

Vertical Distribution of Bacterivorous Nematodes under Different Land Uses

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Abstract: The vertical distribution of dominant genera of bacterivorous nematodes to 150-cm depth in an aquic brown soil was compared after 14 years of four contrasting land uses, i.e., cropland-rice (CR), cropland-maize (CM), abandoned cropland (AC), and woodland (WL). The study was conducted at the Shenyang Experimental Station of Ecology, a Chinese Ecosystem Research Network (CERN) site in Northeast China. Data were analyzed using two-way analysis of variance with land use and depth as independent variables. More than 70% of *Chiloplacus*, *Eucephalobus*, and *Monhystera* spp. were present in the uppermost soil layer (0 to 5 cm) in the CR treatment. In contrast, *Chiloplacus* and *Prismatolaimus* spp. were distributed down to 100-cm depth in the AC and CM treatments, respectively. Differences in numbers of *Acrobeles*, *Acrobeloides*, *Cephalobus*, *Chiloplacus*, *Eucephalobus*, *Monhystera*, *Plectus*, and *Prismatolaimus* were found among land uses and at various depths. Soil C and N were correlated positively with numbers of *Monhystera* and *Plectus* in the CR treatment, *Acrobeloides* in the CM treatment, and *Acrobeles* and *Acrobeloides* in the AC treatment. Soil pH was correlated negatively with *Monhystera*, *Plectus* (CR), and *Acrobeloides* (CM, AC). The relationship of pH with *Acrobeles* depended on land use: positive in the WL treatment and negative in the AC treatment. Our results suggested that *Cephalobus* and *Prismatolaimus* in the CR treatment, and *Chiloplacus* and *Prismatolaimus* in the WL treatment, were insensitive to soil properties measured. Differences in vertical distribution should be considered when studying dominant bacterivorous nematode genera among land uses.

Key words: aquic brown soil, bacterivorous nematodes, CERN site, dominant genera, land use, vertical distribution.

Nematodes occupy a central position in the soil food web and play significant roles in ecological processes such as nitrogen cycling and plant growth patterns (Neher, 2001). Bacterivorous nematodes are key microfaunal grazers that regulate ecological processes of decomposition and nutrient cycling, thereby indirectly affecting primary production (Freckman, 1988). An increase in the abundance of this group often enhances microbial activity in soils with a non-limiting supply of nitrogen (Wasilewska, 1998). Bacterivorous nematodes are better bioindicators of the rate of decomposition of organic matter than the abundance of bacteria because, through their higher position in the food chain, they integrate both biotic and abiotic factors (Griffiths et al., 1994; Wasilewska, 1998). Other evidence indicates that bacterivorous nematodes can increase soil mineral nitrogen availability, crop growth, and nitrogen uptake in microcosm and field experiments (Ferris et al., 1997; Ingham et al., 1985; Li and Hu, 2001). Thus, any change in land management that affects bacterivorous soil nematodes has the potential to influence critical ecological processes (Yeates and King, 1997).

Different land uses affect the vertical distribution of bacterivorous nematodes and the dominant genera present (Hánél, 2003; Ilieva-Makulec, 2000; Ou et al., 2005; Sohlenius and Sandor, 1987; Yeates et al., 2000). Sohlenius and Sandor (1987) suggested that numbers

of *Acrobeloides* and *Cephalobus* at 0 to 30-cm depth were greater in soil with grass than with barley. Hánél (2003) reported that *Acrobeloides* prevailed in soil with maize, whereas *Eucephalobus* was dominant in fallow arable soils. In the North Negev Desert of Israel, the dominant genera of bacterivorous nematodes in a 50-cm soil profile were *Acrobeles*, *Acrobeloides*, and *Cervidellus* under the canopy of *Atriplex halimus* and *Hammada scoparia*, but *Acrobeloides* and *Cephalobus* under *Acacia* trees (Pen-Mouratov et al., 2003, 2004).

Little information is available concerning the effects of land uses on vertical distribution of dominant genera of bacterivorous nematodes in China. To understand the roles of bacterivorous nematodes on soil ecological processes, it is necessary to study the relationships between land use and dominant genera of bacterivorous nematodes. The objectives of this study were to (i) determine the vertical distribution of dominant genera of bacterivorous nematodes under different land uses (cropland, abandoned cropland, and woodland) at a Chinese Ecosystem Research Network (CERN) site and (ii) describe the relationships between dominant genera of bacterivorous nematodes and selected chemical properties in an aquic brown soil.

