus'		8.0	14.5**
Exp. 2	June August	radishes and mustard v. rapeseed 'Essex'/rye radishes and mustard v. rapeseed 'Essex'/rye		17.6 12.4	31.6**** 24.2***
	November June-Aug	radishes v. rapeseed 'Essex'		14.8	9.9*
		radishes v. rapeseed 'Essex'/rye		23.9	49.0****

†, \*, \*\*, \*\*\*, \*\*\*\*, P ≤ 0.10, P ≤ 0.05, P ≤ 0.01, P ≤ 0.001, P ≤ 0.0001

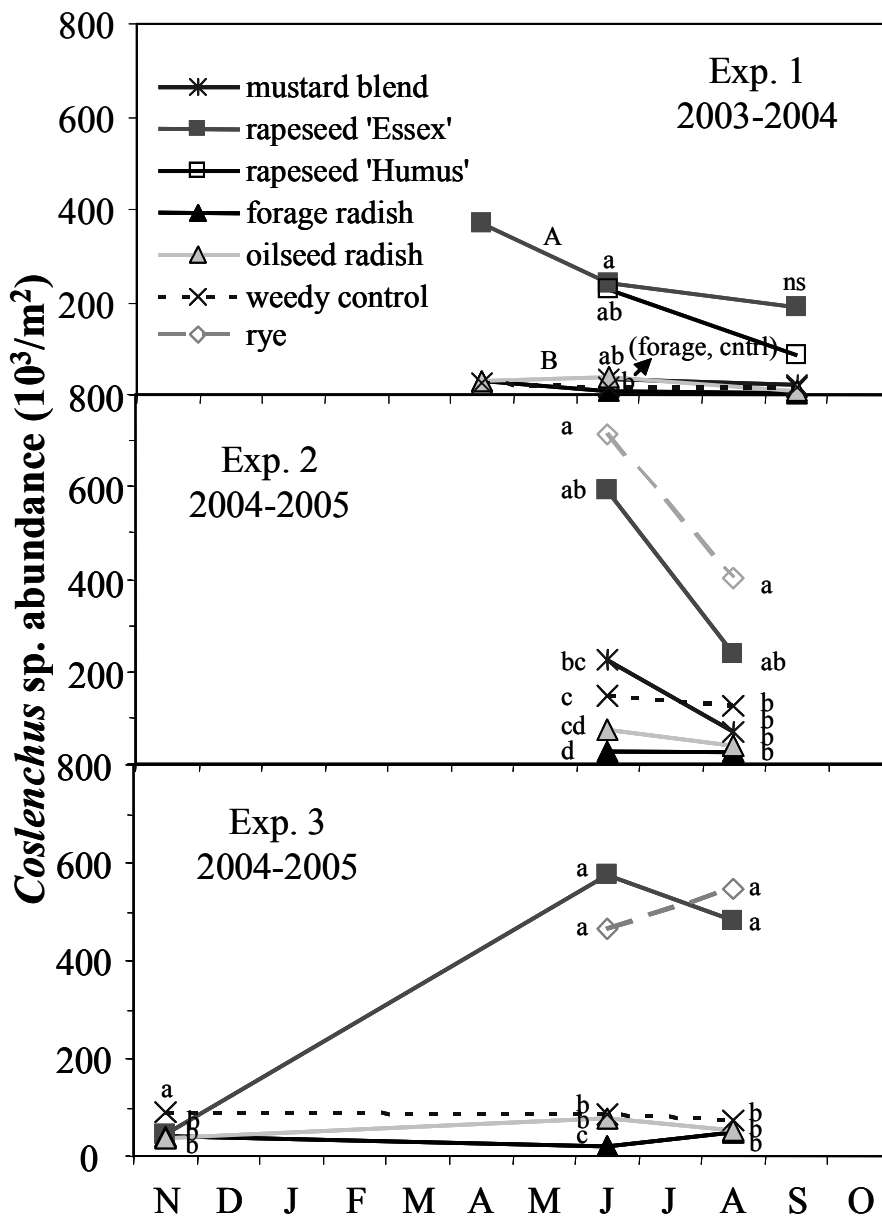
<sup>a</sup> Plant associates not included.

<sup>b</sup> Half of plant associate abundance was assigned to the fungivore trophic group.

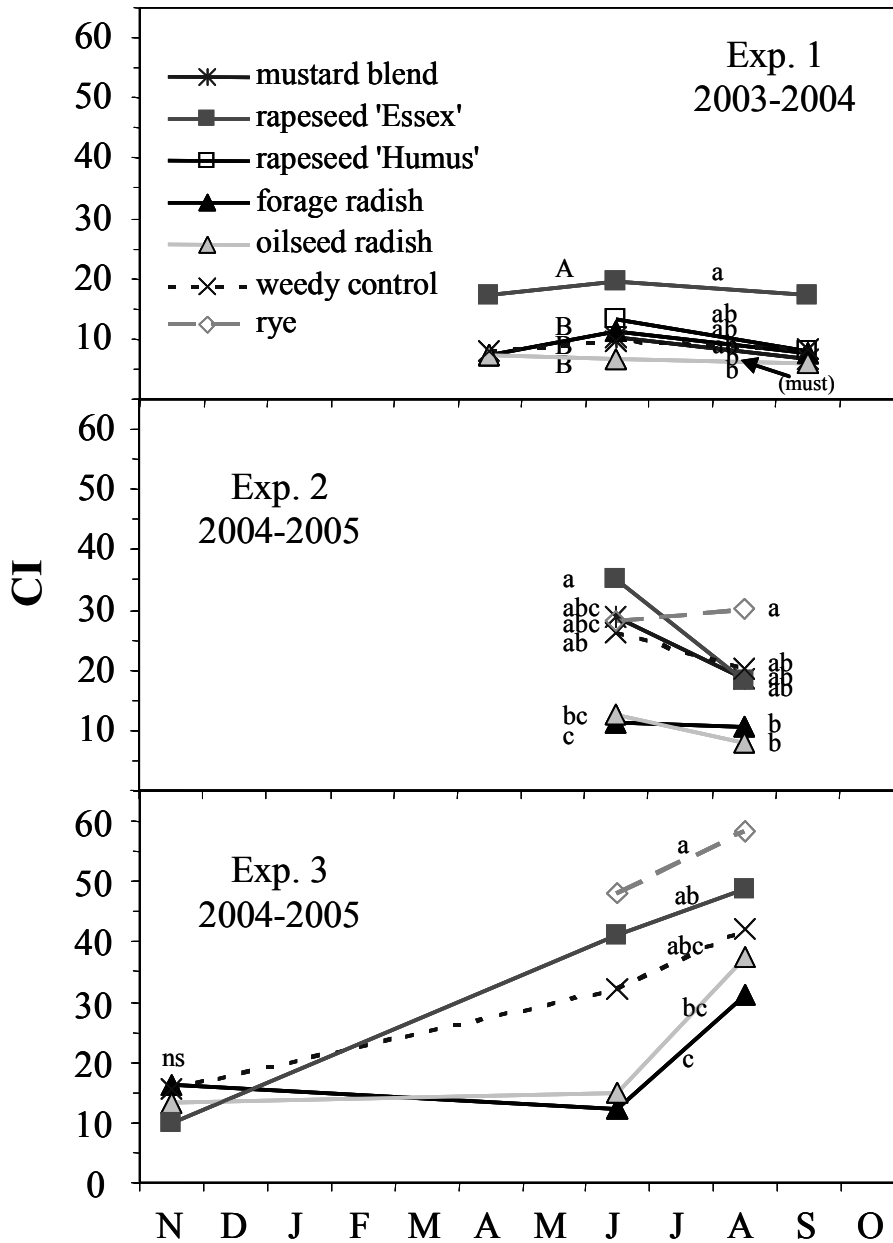


**Figure 4.7.** Total fungivore abundance (not including plant associates) over time at two sites in Maryland after cover crop treatments were sown in fall (August) and terminated in December/January (radishes and mustard) or mid-late April (rapeseed and rye). Notice y axis values are different for each experiment. Capital letters represent means across three dates, and lowercase letters represent means on a given date or across two dates. Means with the same letter are not significantly at  $P \leq 0.10$  (HSD) ( $n=4$ ).





**Figure 4.8.** *Coslenchus* population densities over time at two sites in Maryland after cover crop treatments were sown in fall (August) and terminated in December/January (radishes and mustard) or mid-late April (rapeseed and rye). Capital letters represent means across three dates, and lowercase letters represent means on a given date. Means with the same letter are not significantly at  $P \leq 0.10$  (HSD) ( $n=4$ ).



**Figure 4.9.** The channel index (CI) over time at two sites in Maryland, after cover crop treatments were sown in fall (August) and terminated in December/January (radishes and mustard) or mid-late April (rapeseed and rye). Capital letters represent means across three dates, and lowercase letters represent means on a given date or across two dates. Means with the same letter are not significantly different at  $P \leq 0.10$  (HSD) ( $n=4$ ).

**Table 4.9.** Contrasts between winter-susceptible (radishes and mustard) and winter-hardy (rapeseed and rye) cover crops for community indices related to stability. Contrasts were conducted for each date or set of dates graphed in Appendix V, Figures 4.10 and 4.11.

Site	Date	Covers Contrasted	Winter Terminated	Spring Terminated
<b>Bacterivore Maturity Index<sup>a</sup></b>				
Exp. 1	April-Sept	radishes v. rapeseed 'Essex'	1.88	1.70*
	April	radishes v. rapeseed 'Essex'	1.90	1.65**
	June	radishes/mustard v. 'Essex'/'Humus'	1.76	1.66
	September	Radishes/mustard v. 'Essex'/'Humus'	1.91	1.81
Exp. 2	June-Aug	Radishes/mustard v. 'Essex'/rye	1.87	1.69***
Exp. 3	Nov-Aug	radishes v. rapeseed 'Essex'	1.91	1.81
	June	radishes v. rapeseed 'Essex'/rye	1.77	1.91
	Aug	radishes v. rapeseed 'Essex'/rye	2.09	1.94 <sup>†</sup>
<b>Fungivore Maturity Index<sup>b</sup></b>				
Exp. 1	April	radishes v. rapeseed 'Essex'	3.52	3.23 <sup>†</sup>
	June-Sept	radishes/mustard v. 'Essex'/'Humus'	3.00	2.89
Exp. 2	June	radishes/mustard v. 'Essex'/rye	2.56	2.20**
	August	radishes/mustard v. 'Essex'/rye	3.02	2.74 <sup>†</sup>
Exp. 3	November	radishes v. rapeseed 'Essex'	2.44	2.64
	June	radishes v. rapeseed 'Essex'/rye	2.78	2.83
	August	radishes v. rapeseed 'Essex'/rye	2.71	2.86
<b>ΣMI 2-5<sup>c</sup></b>				
Exp. 1	April-Sept	radishes v. rapeseed 'Essex'	3.08	2.87****
	June-Sept	radishes/mustard v. 'Essex'/'Humus'	3.15	3.01**
Exp. 2	June	radishes/mustard v. 'Essex'/rye	2.75	2.42***
	August	radishes mustard v. 'Essex'/rye	3.33	2.91****
Exp. 3	Nov	radishes v. rapeseed 'Essex'	2.83	2.88
	June	radishes v. rapeseed 'Essex'/rye	3.21	2.75****
	August	radishes v. rapeseed 'Essex'/rye	2.94	2.75*
<b>Structure Index<sup>d</sup></b>				
Exp. 1	April-Sept	radishes v. rapeseed 'Essex'	83.3	78.1*
	June	radishes/mustard v. 'Essex'/'Humus'	88.0	81.4*
	Sept	radishes/mustard v. 'Essex'/'Humus'	80.4	78.4
Exp. 2	June-Aug	radishes/mustard v. 'Essex'/rye	75.8	59.9****
Exp. 3	November	radishes v. rapeseed 'Essex'	74.4	76.4
	June-Aug	radishes v. rapeseed 'Essex'/rye	85.0	71.2***

