EFFECTS OF IMPROVED FALLOWS ON THE DIVERSITY OF PLANT-PARASITIC NEMATODES IN THE AGROFORESTRY SYSTEMS OF WESTERN KENYA

By

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DECLARATION

This thesis is my original work and has not been presented for a degree in any other university or any other award.

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DEDICATION

To all my Family,Relatives and Friends;

In memory of my Dear Parents, Mor and Khoudia. You nurtured me with love and had the wisdom to send me to school. You may not be here to witness my gratefulness, but your efforts have not been in vain.

May your souls rest in eternal peace, Amen!

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ABSTRACT

In recent years, fast growing nitrogen-fixing shrubs of the family Fabaceae, *Sesbania sesban* (L.) Merr., *Crotalaria grahamiana* Wight & Arn. and *Tephrosia vogelii* Hook. f., have been intensively used in western Kenya to improve soil fertility, control soil erosion and increase crop yield. Local farmers have recognised the benefits of rotating these plant species with crops, and this has facilitated the rapid spread of this *improved fallow* technology in the area. Research has been conducted to understand the implications of this new land use system vis-à-vis the physical, chemical and biological characteristics of the soil. The scope of this study was to investigate the impact of this practice on the abundance, diversity and damage potential of plant-parasitic nematodes.

There was a dramatic increase in nematode populations when the improved fallow shrubs were planted in agricultural lands. Spiral nematodes (*Scutellonema* spp. and *Helicotylenchus* spp.), root knot (*Meloidogyne* spp.) and root lesion (*Pratylenchus* spp.) nematodes were the most abundant species in the area. Spiral nematodes had high populations in all the improved fallows, while root knot nematodes were most abundant in the *Sesbania* and *Tephrosia* fallows. The highest populations of root lesion nematodes were found in the *Crotalaria* fallows and in the cultivated plots. The distribution of plant-parasitic nematodes was correlated to that of some soil physico-chemical properties of the soil, which validates the potential of nematodes as biological indicators of soil status. Nematode abundance fluctuated strongly during the year with peaks observed at the onset and in the middle of the rainy seasons and the lowest populations in dry seasons. Although all nematodes were sensitive to seasonal changes, this study showed clearly that the species had different survival strategies. For example, root lesion nematodes, *Pratylenchus* spp., which were dominant in the study site, showed very strong fluctuations in the year. This behaviour, however, contrasted with that of *Scutellonema* spp., which had fairly constant populations over the year. Planting crops and fallow trees in rows had a significant impact on the horizontal distribution of nematodes. Most species were aggregated along the rows, with higher populations in the rows located in the lower part of the slopes. Other distribution patterns such as clumping were also observed in this study, especially with root knot and spiral nematodes.

The nematode communities that emerged when shrubs were planted in the fields negatively affected subsequent crops. Beans were very sensitive to root knot nematodes and suffered heavy loses in the *Tephrosia* soil. Maize was resistant to root knot nematodes, but was damaged by the spiral nematodes, *Scutellonema* spp., especially in low soil fertility. Beans were also sensitive to the spiral nematodes. This is a reminder that the interactions between plants and pest organisms such as nematodes must be considered among other criteria when choosing trees or shrubs to be planted in croplands. Since these interactions can be deleterious to crop growth (and consequently yield), a genuine understanding of the host range and the pathogenic function of the plant-parasitic nematodes occurring in the area may be a prerequisite. Neglecting the role of nematodes in the improved fallow systems in western Kenya may well jeopardise the future of agroforestry in the area.

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CHAPTER 1

1.0. GENERAL INTRODUCTION

1.1. Introduction

The benefits of associating woody perennials and crops have been recognised since the early days of agriculture (Nair, 1993). Agroforestry systems are multiple, and their objectives range widely from producing food and tree products for local consumption and income generation, fodder and fuelwood, to soil restoration and protection of the environment (Cooper *et al.*, 1996; ICRAF, 1996; Rao *et al.*, 1998).