MATERIALS AND METHODS

This study was conducted at the Shenyang Experimental Station of Ecology (41°31'N, 123°22'E), Chinese Academy of Sciences, a CERN site in the lower reaches of the Liao River plain in northeast China. The station is located in the continental temperate monsoon zone, with a dry-cold winter and a warm-wet summer. The annual mean temperature is 7.0 °C to 8.0 °C, annual precipitation averages 650 to 700 mm, and annual non-frost period is 147 to 164 days. The soil is an aquic brown soil (silty loam Hapli-Udic Cambisols in Chinese soil taxonomy), which is suitable for growing

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maize, soybean, and rice (Ou et al., 2005). Before the establishment of the station in 1989, all land was paddy fields with comparatively homogeneous and sufficient soil fertility; after 1989, part of the land was converted to maize production, remained fallow, or converted to woodland (Zhang et al., 2004b).

On 14 November 2003, soil samples were collected from four types of land use, i.e., cropland-rice (*Oryza sativa*) (CR), cropland-maize (*Zea mays*) (CM), abandoned cropland (dominant weeds were *Ambrosia lavandulaefolia*, *Conyza canadensis*, *Humulus scandens*, *Metaplexis japonica*) (AC), and woodland (*Populus canadensis*) (WL), respectively. Three replicate profiles for each land use pattern were sampled to a depth of 0 to 150 cm and subdivided into layers of 0 to 5, 5 to 10, 10 to 20, 20 to 30, 30 to 40, 40 to 60, 60 to 80, 80 to 100, 100 to 120, and 120 to 150 cm (Zhang et al., 2004b).

Soil properties were measured at each depth for each different land use. Specifically, soil bulk density was determined by using a stainless steel ring to delineate a known volume of soil that was oven-dried at 105 °C. Soil total organic carbon, total nitrogen, and pH were measured according to Zhang et al. (2004a,b).

Bacterivorous nematodes were extracted from 100 g of soil (fresh weight) from each sample using sugar flotation and centrifugation (Liang et al., 2001b), and nematode populations expressed as number of nematodes per 100 cm³ (Norton and Niblack, 1991). All extracted nematodes in each sample were counted and identified to genus, using an inverted compound microscope, based on stoma and esophageal morphology (Liang et al., 2001a, 2003; Yin, 2000).

Statistical analysis was performed for genera representing a relative abundance greater than 10 % of total bacterivorous nematodes under different land uses. Statistical probabilities were derived from two-way analysis of variance with land use and soil depth as independent variables. Linear correlations between generic density of dominant bacterivorous nematodes and selected soil chemical properties were quantified using Pearson's correlation coefficients. All nematode data were ln (x + 1) transformed prior to statistical analysis (Verschoor et al., 2001) using SPSS statistical software (SPSS Inc., Chicago, IL). Differences with $P < 0.05$ were considered significant and $P < 0.01$ highly significant.

RESULTS

Dominant genera of bacterivorous nematodes under land uses: In this study, 9, 10, 11, and 13 bacterivorous nematode genera were identified in the CR, CM, AC, and WL treatments, respectively. *Cephalobus*, *Monhystera*, *Plectus*, and *Prismatolaimus* were dominant genera in the CR treatment; *Acrobeloides* and *Chiloplacus* in the CM treatment; *Acrobeles*, *Acrobeloides*, *Cephalobus*, and *Eucephalobus* in the AC treatment; and *Acrobeles*, *Cephalobus*, *Chiloplacus*, and *Prismatolaimus* in the WL treatment (Table 1).

TABLE 1. Proportional contribution (%) of bacterivorous nematode genera to the nematode assemblage in a 150-cm soil profile under different land uses.

Genus	Land use ^a			
	CR	CM	AC	WL
<i>Achromadora</i>	0.0	0.0	0.0	1.0
<i>Acrobeles</i>	0.0	6.9	20.9	13.9
<i>Acrobeloides</i>	5.8	11.6	36.9	9.3
<i>Cephalobus</i>	16.0	7.8	14.7	18.3
<i>Cervidellus</i>	0.0	2.4	0.0	0.0
<i>Chiloplacus</i>	6.2	57.0	0.9	11.2
<i>Domorganus</i>	1.4	0.1	0.0	0.0
<i>Eucephalobus</i>	1.4	7.1	10.3	8.2
<i>Heterocephalobus</i>	0.0	0.0	0.0	0.3
<i>Mesorhabditis</i>	0.0	0.0	5.9	1.1
<i>Monhystera</i>	16.0	0.0	0.0	0.0
<i>Panagrolaimus</i>	1.0	0.9	0.3	2.1
<i>Plectonchus</i>	0.0	0.0	0.0	1.2
<i>Plectus</i>	41.7	0.0	5.5	0.7
<i>Prismatolaimus</i>	10.3	5.3	2.2	26.4
<i>Protorhabditis</i>	0.0	0.0	0.1	0.0
<i>Rhabditis</i>	0.0	0.9	2.3	6.1

^a CR, cropland-rice; CM, cropland-maize; AC, abandoned cropland; WL, woodland.