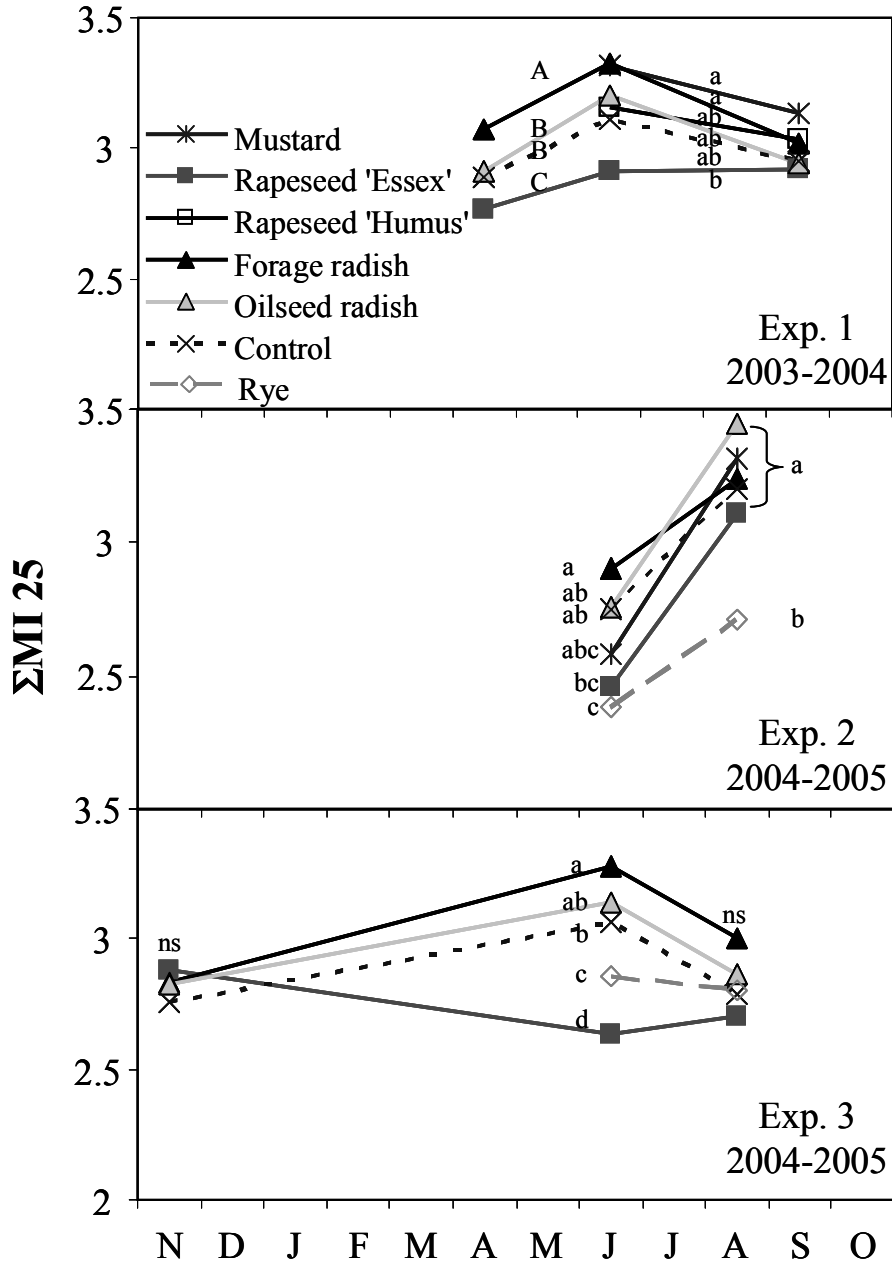
<sup>†</sup>, \*, \*\*, \*\*\*, \*\*\*\*  $P \leq 0.10$ ,  $P \leq 0.05$ ,  $P \leq 0.01$ ,  $P \leq 0.001$ ,  $P \leq 0.0001$

<sup>a</sup> Dauer larvae not included.

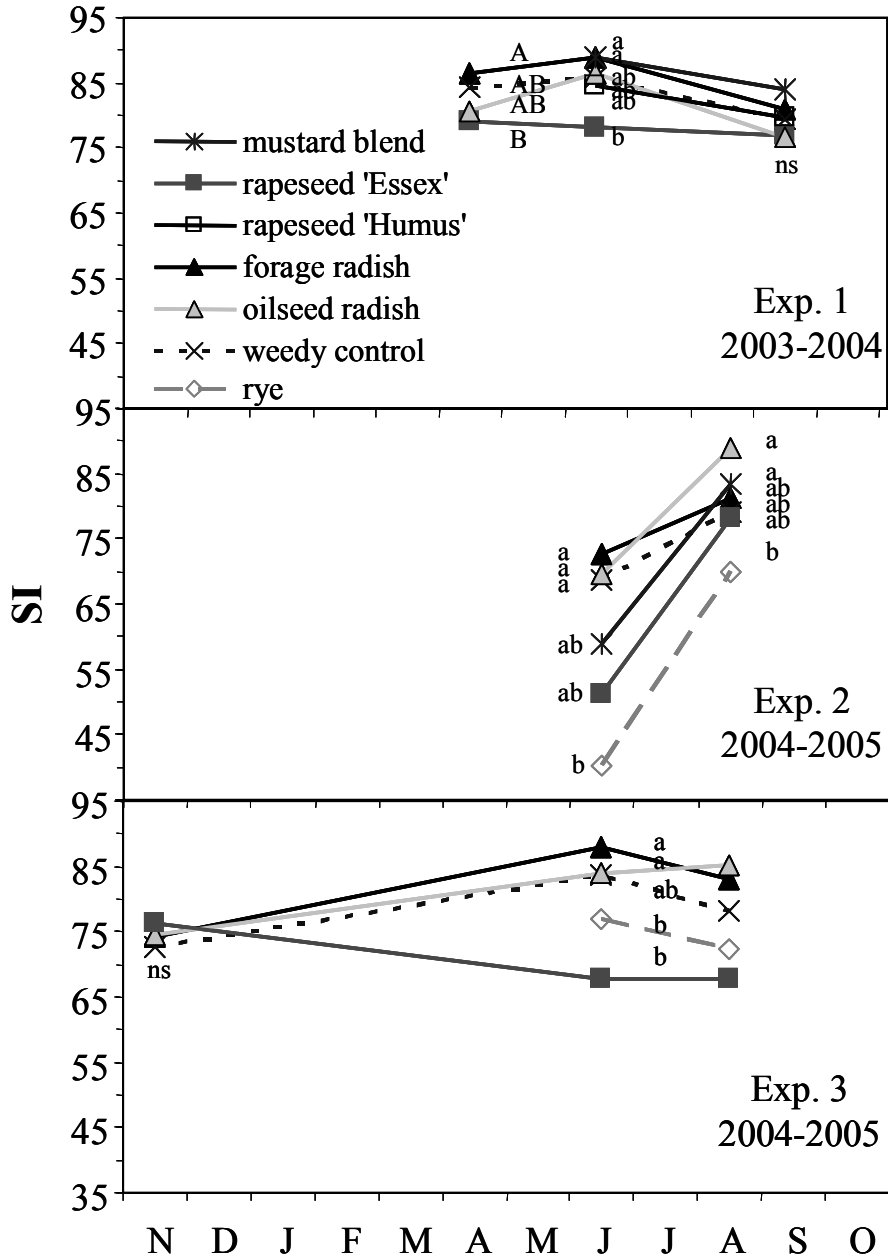
<sup>b</sup> Plant associates not included.

<sup>c</sup> Total free-living and plant-parasitic nematodes cp-2-5.

<sup>d</sup> Half of plant associate abundance was assigned to the fungivore trophic group.



**Figure 4.10.** Total Maturity Index 2-5 ( $\Sigma MI_{25}$ ) over time at two sites in Maryland, after cover crop treatments were sown in fall (August) and terminated in December/January (radishes and mustard) or mid-late April (rapeseed and rye). Capital letters represent means across three dates, and lowercase letters represent means on a given date or across two dates. Means with the same letter are not significantly different at  $P \leq 0.10$  (HSD) ( $n=4$ ).



**Figure 4.11.** The structure index (SI) over time at two sites in Maryland, after cover crop treatments sown in fall (August) and killed in December/January (radishes and mustard) or mid-late April (rapeseeds and rye). Capital letters represent means across three dates, whereas lowercase letters represent means at a given date or across two dates. Means represented with the same letter are not significantly different HSD ( $P \leq 0.10$ ) ( $n=4$ ).

## CHAPTER V – CONCLUSION

Nematodes, being the most abundant mesofauna on earth, are significant contributors to agroecological processes. Decades of research on controlling plant-parasitic nematodes has mostly informed us that common sense practices like crop rotation, equipment cleaning, resistant cultivars, frequent population monitoring, and maintenance of an ecologically active soil are the most effective means for preventing yield loss caused by plant-parasitic nematodes. Increased research on cover crop use for nematode control has added a few cover crops like sunnhemp and sorghum-sudangrass to the management tool box (Kratochvil et al., 2004; Wang et al., 2006), however not all agronomic crop rotations will accommodate these summer cover crops. This research showed little potential for nematode suppression by brassicaceous cover crops in Maryland grain cropping systems, as managed in these experiments. Bioassays suggested that insufficient quantities of rapeseed biomass were grown in one year. In other years, lack of maceration, irrigation, or incorporation may have resulted in insufficient isothiocyanate evolution, an important agent of biocontrol with brassicaceous cover crops (Matthiessen et al., 2004). Sufficient quantities of radish biomass were grown, and therefore it appears that suppression of nematodes in winter, when nematodes are less active, may not be an effective means of control. This study did, however, show the beneficial effect of rye and clover when combined with brassicaceous cover crops. Rye increased yields in 2005 apparently due to greater soil moisture. *Heterodera glycines* was suppressed in rye, relative to brassicaceous cover crops, in June of both years, for unknown reasons. Total nematode abundances were increased by rye or clover

across experiments on at least one date. Increased abundances of Trichodoridae in rye plots in two experiments may be associated with greater total nematode populations.

Future research should focus on building soil capacity to provide pest suppression (Sánchez-Moreno and Ferris, 2007). Polyculture cover crops should be used, and they should be selected for their differing quality (soluble, non-soluble, lignin, etc.) of carbon, which is likely to sustain a more diverse array of bio-control organisms (Sun and Liu, 2006). More attention should be given to plant-parasitic nematodes in the context of soil ecology, rather than pest suppression. Some studies have shown that moderate plant-parasitic nematode populations can support plant growth by increasing the amount of root exudates leaking into the soil and thereby increasing microbial activity in the rhizosphere (Bardgett et al., 1999; Tu et al., 2003). Other studies suggest that plant-parasitic nematode diversity prevents population explosions of one type of plant-parasitic nematode (common to soils after fumigation) and that plant health is improved under a diversity of plant-parasitic nematodes (Lavelle et al., 2004). Future research should look for correlation between free-living nematodes and plant-parasitic nematodes to identify possible synergies between genera or guilds. Sensitivity or insensitivity of plant-parasitic nematodes to pollutants (*Pratylenchus* to copper) (Ekschmitt and Korthals, 2006) and physical disturbance (*Trichodorus* to compaction) (Bouwman and Arts, 2002) suggests that plant-parasitic nematodes could be incorporated into indices designed for specific disturbances. Strong correlations between Dolichodoridae nematodes and sand grain sizes (n=24) or soil moisture (n=76), observed in this study, may have been confounded with absence of a good host. However, the correlations may also be indicative of an

ecological attribute of the Dolichodoridae family, associated with moisture or pore space that could eventually be useful in a disturbance index.