In the densely populated highlands of western Kenya, large-scale experimentation showed that the rotation of fast-growing trees/shrubs and crops, also known as improved fallow, can significantly improve soil fertility and increase crop yield. Research conducted in the area for the last few years allowed a fair understanding of the mechanisms through which trees improve soils, but more often than not, physical and chemical descriptors have been used to characterise soil. Comparatively, knowledge on the biological processes of the soil has so far been limited. Yet, there is strong evidence that the introduction of trees in croplands may have some influence on soil biota.

The choice of nematodes for this study was justified by several factors. Nematodes are the most abundant metazoa on earth and play crucial functions in the soil ecological processes (Viglierchio, 1991; Yeates *et al.*, 1993; Giller *et al.*, 1997; Nielsen, 1998). However, most soil faunal studies in the tropics have been conducted on the macrofauna, especially termites and earthworms.

This study intended to contribute to the elucidation of the complex relationships that relate nematode biodiversity, soil quality and crop production. Nematodes have been recognised as good bio-indicator organisms that can be reliably used to predict trends in soil status (Yeates *et al.*, 1993; Bongers and Bongers, 1998). In addition, understanding the damage potential of plant-parasitic to crops will be helpful in defining soil management strategies.

1.2. Objectives of the study

1.2.1. General objective

To explore the diversity of plant-parasitic nematodes in the improved fallow systems and to assess their potential impact on maize and bean production in the highlands of western Kenya.

1.2.2. Specific objectives

(1) To characterise the nematode communities in different cropping systems

(2) To study the effects of some agroforestry practices on the temporal structures of nematodes

(3) To describe the spatial micro-distribution of nematodes in the agroforestry systems

(4) To assess crop damage by plant-parasitic nematodes as influenced by the practice of improved fallow

1.3. Hypotheses

(1) Abundance and diversity of nematodes are influenced by the cropping system

(2) Improved fallows can change the abundance of specific nematode species and influence the diversity of nematode communities

(3) The plant-parasitic nematode communities that develop during improved fallows can negatively affect subsequent crops

1.4. Organisation of the thesis

This thesis comprises of seven chapters. Chapter 1 introduces the topic. Chapter 2 reviews some literature relevant to the study. Chapter 3 reports on a survey conducted in the maize-producing zone of western Kenya to describe the nematofauna associated with different cropping systems. Chapter 4 addresses the temporal dynamics of nematode communities as influenced by agroforestry practices and the application of rock phosphate. The study of the spatial microstructures of nematodes in crops and improved fallow is described in the 5th chapter. Chapter 6 reports on a greenhouse experiment testing the possible relationships between improved fallows, nematode communities and plant growth. The final chapter is dedicated to the general discussion and definitive conclusions about the results of this study, as well as the definition of potential areas for future investigation.

CHAPTER 2

2.0. LITERATURE REVIEW

2.1. Multiple cropping in Tropical Africa

Agricultural diversification is an old strategy developed by farmers to prevent risks of crop failure. Mixing different crop species in one piece of land is a common feature in tropical Africa, especially in the low-input cropping systems (Vandermeer, 1989; Innis, 1997). Although in traditional peasant agriculture the decision to associate different crop species is essentially based on the needs, experience and empirical knowledge of the farming communities (Bridge, 1987), beneficial roles of intercropping have been in many aspects:

(1) Different plant species are likely to have different water and nutrient requirements. Thus, appropriate crop combinations can allow farmers to diversify food production while preventing rapid exhaustion of the land.

(2) There are positive interactions between plants. For example, the nitrogen biologically fixed by legumes can benefit non-leguminous intercrops.

(3) Species from different botanical families may not share the same pests and diseases (van Emden, 1998). Among the mechanisms involved in the reduction of pest incidence in mixed crops, the establishment of physical barriers limiting pest movement is the most documented (Altieri, 1994; Finch, 1996). This has been observed in agroforestry systems (Ogol *et al.*, 1999).

Different multiple cropping systems exist in Tropical Africa and can be typically categorised into sub-regions.