Differences in the numbers of *Acrobeles*, *Acrobeloides*, *Cephalobus*, *Chiloplacus*, *Eucephalobus*, *Monhystera*, *Plectus*, and *Prismatolaimus* were observed among land uses and depths (Table 2).

Vertical distribution of dominant genera: More than 70% of *Chiloplacus*, *Eucephalobus*, and *Monhystera* present were at 0 to 5-cm depth in the CR treatment, whereas the maximum relative abundance of *Plectus* occurred at 20 to 30-cm depth in the WL treatment (Fig. 1). The CR treatment was the only land use containing *Monhystera* and the only one lacking *Acrobeles*. *Acrobeles* and *Prismatolaimus* tended to be more abundant at 0 to 10-cm depth in the AC treatment, whereas *Chiloplacus* was distributed evenly across all soil depths in the WL treatment. The percentage of *Acrobeles* decreased with depth under the WL treatment, to 30 cm. These results suggest that different genera dominate at differing depths under different land uses.

Correlations between abundance of dominant genera and selected soil chemical properties: Numbers of *Monhystera* and *Plectus* in the CR treatment correlated positively with

TABLE 2. Analysis of variance (F-values) for dominant genera of bacterivorous nematodes with soil and land use effects.

Genus	Land use (F)	Depth (F)
<i>Acrobeles</i>	8.04**	4.69**
<i>Acrobeloides</i>	17.46**	5.34**
<i>Cephalobus</i>	9.59**	8.89**
<i>Chiloplacus</i>	60.16**	2.89**
<i>Eucephalobus</i>	3.45**	2.75**
<i>Monhystera</i>	17.81**	4.98**
<i>Plectus</i>	13.69**	2.12**
<i>Prismatolaimus</i>	7.64**	3.27**

*: $P < 0.05$; **: $P < 0.01$ ($n = 120$).