Free-living nematode community analysis has made rapid progress in the last decade. Indices are being used to refine timing of management practices, such as cover crop biomass amendment and irrigation, to maximize synchrony of nutrient availability with cash crop demands (Wang et al., 2004; Ferris et al., 2004). Winter-kill of radishes and mustard increased community succession by summer, compared to spring-terminated cover crops, despite other disturbances. Spring-termination of rapeseed and rye increased fungivore activity. Canonical Discriminant Analysis (CDA), using nematode response variables to create linear functions which maximally separate treatment means, showed that mustard affected the nematode community differently than radishes. Therefore, cover crop type and not only timing of termination influenced nematode community response. Several studies show that plant or litter identity affects the nematode community more than plant or litter diversity (De Deyn et al., 2004; Wardle et al., 2006). Large quantities of N in radishes distinguished this cover crop from the others and activated the bacterivore food web component in early spring. Higher carbon contents of rapeseed and rye probably were probably strongly associated with fungivore response. Use of radishes in organic production systems may be an effective means of priming the food web for optimum nutrient availability during crop demand. Spring-terminated cover crops increased total nematode population density and reduced percentages of plant-parasitic nematodes on some dates. It was not clear if destabilization of the plant-parasitic nematode community was more beneficial for plant growth. Application of fertilizers probably reduced cash crop dependency on biological fertility and increased



tolerance of root-herbivory, which may explain why correlations between nematode indices and summer crop yield were not observed.

Two major effects on nematodes caused by cover crops in this study were problematic for placement in index calculations—dauer larvae and *Coslenchus* (a plant associate abundant in rapeseed and rye). Standardization of the enrichment index (EI) and dauer abundance showed that the presence of dauer larvae populations was not always indicative of enriched conditions, as defined by the EI (Appendix VI). Inclusion of half of the plant associate abundance in the EI, channel index (CI), and structure index (SI) accounted for many treatment effects, but is justifiable in that the weightings are derived from nematode community analysis that includes plant associates as part of the cp-2 guild. Continued evidence of fungal feeding behavior in the Tylenchidae family (McSorley and Frederick, 1999; Okada et al., 2005) also supports allocation to the fungivore group, though *Coslenchus* has yet to be studied intensively.

Soil texture was an influential property in this study, both for general site characterization and in influencing nematode community structure on a given date. The two Maryland sites had large abundances of omnivores and predators and rarely had degraded structure ( $SI < 50$ ), which is probably a texture effect given the repeated disturbances in agricultural regimes. Dauer larvae and the EI were correlated with percent sand or sand size fractions on some dates, suggesting an interaction between bacterivore prey and soil texture. A growing body of literature shows the strong influence of soil properties on nematode community structure (Bjørnlund and Christensen, 2005; Frouz et al., 2001; Griffiths et al., 2002, 2003). Future researchers might consider developing indices which are calculated only with sentinel taxa—genera

or families known to be good indicators for a given condition—sensitive to soil properties, such as texture, moisture, pH, salinity, or organic matter. Standardization of index data, with graphical depiction, as illustrated in Appendix VI (Fig. 5-7), could then be used to elucidate what environmental properties are might be driving or masking signs of stress in the soil food web.

Brassicaceous cover crops have attributes attractive to farmers, and therefore nematode faunal analysis should continue to be used for understanding how to best fit these cover crops into rotations and how to meet the management goals of grain production systems in Maryland. More frequent sampling during cover crop growth and immediately after termination is recommended, as well as research on sites with different soil textures and without fall fertilization.

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## APPENDIX I – SAS CODES

### 1. Analysis of Covariance with Full Factorial Data

```
title1 Lesrec over time;
dm 'log;clear;out;clear;';
PROC IMPORT OUT= WORK.lesovertime
    DATAFILE= "C:\Documents and Settings\Lisa\My Documents\My Documents\My Documents\Lisa Research\Field Work\LESREC\Nematodes\Data for Thesis\Field 39 main experiment ppn over time with April 3.xls"
    DBMS=EXCEL REPLACE;
    SHEET="factorial exp$";
    GETNAMES=YES;
    MIXED=NO;
    SCANTEXT=YES;
    USEDATE=YES;
    SCANTIME=YES;
RUN;

data new;
set lesovertime;
if month='JUN_FIVE';
logdolich=log(dolich_area + 1000);
run;

proc sort data=new;
by month;
run;

proc mixed data=new;
class brass nonbrass rep ;
model DOLICH_AREA= brass|nonbrass|pctmois /ddfm=satterth outp=d;
random rep;
lsmeans brass nonbrass /pdiff adjust=tukey;
run;
quit;
*Non-significant interactactions were dropped step-wise from the model
```

## 2. C-p Trophic Group Classifications and One-way ANOVA (Mixed and Glimmix) With MACRO for Letter Assignment to Means

```
title1 Lesrec Interseed and Insurance community;  
dm 'log;clear;out;clear;';
```

```
PROC IMPORT OUT= WORK.means  
    DATAFILE= "C:\Documents and Settings\Lisa\My Documents\My  
Documents\My Documents\Lisa Research\Field Work\Les_Hay\Final Spreadsheet  
Community ID Les Hay New2.xls"  
    DBMS=EXCEL REPLACE;  
    SHEET="By Area$";  
    GETNAMES=YES;  
    MIXED=NO;  
    SCANTEXT=YES;  
    USEDATE=YES;  
    SCANTIME=YES;
```

```
RUN;
```

```
quit;
```

```
data newmeans;
```

```
set means;
```

```
where uniqueid ='h';
```

```
Totalnod=(Total_msq - Dauer);
```

```
auc=(Achromadora + Achromadora2);
```

```
plantassoc=(Boleodorus+ Coslenchus + Ditylenchus +Filenchus + Psilenchus  
+Tylenchidae + Tylenchus +Miculenchus + Laimaphelenchus);
```

```
fung=(Aphelenchoides + Aphelenchus + Diphtherophora+ Leptonchus+  
Tylencholaimus+ Tylencholaimellus+ Tyloilaimophorous);
```

```
bact=(Acrobeles + Acrobelloides + Alaimus + Amphidelus + Anaplectus +Ceratoplectus+  
Cervidellus + Cruznema +Cylindrolaimus +Bastiana +Diploscapter + Drilocephalobus  
+ Eucephalobus + Eumonhystera + Eumonhystera2 + Eumonhystera3  
+Mesorhabditis +Panagrolaimidae +Plectus +Prismatolaimus +Pristionchus  
+Prodontorhabditis +Rhabditidae+ Rhabditis+ Tylocephalus + Wilsonema  
+ Zeldia +Bunonema +Cephalobus+ Odontolaimus + Teratocephalus);
```

```
bactd=bact + dauer;
```

```
ppn=( Helicotylenchus+ Heterodera +Hoplolaimus+ Longidorella +Paratrichodorus  
+Pratylenchus +Quinisulcius + Trichodorus + Tylenchorhynchus + Xiphinema +  
Pungentus + Macroposthonia);
```

predator=(Clarkus + Discolaimus + Mylonchulus + Nygolaimus + Paractinolaimus  
+ Paravulvulus + Tobrilus + Seinura +  
Thonus + Thonus\_Han + Paraxonchium + Triplya + Anatonchus);

omni= (Aporcelaimellus + Aporcelaimus + Dorylaimidae + Dorylaimus2 + Dory1  
+ Dory2 + Ecumenicus  
+ Eudorylaimus + Labronema + Lordellonema + Mesodorylaimus + Microdorylaimus +  
Sectonema);

bactone= (Cruzema + Diploscapter + Panagrolaimidae + Mesorhabditis + Pristionchus  
+ Prodontorhabditis + Rhabditidae  
+ Rhabditis + Bunonema );

bacttwo= (Acrobeles + Acrobelloides + Anaplectus + Ceratoplectus + Cervidellus +  
Cylindrolaimus + Drilocephalobus  
+ Eucephalobus + Eumonhystera + Eumonhystera2 + Eumonhystera3 + Plectus +  
Tylocephalus + Wilsonema +  
Zeldia + Cephalobus);

bact3= (Bastiana + Odontolaimus + Prismaolaimus + Teratocephalus);

bact4= (Alaimus + Amphidelus );

fung2= (Aphelenchoides + Aphelenchus );

fung3= (Diphtherophora + Tylophorina );

fung4= (Leptonchus + Tylencholaimus + Tylencholaimellus);

pred2= Seinura;

pred3= (Tobrilus + Triplya);

pred4= (Clarkus + Mylonchulus + Thonus + Thonus\_Han + Anatonchus);

pred5= (Discolaimus + Nygolaimus + Paractinolaimus + Paravulvulus + Paraxonchium);

omni4= (Dorylaimidae + Dorylaimus2 + Dory1 + Dory2 + Ecumenicus  
+ Eudorylaimus + Labronema + Lordellonema + Mesodorylaimus + Microdorylaimus);

omni5= (Aporcelaimellus + Aporcelaimus + Sectonema );

ppn2= (Quinisulcius + Tylenchorhynchus);

ppn3= (Helicotylenchus + Heterodera + Hoplolaimus + Pratylenchus + Macroposthonia);

ppn4= (Longidorella + Paratrachodorus + Trichodorus );

ppn5= Xiphinema;

Cephalobidae= (Eucephalobus + Acrobelloides);

Thon= (Thonus + Thonus\_Han);

Dorylaimidae tot= (Dorylaimidae + Dorylaimus2 + Dory1 + Dory2 + Eudorylaimus);

Qudsianematidae= Labronema;

Aporcelaimidae= Sectonema;

Leptonchidae= Tylencholaimellus + Tylencholaimus;

Totalbactd= bact + Dauer;

Tylenchs= Tylenchidae + Tylenchus;

Tylenchids= Tylenchs + Filenchus;

PredatorsTob= Tobrilus + Triplya;

```

logpred5=sqrt(pred5 + 1000);
BaMI= (bactone/bact) + (bacttwo/bact)*2 + (bact3/bact)*3 + (bact4/bact)*4;
sqrtbami=sqrt(BaMI);

run;

proc mixed data=newmeans;
class cover rep;
model BaMI= cover/ddfm=satterth outp=f;
random rep;
lsmeans cover/pdiff adjust=tukey;

*begin MACRO code
ods output diffs=ppp;
ods output lsmeans=mmm;
ods listing exclude diffs;
ods listing exclude lsmeans;
run;
%include 'c:\Documents and Settings\Lisa\My Documents\stats\pdmix800.sas';
%pdmix800(ppp,mmm,alpha=.10,sort=yes);

*end MACRO code

proc univariate normal plot data=f;
var resid;
run;

proc plot data=f;
plot resid*pred;
plot resid*cover;
run;
quit;

proc glm data=newmeans;
class cover;
model BaMI =cover/ss3;
means cover/hovtest welch;
run;
quit;

proc glimmix data=newmeans;
class cover rep;
model BaMI = cover/ddfm=satterth dist=nb;
random rep;
lsmeans cover/pdiff adjust=tukey ilink lines;run;

```



### 3. Community Indices with Variance Grouping and Correlation

```
title1 Lesrec Exp. 1 and 2 Community;
dm 'log;clear;out;clear;';
PROC IMPORT OUT= WORK.community2
    DATAFILE= "C:\Documents and Settings\Lisa\My Documents\My
Documents\My Documents\Lisa Research\Field Work\Les_Hay\Final Spreadsheet
Community ID Les Hay New2.xls"
    DBMS=EXCEL REPLACE;
    SHEET="By Area$";
    GETNAMES=YES;
    MIXED=NO;
    SCANTEXT=YES;
    USEDATE=YES;
    SCANTIME=YES;
RUN;
quit;
data indices;
set community2;
where uniqueid ='g' ;

*Indices;

Totalnod= (Total_msq - dauer);
one=(Cruz nema + Diploscapter + Panagrolaimidae + Mesorhabditis + Pristionchus +
Prodontorhabditis + Rhabditidae
+ Rhabditis+ Bunonema);

two= (Acrobeles + Acrobeloides + Anaplectus + Aphelenchoides +Aphelenchus +
Ceratoplectus + Cervidellus + Coslenchus + Cylindrolaimus + Boleodorus +
Ditylenchus + Drilocephalobus + Eucephalobus
+Eumonhystera + Eumonhystera2 + Eumonhystera3+ Filenchus +Miculenchus
+Plectus +Psilenchus +Quinisulcius+ Seinura +Tylenchidae + Tylenchus +
Tylenchorhynchus+ Tylocephalus+ Wilsonema+ Zeldia +
Laimaphelenchus+ Cephalobus);

three= (Achromadora + Achromadora2 +Bastiana +Diphtherophora + Helicotylenchus+
Heterodera +Hoplolaimus +Odontolaimus + Pratylenchus+ Pristmatolaimus+ Tobrilus
+Triplya+ Tyloolaimophorous + Macroposthonia + Teratocephalus);

four= (Alaimus + Amphidelus + Clarkus + Dorylaimidae+ Dorylaimus2 +Dory1
+ Dory2+ Ecumenicus + Eudorylaimus +Labronema +Leptonchus +Longidorella
+Lordellonema +Mesodorylaimus +Microdorylaimus+Mylonchulus +Paratrichodorus
+Thonus + Thonus_Han + Trichodorus+ Tylencholaimus + Tylencholaimellus
+Pungentus + Anatonchus);
```

five= (Aporcelaimellus + Aporcelaimus +Discolaimus + Nygolaimus +Paractinolaimus +Paravulvus+ Paraxonchium +Sectonema +Xiphinema);

pp3=(Helicotylenchus +Hoplolaimus +Heterodera +Pratylenchus + Macroposthonia);

pp4=(Longidorella +Paratrichodorus+Trichodorus+ Pungentus);

pp5=(Xiphinema);

free3=three-pp3;

free4=four-pp4;

free5=five-pp5;

freetothi=free3 + free4 + free5;

freetot= (one + free2 + free3 + free4 + free5);