2.1.1. The humid Tropics

Agriculture in the humid tropics of Africa is characterised by the coexistence of two systems (ICRAF, 1996). The first is a sedentary form of agriculture based on high value perennial crops (cocoa, coffee, oil palm and rubber) destined for exportation. When trees are at their early stage, annual crops are usually planted in the alleys. This system is more sustainable and less injurious to the environment. The second is based on shifting cultivation, where the natural forest is progressively cleared for food production.

The magnitude of land degradation in the humid tropics depends on the balance between these two farming systems. Decline of soil fertility is endemic in tropical Africa (Stoorvogel *et al.*, 1993), but it may be less widespread in the humid tropics, especially in the cash crop systems, where the use of fertilisers is fairly adequate and trees permanently cover the soil. However, the collapse of the cocoa and coffee prices on the world market in the past few years has dampened the farmers' enthusiasm towards these cash crops. This resulted in a shift of interest and an upset of the agricultural set-up, as growers had no alternative but to increase their food crop production to secure their livelihood. This, added to an unchecked harvest of timber products, has exacerbated deforestation and land degradation in countries like Côte d'Ivoire, Ghana and Nigeria (ICRAF, 1996).

2.1.2. The Sahelian system

The peasants of the Sahel practise a tree-crop-animal integrated system known as Parkland. In these semi-arid lands, planting trees like in humid zones is not realistic. Instead, farmers keep and protect self-regenerating, indigenous, trees like *Vitellaria paradoxa* (Sapotaceae), *Parkia biglobosa* (Mimosaceae) and *Faidherbia albida* (Mimosaceae) in their fields and use natural fallow, animal manure and crop residues to sustain their land resources. The food crops cultivated include millet, sorghum and cowpea while cash crops are mainly groundnut and cotton. The cultivation phases last between 10 and 15 years with cereal/cash crop rotations, punctuated by short-term weed fallows of 1-5 years. Trees are used to improve soil fertility and to generate a wide range of products including fodder, firewood and medicine. *F. albida* is a high-value tree due to its soil-improving properties: 'the albida effect' (Skerman, 1982; Rao *et al.*, 1998).

The Parkland system is a good illustration of tree-crop-livestock integration. Animals graze in the fallows during the rainy season and are parked near the habitations, where they produce substantial amounts of manure. After harvest, they are fed on the millet stovers and the groundnut and cowpea straw. In the dry season, the animals graze freely on the crop residues and receive forage from *F. albida* (Milleville, 1980; Dugue, 1986; Raymond, 1987). However, erratic rainfall pattern, exacerbated by high demographic pressure, is strongly threatening the viability of this system.

2.1.3. The highlands of East Africa

The highlands of East Africa possess some of the best lands for agriculture in the continent. They are reputed for having a rich and diverse agricultural production and are considered as the storehouse of the sub-region

(ICRAF, 1995). This is illustrated by the fact that the Kenya Highlands represent only 15% of the country's land area but yield most of the export crops such as coffee and tea, and 50% of the staple foods: maize, beans, bananas, wheat and dairy products (AFRENA, 1991). They support 50% of the total human population. Mixed cropping (perennials and annuals) is a common practice in the highlands. This responds to the double objective of a maximum utilisation of the more productive lands and a minimisation of risks in the eroded and exhausted soils. Agroforestry is also practised (Dupriez, 1980; Acquier *et al.*, 1981; Jones and Egli, 1984). However, soil degradation as a result of high population pressure and poor land management has currently become a widespread and serious constraint to farm productivity (ICRAF, 1995).

2.2. Fallow agriculture and agroforestry

2.2.1. Natural fallow

Leaving croplands on fallow has been an efficient way of replenishing soil fertility. The long-term fallows (10-30 years) enabled soils to regain fertility and secure moderate crop yield (Greenland and Nye, 1959; Nair, 1993). Fallowing has always been an important component of the traditional farming systems and is still practised in small-scale farming, where purchase of fertilisers is beyond the reach of resource-poor farmers. Fallows mitigate soil degradation and avail nutrients to subsequent crops through the accumulation of organic matter in the soil (Feller *et al.*, 1993; Manlay and Masse, 1994). The floral succession that occurs is favourable to the disappearance of weeds and has an effect on soil organisms. For example, earthworm biomass and abundance of termites have been found to increase with the age of the fallow (Feller *et al.*, 1993; Sarr *et al.*, 1994). Fallowing also increases the number of free-living nematodes while reducing the populations of plant-parasitic nematodes in the soil (Hominick, 1999; Kandji *et al.*, 2001).