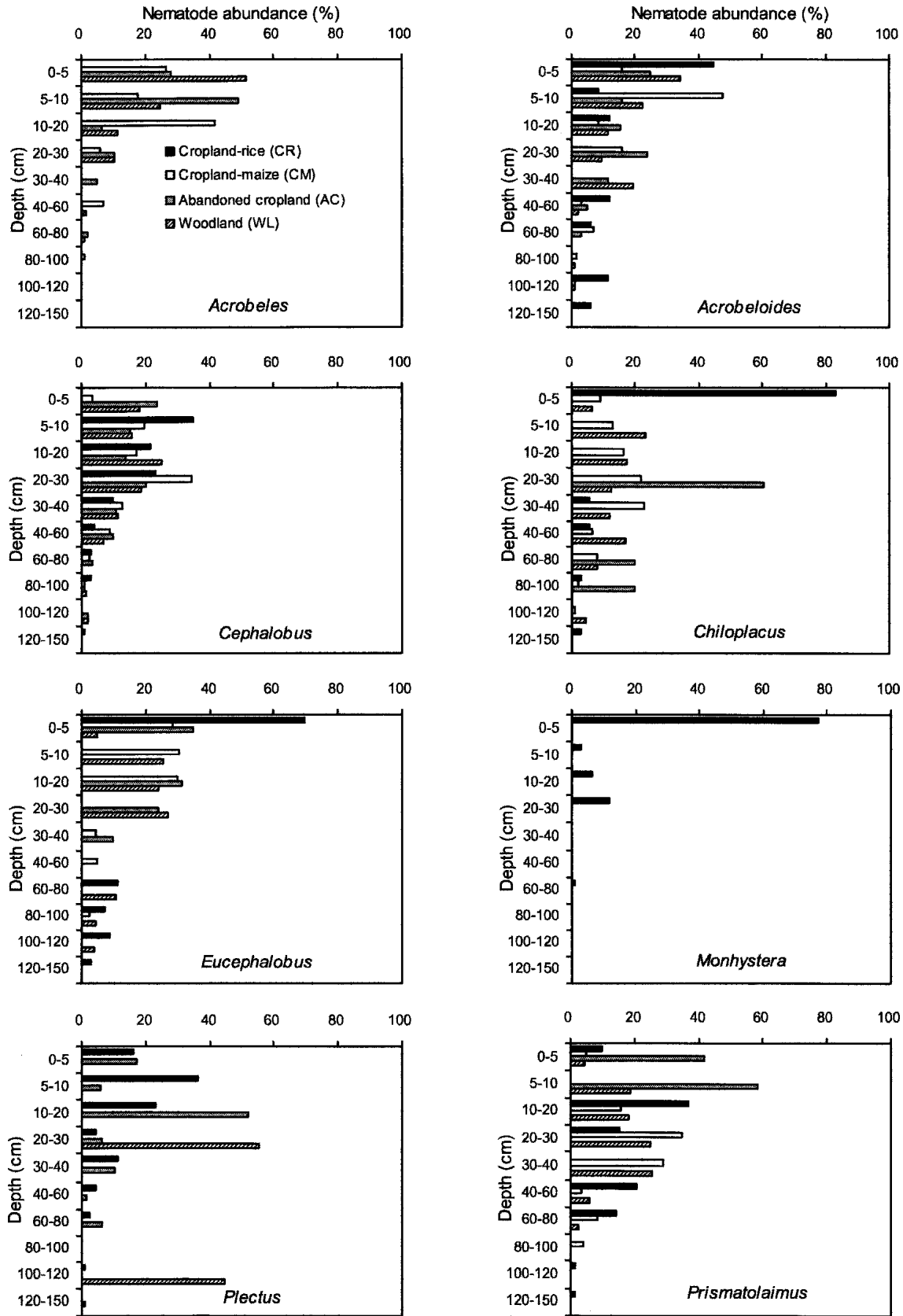


FIG. 1. Vertical distribution of dominant genera of bacterivorous nematodes (mean abundance of nematodes in each soil layer expressed as percentage of the total abundance in a 150-cm soil profile) under different land uses.

total C and total N ($r = 0.47\text{--}0.57$) (Table 3). Similar trends were observed for densities of *Acrobeloides* in the CM and AC treatments. *Acrobeloides* in the AC and WL treatments was correlated positively with total C and total N ($r = 0.44\text{--}0.64$). Soil pH was correlated negatively with *Monhystera*, *Plectus* (CR), and *Acrobeloides* (CM, AC). The relationship of pH with *Acrobeloides* depended on land use, being positive in the WL treatment ($r = 0.43$) but negative in the AC treatment ($r = 0.38$). *Cephalobus* and *Prismatolaimus* under the CR treatment, and *Chiloplacus* and *Prismatolaimus* in the WL treatment, were insensitive to the soil properties measured in this study (Table 3).

DISCUSSION

Different genera of bacterivorous nematodes were dominant in different land uses. In our study, *Acrobeloides* and *Eucephalobus* dominated in the CM and AC treatments, respectively. This observation agrees with that of Hanel (2003) for cultivated and fallow fields in the Czech Republic. *Cephalobus* was the most dominant genus in the CR treatment, which is similar to observations by Ilieva-Makulec (2000) in a cultivated peat meadow soil of northeast Poland. *Acrobeloides* and *Cephalobus* prevailed in the WL treatment, which agrees with the results of Yeates et al. (2000) for a soil under *Pinus radiata* in New Zealand.

Vertical distributions of the dominant genera of bacterivorous nematodes depended on land use. Differences in the vertical distribution of nematode genera may reflect the suitability in the various strata of factors such as temperature, moisture regime, and pore size (Greet, 1978; Nicholas, 1975; Yeates, 1980). Three genera (*Chiloplacus*, *Eucephalobus*, and *Monhystera*) were