/\*Ferris et al. 2001 Indices\*/

bacttwo= (Acrobeles + Acrobelloides + Anaplectus +Ceratoplectus + Cervidellus +  
Cylindrolaimus + Drilocephalobus+ Eucephalobus + Eumonhystera + Eumonhystera2 +  
Eumonhystera3 + Plectus + Tylocephalus + Wilsonema+Zeldia + Cephalobus);

bacttwo= (Acrobeles + Acrobelloides + Anaplectus +Ceratoplectus + Cervidellus +  
Cylindrolaimus + Drilocephalobus  
+ Eucephalobus + Eumonhystera + Eumonhystera2 + Eumonhystera3 + Plectus +  
Tylocephalus + Wilsonema+  
Zeldia + Cephalobus)/Totalnod;

bactonep=(Cruznema + Diploscapter+ Panagrolaimidae +Mesorhabditis +Pristionchus  
+Prodontorhabditis+ Rhabditidae  
+ Rhabditis+ Bunonema )/Totalnod;

bactone= (Cruznema + Diploscapter+ Panagrolaimidae +Mesorhabditis +Pristionchus  
+Prodontorhabditis+ Rhabditidae  
+ Rhabditis+ Bunonema );

bact3= (Bastiana +Odontolaimus + Prismaolaimus + Teratocephalus);

bact4= (Alaimus + Amphidelus );

fung2= (Aphelenchoides + Aphelenchus);

logfung2=log(fung2 +1000);

plantassoc=(Boleodorus+ Coslenchus + Ditylenchus +Filenchus + Psilenchus  
+Tylenchidae + Tylenchus +Miculenchus + Laimaphelenchus);

fungpa=plantassoc/2;

split=fungpa + fung2;

```

b2=(bacttwo + split)*(0.8);
e2=(bactone*3.2) + (split*0.8);
s=(1.8*free3) + (free4*3.2) + (free5*5.0);

```

```

EI= 100*(e2/(e2+b2));
SI= 100*(s/(s+b2));
CI=100*((split*0.8)/e2);

```

```

fung=(Aphelenchoides + Aphelenchus + Diphtherophora+ Leptonchus+
Tylencholaimus+ Tylencholaimellus+ Tylolaimophorous);

```

```

fung3=(Diphtherophora + Tylolaimophorous);
fung4=(Leptonchus + Tylencholaimus + Tylencholaimellus);

```

```

bact=(Acrobeles + Acrobelloides + Alaimus + Amphidelus + Anaplectus +Ceratoplectus+
Cervidellus + Cruznema +Cylindrolaimus +Bastiana +Diploscapter + Drilocephalobus
+ Eucephalobus+ Eumonhystera + Eumonhystera2 + Eumonhystera3
+Mesorhabditis +Panagrolaimidae +Plectus+Prismatolaimus +Pristionchus
+Prodontorhabditis +Rhabditidae+ Rhabditis+ Tylocephalus + Wilsonema
+ Zeldia +Bunonema +Cephalobus+ Odontolaimus + Teratocephalus);

```

```

bactd=bact + dauer;

```

```

predator=(Clarkus + Discolaimus +Mylonchulus + Nygolaimus +Paractinolaimus
+Paravulvulus +Tobrilus + Seinura +
Thonus + Thonus_Han + Paraxonchium + Triplya + Anatonchus);

```

```

omni= (Aporcelaimellus + Aporcelaimus +Dorylaimidae +Dorylaimus2 +Dory1
+Dory2 +Ecumenicus+ Eudorylaimus +Labronema +Lordellonema
+Mesodorylaimus +Microdorylaimus + Sectonema);

```

```

IF COVER='RYE' or cover='MUSTARD' THEN VARGROUP='A'; ELSE
VARGROUP='B';
IF COVER='FORAGE' or COVER='OILSEED' or cover='MUSTARD' THEN
KILL='WINTER';
IF COVER='RAPEE' or COVER='RAPEH' OR COVER='RYE' THEN KILL='SPRING';
if cover='NONE' THEN KILL='NOT';
run;
proc sort data=indices;
by cover rep ;
run;
proc means mean stderr data=indices;
var EI SI CI mi15 mi25 smi15 smi25 MI35 ppi ppimi BaMI BaMId FB FBB PAF;
by cover;
output out=AugInsur;run;

```

```

proc mixed data=indices;
class cover rep VARGROUP;
model CI = cover /ddfm=satterth outp=a;
*random rep;
repeated /subject=rep type=cs group=VARGROUP R RCORR;
estimate 'wintervspring' cover 2 2 0 2 -3 -3;
*estimate 'wvs' cover 1 0 1 -1 -1;
lsmeans cover /pdiff adjust=Tukey;
/*
ods output diffs=ppp;
ods output lsmeans=mmm;
ods listing exclude diffs;
ods listing exclude lsmeans;
*/
run;
%include 'c:\Documents and Settings\Lisa\My Documents\stats\pdmix800.sas';
%pdmix800(ppp,mmm,alpha=.10,sort=yes);
run;
proc univariate normal plot data=a;
var resid;
run;
proc plot data=a;
plot resid*pred;
plot resid*cover;
plot resid*rep;
run;
quit;

PROC GLM DATA=INDICES;
CLASS cover ;
MODEL CI =cover;
MEANS cover/ HOVTEST WELCH;
RUN;
quit;

proc sort data=indices;
by kill;
run;
proc means data=indices ;
var ci si ei bami dauer coslenchus fung;
by kill;
output out=worm;
run;/*

```

#### 4. Repeated Measures with MACRO for Covariance Structure Selection

```
title1 Repeated Measures CMREC Community;
dm 'log;clear;out;clear;';
PROC IMPORT OUT= WORK.Power
    DATAFILE= "C:\Documents and Settings\Lisa\My Documents\My
Documents\My Documents\Lisa Research\Thesis\ch2\results\Repeated Measures Hay
Insurance.xls"
    DBMS=EXCEL REPLACE;
    SHEET="Sheet1$";
    GETNAMES=YES;
    MIXED=NO;
    SCANTEXT=YES;
    USEDATE=YES;
    SCANTIME=YES;
RUN;
proc print;
run;
data home;
set power;
IF COVER='NONE' then vargroup='a'; else vargroup='b';

RUN;
proc sort data=home;
by cover rep date;
run;

PROC MIXED DATA=HOME;
CLASS COVER DATE REP;
MODEL BaMI= cover |date /ddfm=kr OUTP=life;
RANDOM rep;
REPEATED date /subject=cover*rep r rcorr type=sp(pow)(date);
LSMEANS cover date/PDIFF ADJUST=TUKEY ;
ESTIMATE 'WINTERVSPRING' COVER 1 0 1 -2;
ods output diffs=ppp;
ods output lsmeans=mmm;
ods listing exclude diffs;
ods listing exclude lsmeans;
run;
%include 'c:\Documents and Settings\Lisa\My Documents\stats\pdmix800.sas';
%pdmix800(ppp,mmm,alpha=.10,sort=yes);
run;
```

```

*MACRO FOR COVARIANCE STRUCTURE
%MACRO id_cov(covtype, lbl);
TITLE3 "Covariance Type is &covtype";
ODS OUTPUT FITSTATISTICS=fit_&lbl;
ODS LISTING EXCLUDE ALL;
PROC MIXED DATA=home;
class COVER DATE REP vargroup ;
MODEL bami= COVER|DATE/DDFM=KR;
RANDOM REP;
REPEATED date /SUBJECT=cover*rep TYPE=&covtype ;
QUIT;

DATA fit_&lbl;
SET fit_&lbl;
FORMAT covtype$ 6.;
covtype="&lbl";
RUN;
ODS LISTING;
%MEND id_cov;
%id_cov(un, un);
%id_cov(vc, vc);
%id_cov(cs, cs);
%id_cov(csh, csh);
%id_cov(ar(1), ar1 );
%id_cov(sp(pow)(date), sp_pow);
%id_cov(ante(1), ante1);

DATA fitstats;
SET fit_un;
RUN;
%MACRO fitstats(ctype_lbl);
DATA fitstats;
SET fitstats fit_&ctype_lbl;
IF MOD( _N_,4)=1 THEN stat_id='ResLogLike';
IF MOD( _N_,4)=2 THEN stat_id='AIC  ';
IF MOD( _N_,4)=3 THEN stat_id='AICC';
IF MOD( _N_,4)=0 THEN stat_id='BIC  ';
%MEND fitstats;
%fitstats(vc);
%fitstats(cs);
%fitstats(csh);
%fitstats(ar1);
%fitstats(sp_pow);
%fitstats(ante1);
PROC SORT DATA=fitstats; BY covtype stat_id;
PROC TRANSPOSE DATA=fitstats OUT=tfits;

```

```
VAR value;  
ID stat_id;  
BY covtype;  
RUN;  
DATA tfits; SET tfits; DROP _NAME_ ; RUN;  
TITLE 'Fit Statistics for Candidate Covariance Structures';  
PROC PRINT DATA=tfits; RUN;  
*END MACRO
```

```
PROC UNIVARIATE NORMAL PLOT DATA=life;  
VAR RESID;  
RUN;  
PROC PLOT DATA=life;  
PLOT RESID*PRED;  
plot resid*cover;  
plot resid*rep;  
RUN;  
QUIT;  
PROC GLM DATA=new;  
CLASS cover ;  
MODEL BaMI =cover;  
MEANS cover/ HOVTEST WELCH;
```

## 5. Split-Plot in Time ANOVA

```
title1 split-plot Lesrec Insur;
dm 'log;clear;out;clear;';
PROC IMPORT OUT= WORK.split
    DATAFILE= "C:\Documents and Settings\Lisa\My Documents\My
Documents\My Documents\Lisa Research\Thesis\ch2\results\Split-plot Lesrec Insurance
Indices.xls"
    DBMS=EXCEL REPLACE;
    SHEET="updated_indices_August$";
    GETNAMES=YES;
    MIXED=NO;
    SCANTEXT=YES;
    USEDATE=YES;
    SCANTIME=YES;
RUN;
DATA NEW;
SET split;
if cover='FORAGE' OR COVER='MUSTARD' OR COVER='OILSEED' THEN
KILL='WINTER';
IF COVER='RAPEE' OR COVER='RYE' THEN KILL='SPRING';
IF COVER='NONE' THEN KILL='NOT';
logdauer=log(dauer + 1000);
sqrtcosl=sqrt(coslenchus + 1000);
run;
proc mixed data=NEW;
class cover date rep;
model BAMI= cover|date/ddfm=satterth outp=dog;
random rep rep*cover/ G GCORR;
ESTIMATE 'WINTERVSPRING' COVER 2 2 0 2 -3 -3;
lsmeans date cover/pdiff adjust=tukey;
ods output diffs=ppp;
ods output lsmeans=mmm;
ods listing exclude diffs;
ods listing exclude lsmeans;
run;
%include 'c:\Documents and Settings\Lisa\My Documents\stats\pdmix800.sas';
%pdmix800(ppp,mmm,alpha=.10,sort=yes);
run;
proc univariate normal plot data=dog;
var resid;
run;
proc plot data=dog;
plot resid*pred;
plot resid*cover;
run;quit;
```