2.2.2. Improved fallow as an agroforestry system

2.2.2.1. Roles of improved fallow

Improved fallow entails the planting of fast growing trees or shrubs in depleted croplands to achieve the benefits of natural fallow within a shorter time or smaller area (Prinz, 1987). Rao *et al.* (1998) distinguished (1) the short-duration fallows with fast-growing leguminous shrubs seeking to replenish soil fertility (Plate 2.a) and (2) the medium-to-long-duration fallows with diverse species and aimed at rehabilitating degraded and abandoned lands as well as exploiting tree products.

One comparative advantage of improved fallows is the elimination of the tree-crop competition common in simultaneous agroforestry systems such as hedgerow intercropping. Other benefits for soil restoration and conservation include: (1) increase of soil organic matter (SOM), which affects both physical and chemical fertility; (2) nutrient input, mainly N through biological nitrogen fixation (BNF) and retrieval of leaching minerals from the subsoil and making them available to crops; (3) reduced soil erosion; (4) improved activity of soil organisms (fungi, arthropods, earthworms, nematodes) and (5) weed control (van Reuler and Prins, 1993; Young, 1997; Rao *et al.*, 1998).

2.2.2.2. Improved fallow trees (shrubs)

Improved fallow species are in general fast-growing, nitrogen-fixing trees or shrubs of the family Leguminosae (ICRAF, 1995). *Sesbania sesban*, *Crotalaria grahamiana* and *Tephrosia vogelii* are the main species being evaluated in western Kenya.

Sesbania sesban (L.) Merr. (Fabaceae)

Sesbania sesban (Plate 2.b) is a multipurpose tree (shrub), used as forage for ruminants (Gutteridge and Shelton, 1994), to produce firewood and charcoal, and as a medicinal plant (Allen and Allen, 1981). *S. sesban* fixes atmospheric nitrogen, retrieves leaching nitrate in the subsoil (Mekonnen *et al.*, 1997) and produces high quality mulch and green manure. It also ameliorates soil fertility as short-term rotation fallow (Kwesiga and Coe, 1994; ICRAF, 1996) and is effective for controlling *Striga hermonthica* (Oswald *et al.*, 1996). However, *S. sesban* is prone to pest attack. *Mesoplatys ochroptera* (Coleoptera: Chrysomelidae) is the major insect pest, which can occasionally defoliate the tree to death (Melaku *et al.*, 1996; Sileshi *et al.*, 2000). Root-knot nematodes are also a major problem for *S. sesban* (Desaeger and Rao, 1999; Kandji *et al.*, 2001).

Crotalaria grahamiana Wight & Arn. (Fabaceae)

C. grahamiana (Plate 2.c) is an erect, fast-growing perennial plant. This leguminous shrub has been used in short-term rotations (Peltier, 1959; Polhill, 1982; Godefroy, 1988) and was recently introduced in western Kenya, where it showed potential for one-season improved fallow. However, its cultivation can be limited by pests. In India, *C. grahamiana* has been severely damaged by the flea beetle, *Longitarsus* spp. (Coleoptera: Chrysomelidae) (Kakoty, 1992; Pandit and Pradhan, 1996). In western Kenya, a major threat to *C. grahamiana* is *Ampicalia pactolichus* (Lepidoptera: Arctiidae) (Hailu, pers. com.) and the root-lesion nematodes, *Pratylenchus* spp. (Kandji *et al.*, 2001).