dominant in the upper soil profile of the CR treatment, whereas *Cephalobus*, *Plectus*, and *Prismatolaimus* were found in deeper soil layers in the CR treatment. The different vertical distribution of dominant nematode genera in the CR treatment may be due to the impoverishment of living conditions owing to water-logging and oxygen deficit at greater depths (Sohlenius and Sandor, 1987). Yeates (1980) found that the bacterivores were concentrated in 0 to 5-cm depth but *Cephalobus* extended to 10 to 20-cm depth in the Otiake slit loam soil; in the Patumahoe clay loam soil, 50% *Plectus* were found in the 0 to 2.5-cm depth, and it extended to 20 to 30-cm depth. Further discussion is hindered by lack of knowledge of feeding habits in different land uses. In this study, two peaks of *Plectus* abundance were observed with depth in the WL treatment. These results were contrary to Yeates et al. (2000), who found one peak with depth in soil under *Pinus radiata*. Perhaps differences in climatic condition, soil types, and tree species between the two sites explained the contrasting vertical distribution of *Plectus*. According to Sohlenius (1985), some members of Cephalobidae are common in various types of undisturbed soils, which may account for insensitivity of *Cephalobus* and *Chiloplacus* to contrasting soil properties under different land uses. Whereas *Acrobeloides* are adapted to a stable food supply under ordinary soil conditions (Sohlenius, 1985), they may be at a competitive advantage to other genera in the CM treatment.

Differences in the vertical distribution of different dominant genera of bacterivorous nematodes are probably caused partially by differences in vertical distribution of their food sources (Sohlenius and Sandor, 1987). For example, in our study, distribution of *Monhystera* and *Plectus* in the CR treatment, *Acrobeloides* and *Chiloplacus* in the CM treatment, *Acrobeloides* and *Acrobeloides* in the AC treatment, and *Acrobeloides* and *Cephalobus* in the WL treatment soils were correlated positively with total C and total N. Similar findings were reported by Yeates (1980), who found that the mean nematode population under the 11 established grazed pastures sampled was correlated with the C:N ratio in 20 to 30-cm depth. Vertical distributions of the dominant bacterivorous genera under different land uses are also related to soil pH. While these results demonstrate that pH is an important limiting factor for survival of the dominant genera of bacterivorous nematodes, further work is required to determine whether this pH effect is direct or indirect, through nematode food resources.

Our study showed that dominant genera of bacterivorous nematodes had different vertical distribution under different land uses. We sampled only in late autumn, seasonal variation and species level variation not being considered. Further studies are needed to determine the seasonal and vertical distribution of dominant bacterivorous genera, and their species, under different land uses.

TABLE 3. Correlation coefficients among dominant genera of bacterivorous nematodes and selected soil chemical properties under different land uses.

Land use	Genus	pH	Total C	Total N
Cropland-rice	<i>Cephalobus</i>	-0.10	0.32	0.32
	<i>Monhystera</i>	-0.79**	0.57**	0.55**
	<i>Plectus</i>	-0.49**	0.47**	0.52**
	<i>Prismatolaimus</i>	-0.16	0.11	0.13
Cropland-maize	<i>Acrobeloides</i>	-0.50**	0.45**	0.47**
	<i>Chiloplacus</i>	-0.32	0.52**	0.48**
Abandoned	<i>Acrobeloides</i>	-0.38*	0.44**	0.44*
	<i>Acrobeloides</i>	-0.52**	0.61**	0.60**
	<i>Cephalobus</i>	-0.36	0.61**	0.60**
	<i>Eucephalobus</i>	-0.23	0.39*	0.37*
Woodland	<i>Acrobeloides</i>	0.43*	0.64**	0.61**
	<i>Cephalobus</i>	0.17	0.38*	0.38*
	<i>Chiloplacus</i>	0.06	0.05	0.05
	<i>Prismatolaimus</i>	-0.06	0.02	0.01

*, **: Significant at $P < 0.05$ and $P < 0.01$ levels, respectively.

As we found different land use patterns affected vertical distribution of bacterivorous nematode genera in contrasting ways, such differences in vertical distribution should be considered when comparing dominant bacterivorous genera among land uses.