## 5. Canonical Discriminant Analysis on Final Sample Dates from 3 Experiments

```
title CANDISC LESREC JUN DATA;
dm 'log;clear;out;clear;';
PROC IMPORT OUT= WORK.home
    DATAFILE= "C:\Documents and Settings\Lisa\My Documents\My
Documents\My Documents\Lisa Research\Thesis\ch2\results\Correlations All Sites All
Properties23.xls"
    DBMS=EXCEL REPLACE;
    SHEET="JUN ALLSITES";
    GETNAMES=YES;
    MIXED=NO;
    SCANTEXT=YES;
    USEDATE=YES;
    SCANTIME=YES;
RUN;
DATA NEW;
SET HOME;
IF date ne 'i';
IF COVER NE 'MUSTARD' AND COVER NE 'RAPEH';
fung=(Aphelenchoides + Aphelenchus + Diphtherophora+ Leptonchus+
Tylencholaimus+Tylencholaimellus+ Tylolaimophorous);
bact=(Acrobeles + Acrobelloides + Alaimus + Amphidelus + Anaplectus +Ceratoplectus+
Cervidellus + Cruznema +Cylindrolaimus +Bastiana +Diploscapter + Drilocephalobus
+ Eucephalobus+ Eumonhystera + Eumonhystera2 + Eumonhystera3
+Mesorhabditis +Panagrolaimidae +Plectus+Prismatolaimus +Pristionchus
+Prodontorhabditis +Rhabditidae+ Rhabditis+ Tylocephalus + Wilsonema
+ Zeldia +Bunonema +Cephalobus+ Odontolaimus + Teratocephalus);

predator=(Clarkus + Discolaimus +Mylonchulus + Nygolaimus +Paractinolaimus
+Paravulvulus +Tobrilus + Seinura +Thonus + Thonus_Han + Paraxonchium + Triplya +
Anatonchus);

omni= (Aporcelaimellus + Aporcelaimus +Dorylaimidae +Dorylaimus2 +Dory1
+Dory2 +Ecumenicus+ Eudorylaimus +Labronema +Lordellonema
+Mesodorylaimus +Microdorylaimus + Sertonema);

PPN= Quinisulcius + Tylenchorhynchus + Helicotylenchus + Heterodera + Hoplolaimus
+ Pratylenchus + Macroposthonia + Xiphinema + Longidorella + Paratrachodorus +
Trichodorus;

Cbactone= (Cruznema + Diploscapter+ Panagrolaimidae +Mesorhabditis +Pristionchus
+Prodontorhabditis+ Rhabditidae+ Rhabditis+ Bunonema );

Cbacttwo= (Acrobeles + Acrobelloides + Anaplectus +Ceratoplectus + Cervidellus +
Cylindrolaimus + Drilocephalobus
```

+ Eucephalobus + Eumonhystera + Eumonhystera2 + Eumonhystera3 + Plectus +  
 Tylocephalus + Wilsonema+  
 Zeldia + Cephalobus);  
 Cbact3= (Bastiana + Odontolaimus + Prigmatolaimus + Teratocephalus);  
 Cbact4= (Alaimus + Amphidelus );  
 Cfung2= (Aphelenchoides + Aphelenchus );  
 Cfung3= (Diphtherophora + Tyloilaimophorous );  
 Cfung4= (Leptonchus + Tylencholaimus + Tylencholaimellus);  
 Cpred2= Seinura;  
 Cpred3= (Tobrilus +Triplya);  
 Cpred4= (Clarkus +Mylonchulus +Thonus + Thonus\_Han + Anatonchus);  
 Cpred5= (Discolaimus + Nygolaimus +Paractinolaimus + Paravulvus + Paraxonchium );  
 Comni4= (Dorylaimidae+ Dorylaimus2 +Dory1 + Dory2+ Ecumenicus  
 + Eudorylaimus +Labronema +Lordellonema +Mesodorylaimus +Microdorylaimus);  
 Comni5= (Aporcelaimellus + Aporcelaimus +Sectonema );  
 Cppn2=(Quinisulcius + Tylenchorhynchus);  
 Cppn3=( Helicotylenchus+ Heterodera +Hoplolaimus+ Pratylenchus + Macroposthonia);  
 Cppn4= (Longidorella +Paratrichodorus + Trichodorus ) ;  
 paf2= (Boleodorus+ Coslenchus + Ditylenchus +Filenchus + Psilenchus +Tylenchidae +  
 Tylenchus +Miculenchus +Laimaphelenchus + Aphelenchoides + Aphelenchus);

logfung=log(fung + **1000**);  
 logbact=log(bact + **1000**);  
 logppn=log(ppn + **1000**);  
 logpredator=log(predator + **1000**);  
 logomni=log(omni + **1000**);  
 SQRTbone =SQRT(Cbactone + **1000**);  
 SQRTbtwo = SQRT(Cbacttwo + **1000**);  
 SQRTb3 =SQRT(Cbact3 + **1000**);  
 SQRTb4 = SQRT(Cbact4 + **1000**);  
 SQRTf2 =SQRT(Cfung2 + **1000**);  
 SQRTf3 =SQRT(Cfung3 + **1000**);  
 SQRTf4 = SQRT(Cfung4 + **1000**);  
 SQRTp4 = SQRT(Cpred4 + **1000**);  
 SQRTp5 = SQRT(Cpred5 + **1000**);  
 SQRTo4 =SQRT(Comni4 + **1000**);  
 SQRTo5 = SQRT(Comni5 + **1000**);  
 SQRTppn2 = SQRT(Cppn2 + **1000**);  
 SQRTppn3 =SQRT(Cppn3 + **1000**);  
 SQRTppn4 = SQRT(dauer + **1000**);  
 sqrtpa=sqrt(plantassoc + **1000**);  
 logbone=log(Cbactone + **1000**);  
 logbtwo= log(Cbacttwo + **1000**);  
 logpaf2= log(paf2 + **1000**);  
 logb3= log(Cbact3 + **1000**);  
 logb4= log(Cbact4 + **1000**);

```

logf2 =log(Cfung2 + 1000);
logf3=log(Cfung3 + 1000);
logf4= log(Cfung4 + 1000);
logp4= log(Cpred4 + 1000);
logp5= log(Cpred5 + 1000);
logo4=log(Comni4 + 1000);
logo5=log(Comni5 + 1000);
logppn2= log(Cppn2 + 1000);
logppn3 =log(Cppn3 + 1000);
logppn4 = log(Cppn4 + 1000);
logpa= log(plantassoc + 1000);
logdauer= log(dauer + 1000);
run;

```

```

PROC UNIVARIATE NORMAL PLOT DATA=NEW;
VAR logbone logbtwo      logb3  logb4 logpaf2 logf2  logf3  logf4  logp4  logp5
      logo4  logo5  logppn2      logppn3      logppn4      logpa  logdauer
SQRTbone  SQRTbtwo  SQRTb3      SQRTb4      SQRTf2      SQRTf3
      SQRTf4      SQRTp4      SQRTp5      SQRTo4      SQRTo5
      SQRTppn2  SQRTppn3  SQRTppn4  sqrtpa;
run;

```

```

proc candisc data=new ncan=2 out=outcan;
  class cover;
var logdauer logbone logb4 logf2 sqrtf3 sqrtf4  logp4 logp5 sqrto5 sqrtpa  logppn ;

```

```

%plotit(data=outcan, plotvars=Can2 Can1,
  labelvar=_blank_, symvar=cover, typevar=cover,
  symsize=1, symlen=4, exttypes=cover, ls=80,
  tsize=2.5, extend=close);
  run;
  quit;

```

```

proc corr data=outcan;
VAR logdauer logbone logb4 logf2 sqrtf3 sqrtf4  logp4 logp5 sqrto5 sqrtpa  logppn can1
can2;
run;
quit;
proc print data=outcan;
run;quit;

```

## **APPENDIX II -- SITE CHARACTERIZATION OF NEMATODE COMMUNITIES**

### **1. LESREC, Experiment 1**

Average total nematode abundances ranged between a low of 1.9 million  $m^{-2}$  in September to 2.7 million  $m^{-2}$  in June. Bacterivores and plant parasites were the most abundant trophic groups in this experiment. Bacterivores did not change in abundance over time, while fungivores, omnivores, and predators were highest in June, approximately 6 weeks after tillage, and were lowest in September, among the three dates sampled. Plant associates peaked in April and declined over time, while plant parasites peaked in September.

### **2. LESREC, Experiment 2**

Total average nematode abundance in this experiment was highest in June 2005 at 3.2 million nematodes  $m^{-2}$  and dropped to 1.5 million  $m^{-2}$  by August. Bacterivores, fungivores, and plant associates were most abundant in June, however by August dominant trophic groups were bacterivores and plant parasites. All nematode trophic group abundances were highest in June and dropped significantly by August.

### **3. CMREC, Experiment 3**

Average total nematode abundances were lowest in November at 1.3 million  $m^{-2}$  and leveled at 1.8 million  $m^{-2}$  in June and August. Dominant trophic groups were bacterivores and plant parasites, followed by plant associates. Bacterivores were highest in abundance in November, and declined or leveled, respectively, in August. Plant associates, omnivores, and predators peaked in June, and plant parasites peaked in August.

<b>Trophic Group</b>	<b>LESREC Exp. 1</b>	<b>LESREC Exp. 2</b>	<b>CMREC</b>
<b>Bacterivores</b>	<i>Acrobeloides</i>	<i>Acrobeles</i>	<i>Acrobeles</i>
	<i>Alaimus</i>	<i>Acrobeloides</i>	<i>Acrobeloides</i>
	<i>Mesorhabditis</i>	<i>Alaimus</i>	<i>Anaplectus</i>
	Panagrolaimidae	<i>Mesorhabditis</i>	<i>Mesorhabditis</i>
	<i>Rhabditis</i>	Panagrolaimidae <i>Rhabditis</i>	Panagrolaimidae
<b>Fungivores</b>	<i>Aphelenchoides</i>	<i>Aphelenchoides</i>	<i>Aphelenchoides</i>
	<i>Diphtherophora</i>	<i>Aphelenchus</i>	<i>Aphelenchus</i>
	<i>Leptonchus</i>	<i>Diphtherophora</i>	<i>Diphtherophora</i>
		<i>Leptonchus</i>	
<b>Plant Associates</b>	<i>Coslenchus</i>	<i>Coslenchus</i>	<i>Coslenchus</i>
<b>Omnivores</b>	<i>Aporcelaimellus</i>	<i>Aporcelaimellus</i>	<i>Aporcelaimellus</i>
	<i>Ecumenicus</i>	<i>Ecumenicus</i>	<i>Mesodorylaimus</i>
	<i>Mesodorylaimus</i>	<i>Mesodorylaimus</i>	<i>Microdorylaimus</i>
		<i>Microdorylaimus</i>	
<b>Predators</b>	<i>Discolaimus</i>	<i>Discolaimus</i>	<i>Clarkus</i>
	<i>Mylonchulus</i>	<i>Mylonchulus</i>	<i>Discolaimus</i>
	<i>Nygolaimus</i>	<i>Nygolaimus</i>	<i>Mylonchulus</i>
		<i>Thonus</i>	<i>Nygolaimus</i>

**Table II.1.** List of most common genera/families at each site.

### APPENDIX III – PORE SIZE DISTRIBUTION FOR LESREC AND CMREC

**Table III.1.** Pore size distribution for intact soil cores (5-10 cm deep) at two sites in Maryland where nematode community studies were conducted (n=4 per site).

Site	Equivalent Moisture Tension (kPa)	Percent Water-Filled Pores											
		> 300	300	150	100	30	15	9	6	4.5	≤3		
LESREC	1/2	38.5	4.5	16.2	8.0	4.5	2.2	2.4	1.0	1.5	21.0		
	3/4	34.8	5.3	24.4	12.2	4.3	2.0	2.1	0.8	1.0	13.1		
CMREC	1/3	32.4	1.3	18.8	9.9	4.3	2.5	2.8	1.2	1.6	25.2		
	2/4	28.7	2.4	25.6	9.2	4.7	3.3	2.7	1.4	1.4	20.6		

#### 1. Materials and Methods

Soil samples used for the water retention curve collected in intact soil cores at 5-10 cm deep. Samples were kept sealed for 24 hours and then brought to the lab where they were prepared for placement on a sand table. Plastic mesh was secured to the bottom of the cores using hot glue. The samples were returned to the plastic bags and secured with rubber bands. They remained in the refrigerator for one week, prior to saturation. Samples were saturated rapidly by placement in a tank of water, not through capillary rise.