Tephrosia vogelii Hook. f. (Fabaceae)

This is a soft woody, multipurpose herb or small tree (Plates 2.d and 2.e). The leaves are used as insecticide and molluscide. *Tephrosia* is also used in medicine to procure abortion, as an emetic, a bactericide and to cure skin diseases (Faridah and van der Maesen, 1997). It is used as green manure in coconut plantations in Central Africa and South-East Asia. The nitrogen content per 100g of dry matter is 3.7g for 2-3 months old plants, falling to 1.2g for 10 months old material, while the phosphorus content drops from 0.8 to 0.2g (Faridah and van der Maesen, 1997). *Tephrosia* is also cultivated as an ornamental and hedge plant. However, attempts to cultivate *T. vogelii* failed in many areas mainly due to pest problems. In the USA, heavy infestations by root-knot nematodes have discouraged the plantation of *T. vogelii* as a pesticide crop (Faridah and van der Maesen, 1997). Similar observations were made in western Kenya (Desaeger and Rao, 1999; Kandji *et al*, 2001).

2.3. Soil and plant nematodes

2.3.1. Functional organisation of nematodes

Nematodes are the most abundant metazoa on the planet (Nielsen, 1998). An exhaustive identification of all nematodes in a soil sample is almost impossible. A practical alternative, commonly used in ecological studies, is the definition of functional or trophic groups: ensembles of species having similar effects on ecosystem processes (Bongers and Bongers, 1998). Yeates *et al.* (1993) classified nematodes into 8 groups, based on their feeding behaviour: bacterial feeders, fungal feeders, plant feeders, substrate ingesters, animal predators, unicellular eucaryote feeders, omnivorous feeders, infective stages of animal parasites including insects.

In this study, the above classification was summarised by separating two major groups: plant-parasitic nematodes and free-living nematodes. The term 'plant-parasitic nematode' refers to the species that parasitise roots of higher plants, they bear a strong stylet to puncture plant roots. Under free-living nematodes, are grouped all the other nematodes found in the soil and which have a rather beneficial role on plant growth.

2.3.1.1. Free-living nematodes

Of all nematodes, the free-living are arguably the least known. Yet the microtrophic (bacterial and fungal feeding) nematodes constitute the overwhelming proportion of the soil nematofauna and significantly contribute to the cycling of plant nutrients (Viglierchio, 1991). Positive correlations have been found between total nematode abundance and primary productivity or other correlates such as levels of available phosphorus or nitrogen mineralisation (Elliott *et al*., 1980; Yeates and Coleman, 1982). Nematodes have been reported to enhance decomposition by 16% in field soil and up to 30% in litter (Pradhan *et al*., 1988).

Another fundamental aspect of these microtrophic nematodes is their role in the maintenance of diversity within soil communities (Giller *et al*., 1997). Bacterial and fungal feeding nematodes exert a regulating function over soil micro-organisms. When ecosystems are disturbed through cultivation, these nematodes are among the first groups of organisms to be affected. The system loses its functional stability and its intrinsic property to buffer against soil-borne pathogens and natural vagaries. It is believed that decreased nematode diversity is one of the major factors facilitating the outbreak of plant diseases and nutrient leaching in the soil system (Bongers and Bongers, 1998).

2.3.1.2. Plant-parasitic nematodes

Plant nematodes fall into 4 main groups depending on the mode of association between the parasite and the host plant: ectoparasites, semi-endoparasites, migratory endoparasites and sedentary endoparasites (Siddiqi, 1986; Yeates *et al*., 1993). Under natural vegetation, the free-living nematodes dominate in the communities, but when lands are converted into cultivation, the latter decrease drastically in favour of the plant-parasitic community. Nematodes have long been overlooked as pests because of the often-atypical character of their attack and their secluded habitats (Bridge, 1996; ARC, 1997). As a result, crop losses have seldom been associated with these parasites. But, the advent of chemical nematicides made it clear that nematodes can be a real disaster in croplands and have occasionally caused crop devastation in various parts of the world. Studies based on farm values in 1967 and 1968 declared losses by nematodes in the USA as reaching 1.59 billion dollars yearly (Feldmesser, 1971). In the tropics, losses by nematodes amount to 10-15% of the total agricultural production. Worldwide, 100 billion US dollars are lost annually as a result of nematode damage on crops (Melakeberhan, 1997).