LITERATURE CITED

- Ferris, H., R. C. Venette, and S. S. Lau. 1997. Population energetics of bacterial-feeding nematodes: Carbon and nitrogen budgets. *Soil Biology and Biochemistry* 29:183–1194.
- Freckman, D. W. 1988. Bacterivorous nematodes and organic-matter decomposition. *Agriculture, Ecosystems and Environment* 24: 195–217.
- Greet, D. N. 1978. The effect of temperature on the life cycle of *Panagrolaimus rigidus* (Schneider). *Nemotologica* 24:239–42.
- Griffiths, B. S., K. Ritz, and R. E. Wheatley. 1994. Nematodes as indicators of enhanced microbiological activity in Scottish organic farming system. *Soil Use and Management* 10:20–24.
- Háněl, L. 2003. Recovery of soil nematode populations from cropping stress by natural secondary succession to meadow land. *Applied Soil Ecology* 22:255–270.
- Ilieva-Makulec, K. 2000. Nematode fauna of a cultivated peat meadow in relation to soil depth. *Annales Zoologici Fennici* 50:247–254.
- Ingham, R. E., J. A. Trofymow, E. R. Ingham, and D. C. Coleman. 1985. Interactions of bacteria, fungi, and their nematode grazers: Effects on nutrient cycling and plant growth. *Ecological Monographs* 55:119–140.
- Li, H. X., and F. Hu. 2001. Effect of bacterial-feeding nematode inoculation on wheat growth and N and P uptake. *Pedosphere* 11: 57–62.
- Liang, W. J., I. Lavian, and Y. Steinberger. 2001a. Effect of agricultural management on nematode communities in a Mediterranean agroecosystem. *Journal of Nematology* 33:208–215.
- Liang, W. J., Q. Li, Y. Jiang, W. B. Chen, and D. Wen. 2003. Effect of cultivation on spatial distribution of nematode trophic groups in black soil. *Pedosphere* 13:97–102.
- Liang, W. J., W. M. Zhang, W. G. Li, and Y. X. Duan. 2001b. Effect of chemical fertilizer on nematode community composition and diversity in the Black Soil Region. *Biodiversity Science* 9:237–240. (In Chinese.)
- Neher, D. A. 2001. Role of nematodes in soil health and their use as indicators. *Journal of Nematology* 33:161–168.
- Nicholas, W. L. 1975. *The biology of free-living nematodes*. Oxford: Oxford University Press.
- Norton, D. C., and T. L. Niblack. 1991. Biology and ecology of nematodes. Pp 47–71 in W. R. Nickle, ed. *Manual of agricultural nematology*. New York: Marcel Dekker, Inc.
- Ou, W., W. J. Liang, Y. Jiang, Q. Li, and D. Wen. 2005. Vertical distribution of soil nematodes under different land use types in an aquic brown soil. *Pedobiologia* 49:139–148.
- Pen-Mouratov, S., X. L. He, and Y. Steinberger. 2004. Spatial distribution and trophic diversity of nematode populations under *Acacia raddiana* along a temperature gradient in the Negev Desert ecosystem. *Journal of Arid Environments* 56:339–355.
- Pen-Mouratov, S., M. Rakhimbaev, and Y. Steinberger. 2003. Seasonal and spatial variation in nematode communities in a Negev Desert ecosystem. *Journal of Nematology* 35:157–166.
- Sohlenius, B. 1985. Influence of climatic conditions on nematode coexistence: A laboratory experiment with a coniferous forest soil. *Oikos* 44:430–438.
- Sohlenius, B., and A. Sandor. 1987. Vertical distribution of nematodes in arable soil under grass (*Festuca pratensis*) and barley (*Hordeum distichum*). *Biology and Fertility of Soils* 3:19–25.
- Verschoor, B. C., R. G. M. de Goede, J. W. de Hoop, and F. W. de Vries. 2001. Seasonal dynamics and vertical distribution of plant-feeding nematode communities in grasslands. *Pedobiologia* 45:213–233.
- Wasilewska, L. 1998. Changes in the proportions of groups of bacterivorous soil nematodes with different life strategies in relation to environmental conditions. *Applied Soil Ecology* 9:215–220.
- Yeates, G. W. 1980. Populations of nematode genera in soils under pasture. III. Vertical distribution at eleven sites. *New Zealand Journal of Agricultural Research* 23:117–128.
- Yeates, G. W., M. F. Hawke, and W. C. Rijkse. 2000. Changes in soil fauna and soil conditions under *Pinus radiata* agroforestry regimes during a 25-year tree rotation. *Biology and Fertility of Soils* 31:391–406.
- Yeates, G. W., and K. L. King. 1997. Soil nematodes as indicators of the effect of management on grasslands in the New England Tablelands (NSW): Comparison of native and improved grasslands. *Pedobiologia* 41:526–536.
- Yin, W. Y. 2000. *Pictorial keys to soil animals of China*. Beijing: Science Press.
- Zhang, Y. G., Y. Jiang, W. J. Liang, and F. X. Meng. 2004a. Vertical variation of soil pH and Olsen-P in an aquic brown soil as affected by land use. *Journal of Soil and Water Conservation* 18:89–92. (In Chinese.)
- Zhang, Y. G., Y. Jiang, W. J. Liang, D. Wen, and Y. L. Zhang. 2004b. Vertical variation and storage of nitrogen in an aquic brown soil under different land uses. *Journal of Forestry Research* 15:192–196.