A sand table (right) was used to equilibrate the cores at -1 and -2 kPa. The saturated cores were placed on the surface of the sand, which was leveled manually. A single layer of paper towel was placed on the surface of the sand to increase soil pore connection with sand pores. The chamber was sealed by strapping a lid on the tank. Pressure was applied by adjusting the height of the rubber tubing (by which water exited the tank) a given distance below the saturation height (the center of the core height). Equilibrium was assumed when water stopped dripping from the rubbing tubing. The actual pressure applied was determined by averaging the measurement of a tensiometer with the height of pressure applied by lowering the tubing from the center of the core height.

A pressure membrane apparatus was used to determine the drying moisture retention curve of the eight soil samples at a higher range of pressures. The pressure plates (3 bar) were prepared by wetting them and adding celite to ensure good soil contact with the plates. Four samples were placed in each pressure chamber, and a plate (made by Soil Moisture Co. of Santa Barbara, California) in each chamber served as a porous medium through which water could pass from the soil. The water collected in a rubber seal beneath the plate and drained through a small outlet of the chamber. When water stopped dripping from the outlet, it was assumed that equilibrium was reached. After reaching equilibrium for each pressure applied, the cores were weighed to determine the moisture content. Bulk density was determined by drying soil cores in an oven at 105°C. Bulk density values were low which may have been a methodology error or an effect of winter soil sampling.

## **APPENDIX IV – OTHER METHODS**

### **1. Sand size fractionation**

Plastic centrifuge tubes containing 20 g of soil sample and 30 ml of 0.65% sodium hexametaphosphate solution were shaken for 21.5 hours. Cleaned and dried 50 ml beakers were pre-weighed and labeled. Samples were rinsed out of the tubes and into a 270 mesh screen (0.05 mm diameter). After thorough rinsing, the sand remaining on the sieve was washed into the 50 ml beaker and placed in an oven at 100°C for several days until thoroughly dry. Each beaker with sand was measured and pre-weighed beaker weight was used to obtain the sand size fraction of the soil by subtraction. The sand was then transferred to a stack of sieves and shaken automatically and vigorously for 3 minutes. Sand and sieve were weighed together and then sieve alone, to calculate the mass of the sand size fraction by subtraction. The sand was separated into very coarse (1.0-2.0 mm), coarse (0.5-1.0 mm), medium (250-500 µm), fine (106-250 µm), and very fine (53-106 µm) size fractions.

### **2. pH**

Samples were weighed (5 g) into scintillation vials. Distilled water (5 ml) was added to the soil and shaken (upright) on a shaker for 5-10 seconds. Samples were permitted to settle for 10-15 minutes and then after calibration of pH electrode using buffers 4.0 and 7.0, sample pH was measured. Supernatant was gently stirred with the electrode just prior to reading. During analysis of samples from LESREC Exp. 2, the electrode was re-calibrated for each block of samples, corresponding to field blocks. Samples from CMREC were analyzed after settling one hour.



### 3. Bulk density

Bulk density was determined by weighing the known volume of soil in each sample bag before nematode extraction and removing a ~30 g sub-sample for soil moisture determination. Soil was placed in metal tins, weighed moist, and allowed to dry before being heated to 105 °C for no more than 24 hours.

### 4. Calculation of Nematode Abundance on an Area Basis

$(100 - \% \text{ Moisture determined for BD})/100 = \% \text{ dry soil}$

$\% \text{ dry soil} \times \text{fresh soil weight from nematode extraction} = \text{g dry soil extracted}$

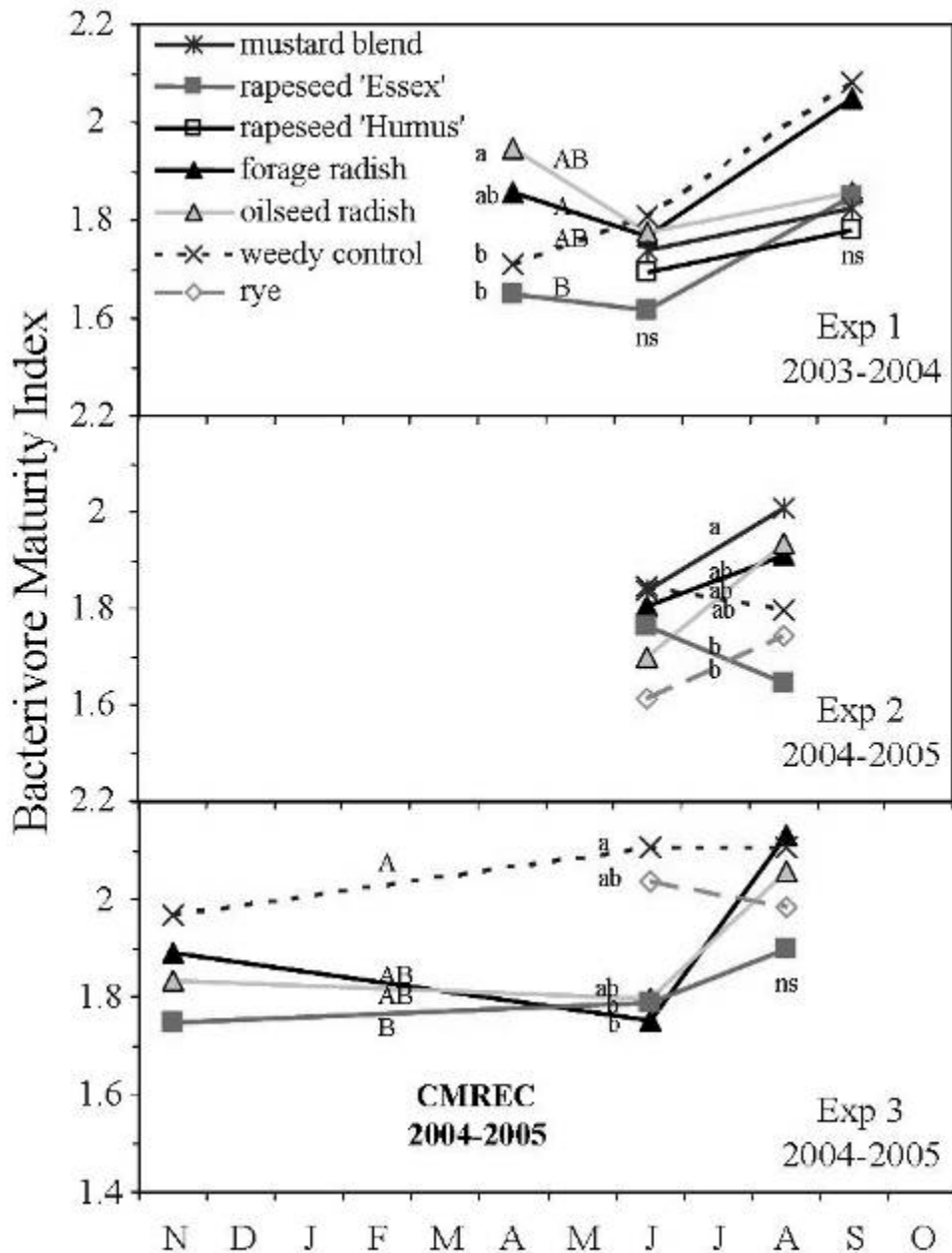
$(\text{individuals counted} \times (10 \text{ ml} / \# \text{ of ml identified})) = \text{total number of nematodes/extracted sample}$

$\text{Total number of nematodes/g dry soil extracted} = \text{nematodes g}^{-1} \text{ dry soil}$

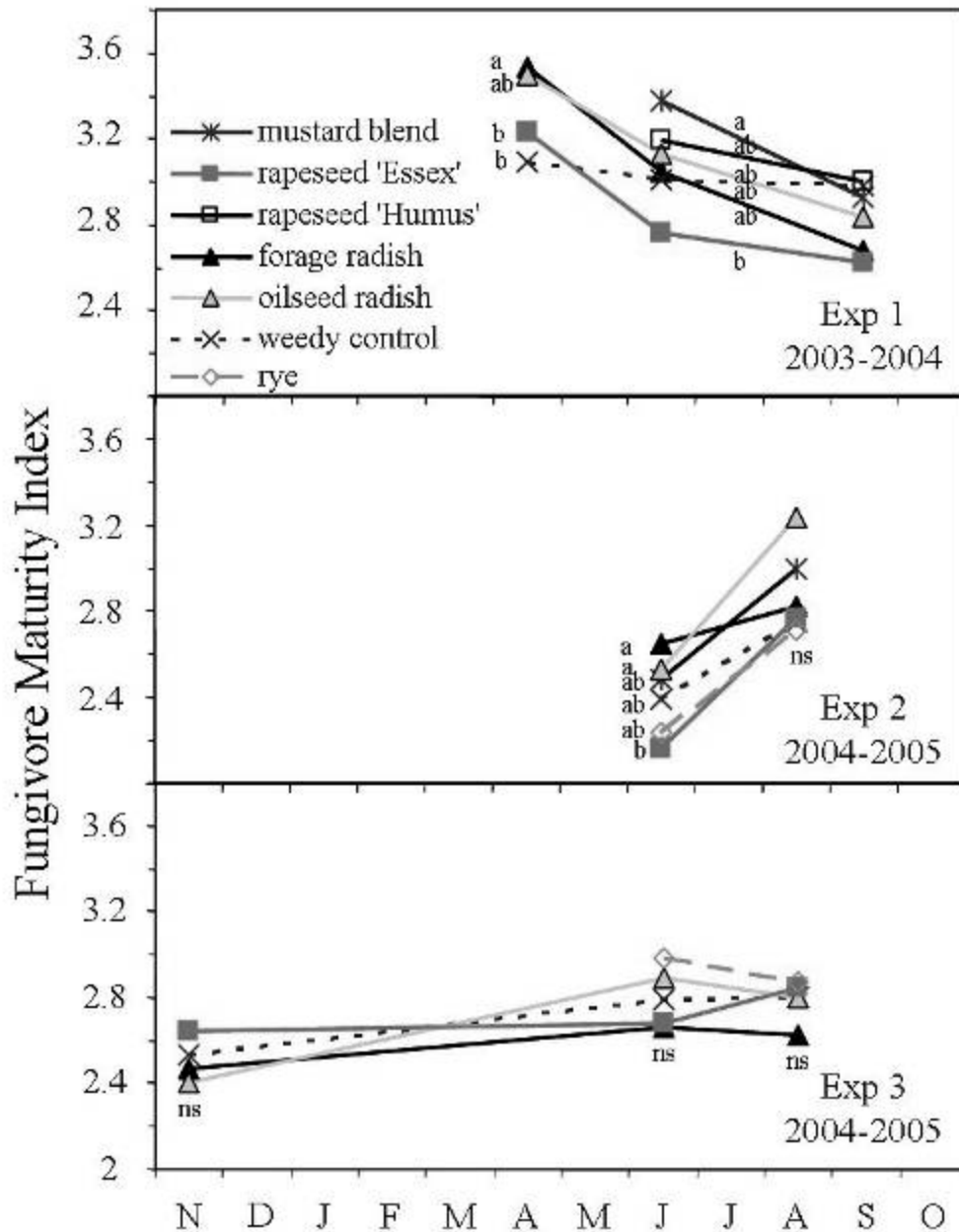
$\text{Nematodes g}^{-1} \text{ dry soil} \times \text{BD (g/cm}^3) = \text{nematodes cm}^{-3}$

$(\text{nematodes cm}^{-3}) \times (15 \text{ cm deep} \times 100 \text{ cm} \times 100 \text{ cm}) = \text{nematodes m}^{-2}$