2.3.2. Nematodes and the soil environment

Comprehensive nematological studies cannot be carried out unless appropriate knowledge on nematode biology and the different environmental factors influencing their abundance and distribution is established. Nematode studies can be considered at two different scales. There is a macro-distribution, which is determined by the climate, the soil characteristics and the agricultural history as opposed to the micro-distribution determined by the availability of the food resource and the biology of the different species (Cadet and Albrecht, 1992; Cadet *et al.*, 1995). The establishment of a colony of plant-parasitic nematodes is not possible without the presence of a host plant, but the environmental conditions strongly influence the structure of their communities (Norton, 1989; Luc *et al.*, 1990).

2.3.2.1. The abiotic factors

Nematodes are associated with water films on the surface of soil and organic particles (Decker, 1988). Soil moisture, structure, and texture are therefore key elements for the development of nematodes. The impact of soil water on nematodes is both direct and indirect, viz through the host plant (Wallace, 1971; Vrain, 1986). Nematode dynamics closely depend on the water balance in the soil. When the latter is positive, they are active and reproduction takes place. However, excessive moisture may be lethal to some nematodes since it creates anaerobic conditions (Norton, 1979). In dry conditions, reproduction ceases and nematodes survive inactively in the form of kysts, cysts or eggs. Nematode movement is optimal when the water film approaches 5µm thick. The physical forces exerted by the water film on nematodes are critical for the maintenance of their hydrostatic pressure and the induction of anhydrobiosis (Wallace, 1971; Demeure *et al.*, 1979).

Soil texture and structure influence the movement of nematodes, which is paramount in the root colonisation process and the encounter of the two sexes for amphimictic species. Most nematodes, especially the larger species, develop better in coarse sandy soils, but clay particles are indispensable for the transmission of root exudates (Prot and van Gundy, 1981). Habitat preference of nematodes can, however, vary with the species. For instance, *Scutellonema cavenessi*, a fairly large and amphimictic species, thrived better in coarse soils (Villenave *et al.*, 1997) whereas *Pratylenchus* spp. showed some preference towards clayey soils (Cadet and Debouzie, 1990).

Temperature is important for nematode survival. For each species, there are optima and lethal extremes. Most tropical nematodes have their maximal activity between 25 and 35°C (Jones, 1975) although some species can survive for long at 50°C in anhydrobiotic state (Siddiqi, 1986).

Numerous chemical elements of the soil have been reported to have effects on nematodes although sharp contradictions exist between authors. Barry *et al.* (1974) observed a stimulating role of nitrogen on nematodes although this effect may be indirectly due to the food availability following root growth (Ross, 1959). Elsewhere, ammonium has been reported to have nematicidal properties (Oteifa, 1955; Vrain, 1986). Increase in nematode abundance following phosphorus application has been observed with *Xiphinema americanum* (Kirkpatrick *et al.*, 1964) and *Pratylenchus spp.* (Yeates, 1976), whereas Simon and Rovira (1985) and Das *et al.* (1990) reported a reduction of nematode populations after adding phosphorus to the soil. Many other minerals such as calcium, sodium, magnesium and chlorine have also been reported to have various effects on nematodes (Taylor *et al.*, 1982; Shefelbine *et al.*, 1986; Francl, 1993; Wallace *et al.*, 1993).

The role of organic matter on nematodes has also been extensively studied. Cases of nematode increase (Zoon *et al.*, 1993) as well as of reduction (Dick and Spaull, 1982) have been mentioned as results of organic amendments. The emanation of nematoxic gases during the decomposition of some nitrogenous substances is believed a major cause of nematode reduction (Walker, 1969).