## APPENDIX V – BACTERIVORE AND FUNGIVORE MATURITY INDICES

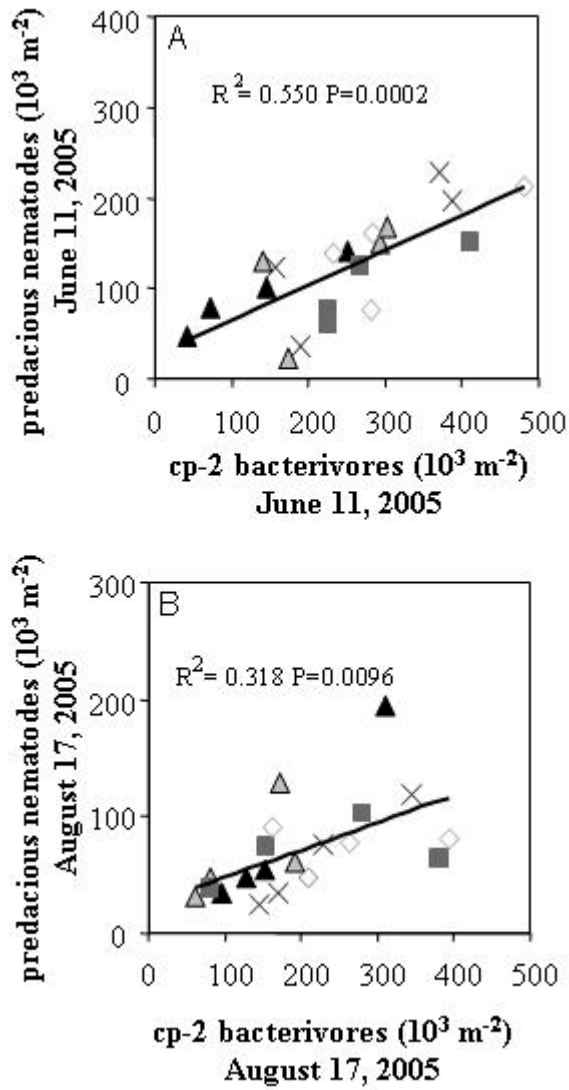


**Figure V.1.** The Bacterivore Maturity Index over time at two sites in Maryland after cover crop treatments were sown in fall (August) and terminated in Dec/Jan (radishes and mustard) or mid-late April (rapeseeds and rye). Summer cash crops were either soybean (LESREC Exp 1) or corn (LESREC Exp 2/CMREC). The BaMI is calculated by weighting (by their respective cp values) and summing the proportions of p-1, cp-2, cp-3, and cp-4, bacterivores to total bacterivores (Table 2). Capital letters represent means across three dates, while lowercase letters represent means on a given date or across two dates. Means with the same letter are not statistically different at  $P < 0.10$  (HSD) ( $n=4$ ).

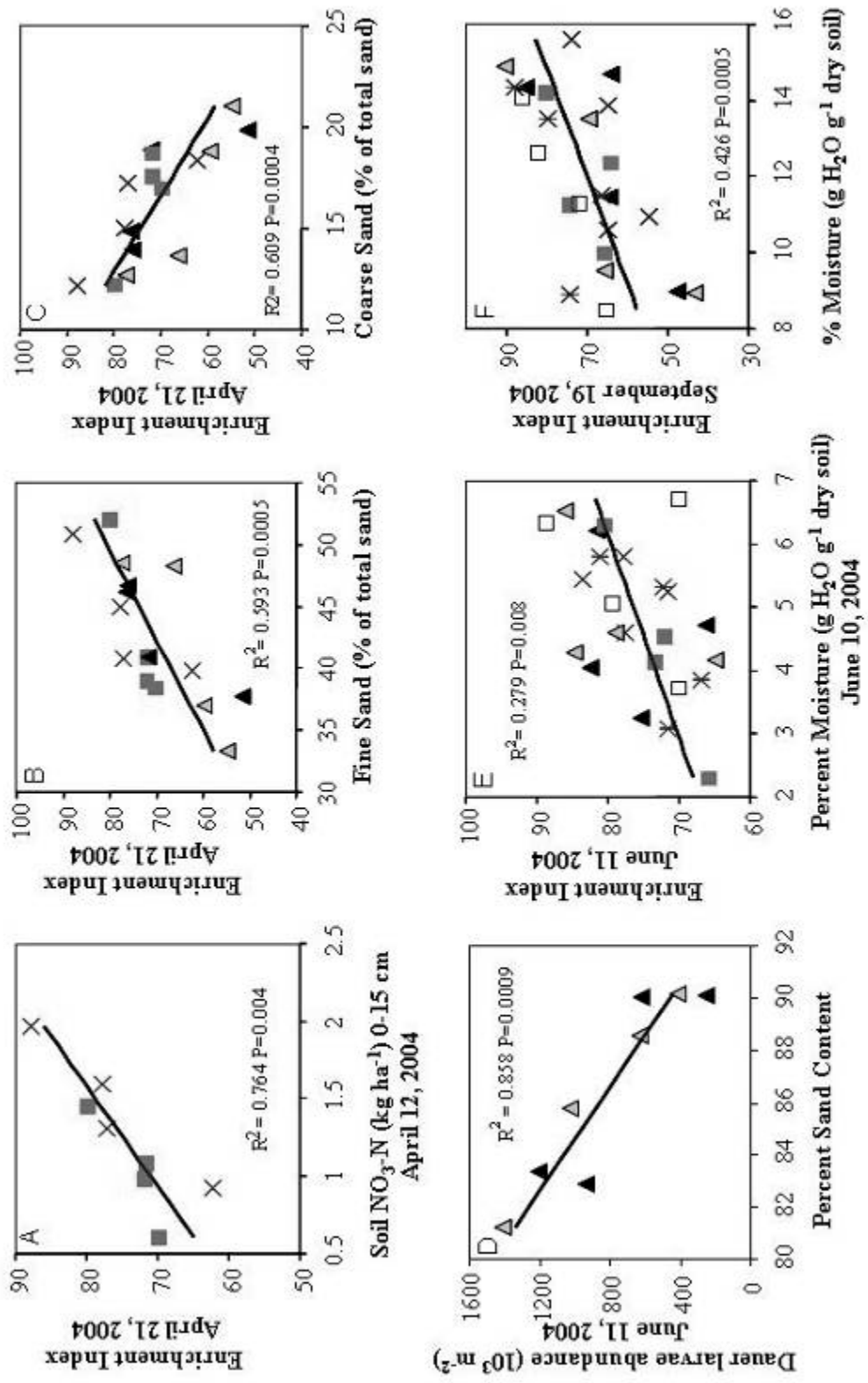


**Figure V.2.** Fungivore Maturity Index across time at two sites in Maryland after cover crop treatments were sown in fall (August) and terminated in Dec/Jan (radishes and mustard) or mid-late April (rapeseeds and rye). The FuMI is calculated by weighting (by their respective cp values) and summing the proportions of cp-2, cp-3, and cp-4 fungivores to total fungivores abundance (Table 4.1). Facultative root hair-fungi feeders are not included in the index. Letters represent means on a given date or across two dates. Means with the same letter are not significantly different at  $P < 0.10$  (HSD) ( $n=4$ ).

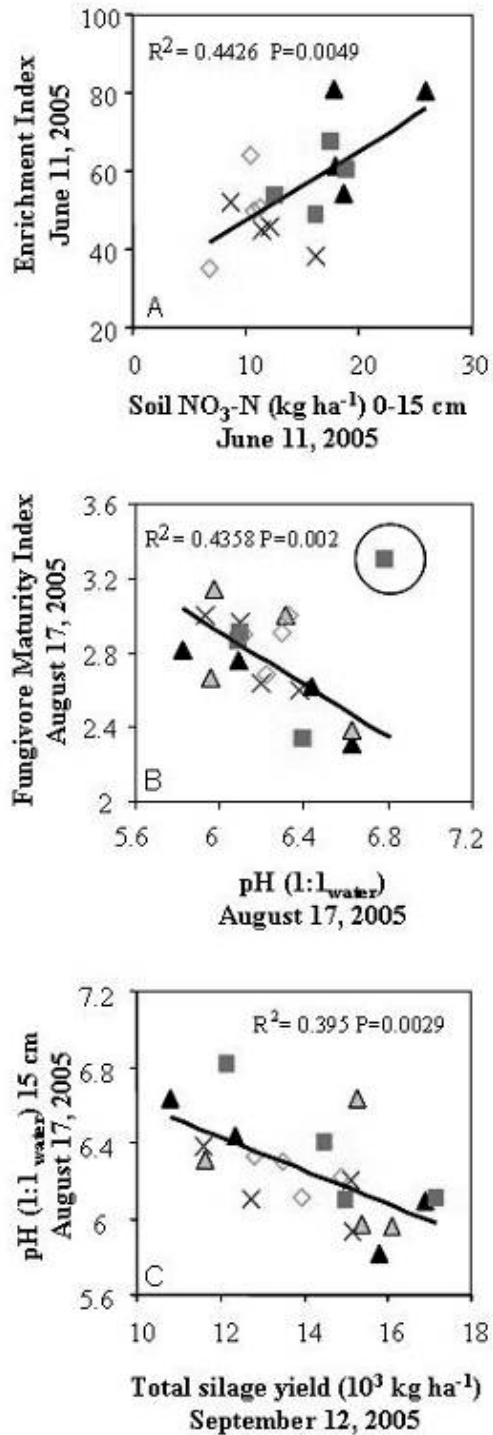
APPENDIX VI – OTHER GRAPHS OF FAUNAL ANALYSIS



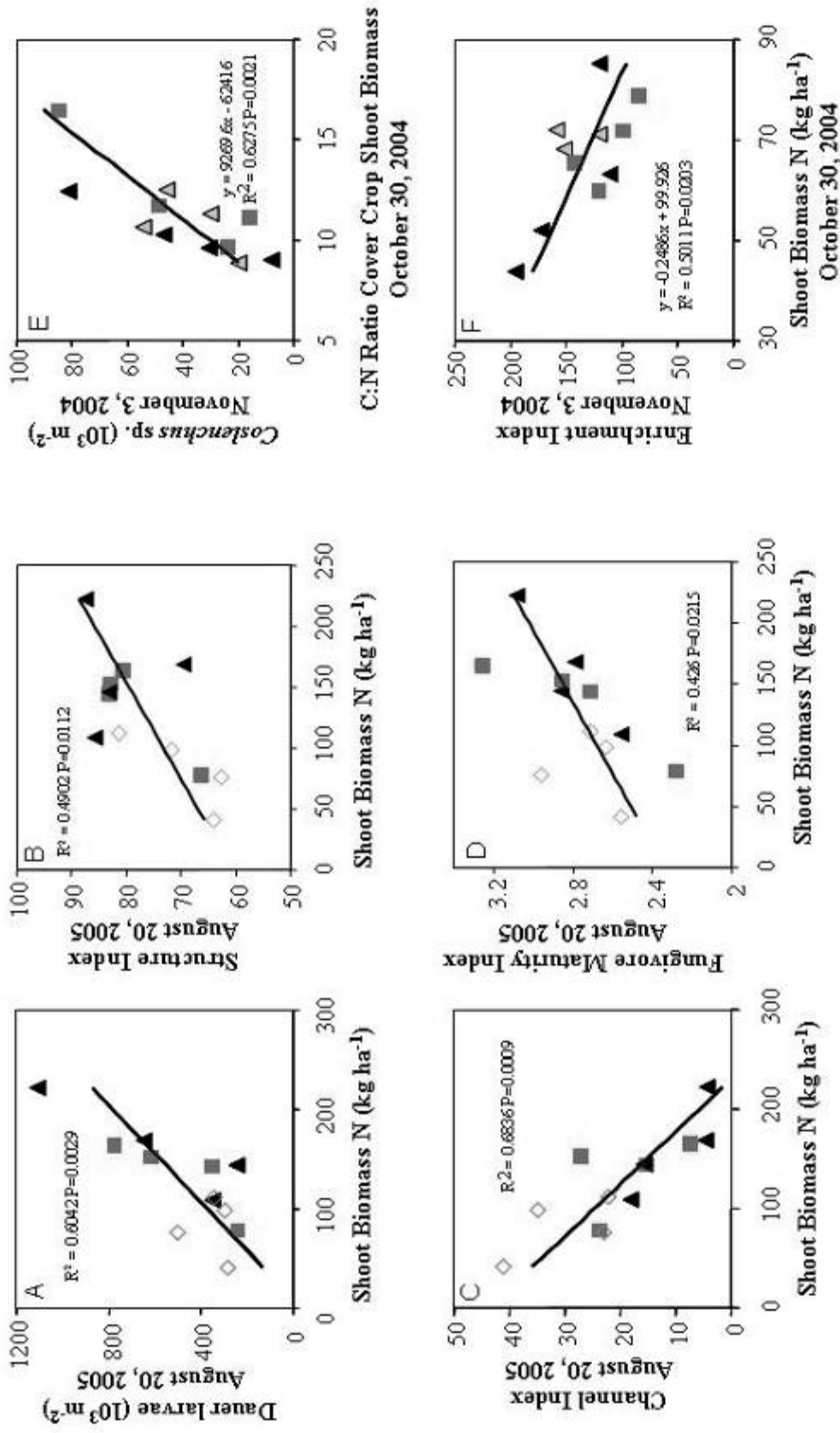
**Figure VI.1.** Correlations between predacious nematodes and cp-2 bacterivores in Exp. 3 in June and August. Symbols represent cover crop treatments: black triangles=forage radish; grey triangles=oilseed radish; squares=rapeseed ‘Essex’; X=weedy control.