2.3.2.2. The biotic factors

Various types of relationships exist both between nematodes themselves, and between them and other soil organisms. The nematode-nematode relationships have been widely studied. Although actual occurrence of overlapping niches and limiting resources is difficult to prove at the scale of the micro-organisms (Queneherve, 1990), competition for space and resources seems inevitable, at least between nematodes of the same trophic function (Cadet, 1998). Interspecific competition is expected to be higher with endoparasitic nematodes as for example between *Heterodera glycines* and *Pratylenchus scribneri* (Lawn and Noel, 1986), and between *Meloidogyne chitwoodi* and *Pratylenchus neglectus* (Umesh *et al*., 1994).

Various types of relationships have been described between nematodes and other soil organisms. Nematode attack on plants is usually followed by secondary bacterial, fungal or viral infections which aggravate crop damage (Siddiqi, 1986). Nematode antagonists have also been identified from various taxa (fungi, bacteria, arthropods, protozoa) and are believed to have a great potential for the biological control of plant-parasitic nematodes (e.g. Mateille *et al*., 1995). Conversely, nematodes prey on, or parasitise, other soil organisms including pests and disease agents. This justifies the renewal of interest towards the entomopathogenic nematodes, which are being extensively researched as a potential component in the integrated management of insect pests (Klein, 1990; Waturu *et al*., 1997).

Plate 2.a. Establishment of a short-duration improved fallow: soil improving shrubs are relay intercropped with the maturing maize in the middle of the long rainy season (Photo Serigne Kandji).

Plate 2.b. A six month old sesbania fallow: after maize harvest, trees grow alone in the field during the short rainy season (Photo Serigne Kandji).

Plate 2.c. A six month old crotalaria fallow (Photo Serigne Kandji).

Plate 2.d. Inflorescence and pods on a mature plant of *Tephrosia vogelii* (Photo Serigne Kandji).

Plate 2.e. A six month old tephrosia fallow (Photo Serigne Kandji).

Plate 2.f. Example of a crotalaria-tephrosia mixed improved fallow (Photo Serigne Kandji).

CHAPTER 3

3.0. DIVERSITY OF PLANT-PARASITIC NEMATODES AND THEIR RELATIONSHIPS WITH SOME SOIL CHARACTERISTICS IN THE IMPROVED FALLOWS OF WESTERN KENYA

3.1. Introduction

There is a tendency amongst the world's conservationists to focus on large, charismatic species, often failing to recognise the agroecosystems and the species they contain as part of the world biodiversity (Vandermeer and Perfecto, 1997). Yet the transformation of managed systems and the loss of inconspicuous species are the very base of the biodiversity crisis. These systems therefore need more research attention.

The agroecosystems of the western Kenya highlands provide an interesting framework for such ecological studies. Continued cultivation of lands without adequate use of inputs has resulted in a widespread and steady decline of soil fertility in the area (Stoorvogel *et al.*, 1993). Subsistence farmers, although aware of this loss of land productivity, lack the financial means to purchase the inorganic fertilisers necessary to boost crop production (Cooper *et al.*, 1996). In the tropics, traditional peasant farmers have been using long-term natural fallows to minimise soil degradation and maintain a reasonable level of crop production (Nye and Greenland, 1960). Natural fallows are still practised in western Kenya (Niang *et al.*, 1998), but if farmers can no longer leave their land for a long enough period because of population pressure, gains in crop production after these short-duration weed fallows may be meaningless (Aweto *et al.*, 1992).

The search for alternatives to natural fallows in the past few years has led a consortium of researchers from the International Centre for Research in Agroforestry (ICRAF), the Kenya Forestry Research Institute (KEFRI) and the Kenya Agricultural Research Institute (KARI) to experiment with a land use system hitherto unknown to the area. This consists of planting for one or two seasons fast growing leguminous trees/shrubs in depleted lands to speed up recovery of soil fertility. This 'improved fallow' technology is now gaining popularity among the farming community and has already been adopted by some farmers who, after a relatively short period, can enjoy substantial increase in maize yield (ICRAF, 1996).