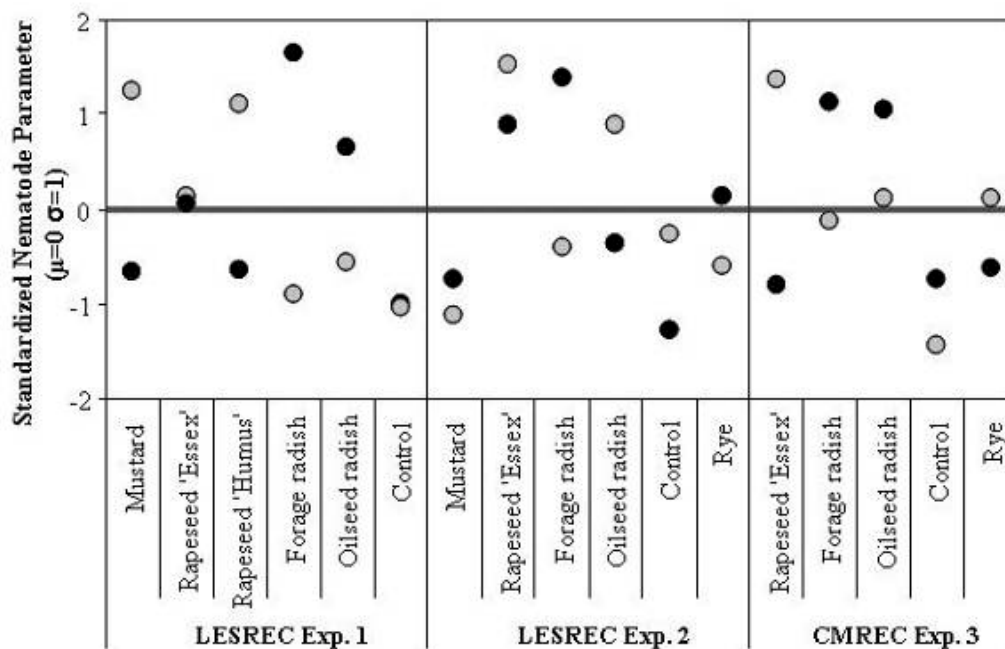
**Figure VI.2.** Correlations between nematode parameters and soil properties in Exp. 1. Symbols represent cover crop treatments: black triangles=forage radish; grey triangles=oilseed radish; filled squares=rapeseed 'Essex'; empty squares=rapeseed 'Humus'; stars=mustard; X=weedy control.



**Figure VI.3.** Correlations between nematode parameters or corn silage yield and soil properties in Exp. 3. Figure B does not include the outlier (circled). Symbols represent cover crop treatments: black triangles=forage radish; grey triangles=oilseed radish; filled squares=rapeseed ‘Essex’; unfilled diamonds=rye; X=weedy control.



**Figure VI.4.** Correlations between plant properties and nematode parameters in August in Exp. 2 (A-D) and during cover crop growth in November in Exp. 3. Symbols represent cover crop treatments: black triangles=forage radish; grey triangles=oilseed radish; filled squares=rapeseed 'Essex'; unfilled diamonds=rye; X=weedy control.



**Figure VI.5.** Depiction of standardized treatment mean deviation from the total mean of all treatments (including control) for dauer larvae (filled circles) and EI (grey filled circles) at a given experiment in fall (September or August).<sup>1</sup>

<sup>1</sup> Simultaneous depiction of nematode community parameters can assist in interpretation of currently available indices. Interpretation of nematode community response through visual means has already been introduced and developed (de Goede et al., 1993; Ferris et al., 2001; Ferris and Bongers, 2006), and aggregation of indices for interpretation of C and N cycling is a common practice in soil quality evaluation (Schloter et al., 2003). Figure 1 suggests that dauer larvae should not be included in calculation of the EI, because both similar and opposing deviations from the mean, for different treatments, suggest that dauer abundance and the EI may indicate different fertility conditions at various times.

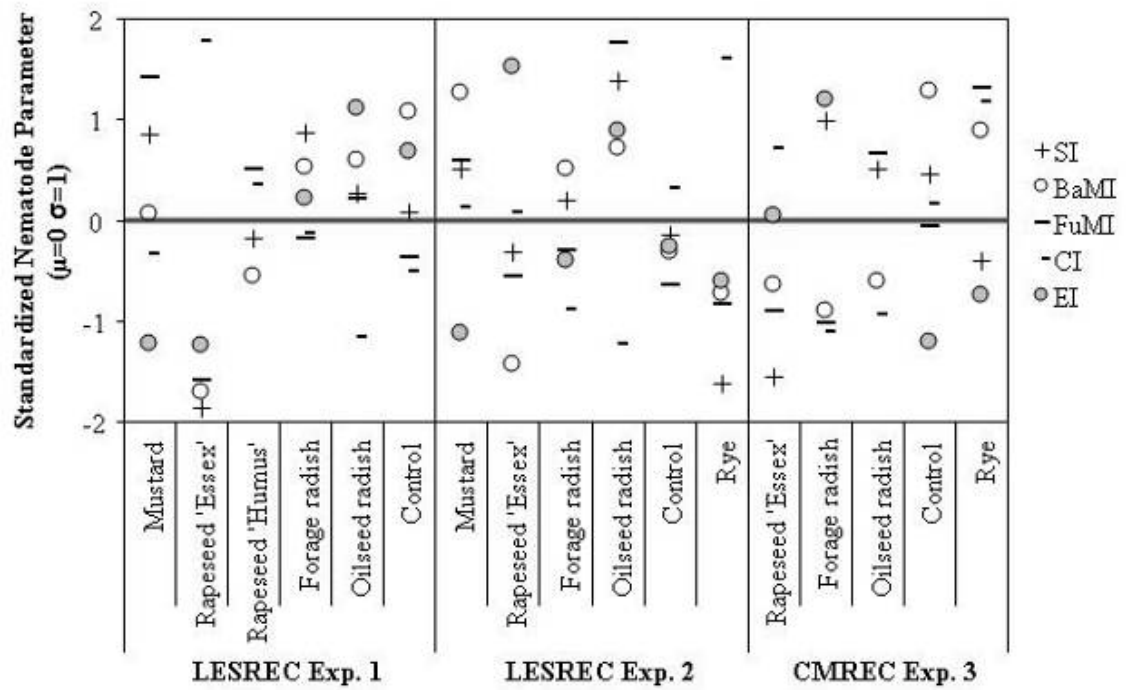
de Goede, R.G.M., Bongers, T., Ettema, C., 1993. Graphical presentation and interpretation of nematode community structure: C-P triangles. *Med. Fac. Landbouww Univ. Gent.* 58, 743-750.

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Schloter, M., Dilly, O.M., Munch, J.C., 2003. Indicators for evaluating soil quality. *Agr. Ecosys. Envir.* 98, 255-262.





**Figure VI.6.** Depiction of standardized treatment mean deviation from the total mean of all treatments (including control) for SI, BaMI, FuMI, CI, and EI at a given experiment in June.

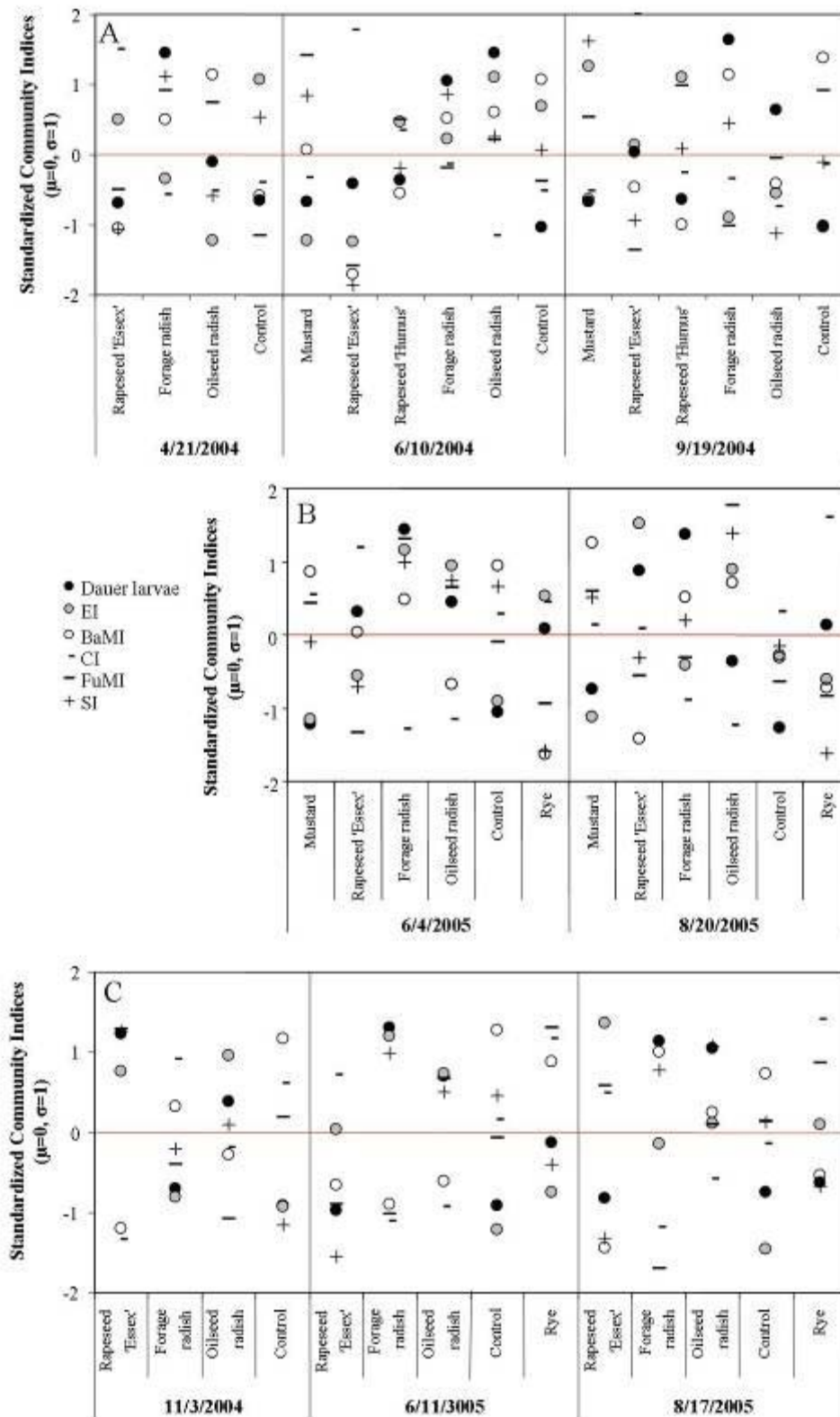


Figure VI.7. Standardized indices presented for Exp. 1 (A), Exp. 2 (B), and Exp. 3 (C).

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