Thus, the food production system, in the study area of western Kenya, may be viewed as a succession of land uses evolving along a continuum of natural (weed) fallows through planted (improved) fallows to cultivated plots. Such a succession not only results in a gradient in terms of level of disturbance, but also generates a diversity of plants and habitats favourable to a high diversity of soil organisms. Paradoxically, this potentially high soil biodiversity is poorly understood. For example, little is known on the nematofauna of western Kenya, despite recent research work that showed that phytophagous nematodes can be a serious yield limiting factor in the area (Desaeger and Rao, 1999). Whilst it is admitted that these pests are part of any existing agroecosystem, they have been found to build up high populations and may reach damaging levels for crops when legume trees (shrubs) are planted in farmlands (Desaeger and Rao, 1999). Therefore, there is a risk of the beneficial role of the improved fallows being reduced to zero if precaution is not taken to develop judicious nematode control methods.

This setback to the sustainability of improved fallow technology has prompted ICRAF to initiate a programme aimed at gathering more information on nematodes and their possible role in the agroforestry systems. This paper reports on a survey aimed at characterising the nematode communities in different cropping systems of western Kenya and assessing the impact of improved fallows on the abundance, diversity and community structure of nematodes, with major emphasis on plant parasites.

3.2. Material and methods

3.2.1. Study area

The study was conducted in the food crop land-use system of the highlands of western Kenya (Figure 3.1). The altitudes range between 1300 and 1600m. The mean monthly temperatures vary from 15 to 29°C. The rainfall ranges between 1500 and 2300mm and follows a bimodal distribution with long rains (March-June) and short rains (September-November). Despite this high total rainfall, dry spells often occur during the growing seasons and negatively affect crop production (AFRENA, 1991).

Soils are usually deficient in nitrogen, phosphorus and many other nutrients, and have a pH in water between 4.0 and 6.5. Acrisols and Ferralsols constitute 75% of the soils in the upland area. Only 11% of the area have soils of high natural quality: Nitisols and Phaoezems. Soil erosion is extensive due to the intensive land use and the heavy rainstorms (AFRENA, 1991).

3.2.2. Soil sampling technique for nematodes

Soil samples were taken from 51 farmers' fields distributed in 5 sites located in Vihiga, Siaya and Kisumu districts, western Kenya, where improved fallow was practised. The fields sampled represented 8 different cropping systems, which were distributed as follows:

1. Pure improved fallow of *Crotalaria grahamiana*: 7 fields
2. Mixed improved fallow of *C. grahamiana* and *S. sesban*: 8 fields
3. Mixed improved fallow of *C. grahamiana* and *T. vogelii*: 6 fields
4. Long-term natural fallow (> 20 years): 5 fields

5. Maize/beans cultivated field: 7 fields
6. Pure improved fallow of *Sesbania sesban*: 5 fields
7. Short-term natural fallow (< 3 years): 7 fields
8. Pure improved fallow of *Tephrosia vogelii*: 6 fields

Soil sampling was done twice, between September and November 1998 (short rains), and between April and June 1999 (long rains). In each plot, a hand auger was used to collect soil from 5 evenly distributed spots from a depth of 0-20 cm. The 5 cores taken from each single plot were then mixed homogeneously to constitute a composite sample. Thus, each plot was represented by one composite sample used to analyse the soil physical and chemical properties and to extract nematodes.

3.2.3. Soil and nematode analyses

3.2.3.1. Soil analyses

The soil analyses were carried out at the ICRAF soil laboratory in Nairobi, using standard methods (see Anderson and Ingram, 1993). The soil properties analysed were soil water content; soil texture: proportions of clay (0-2 μm), silt (2-50 μm) and sand (50- > 200 μm); bulk density; pH (1:2.5 soil water suspension); exchangeable cations: potassium, calcium and magnesium; exchangeable acidity; total soil organic matter; ammonium content; nitrate content; extractable phosphorus.

3.2.3.2. Nematode extraction, identification and counting

Nematological analyses were conducted jointly at the Laboratoire de Biopédologie of IRD (ex ORSTOM) in Bel-Air, Senegal and at the Laboratory of Nematology in the Maseno Agroforestry Research Centre, Kenya. Nematodes were separated from the soil by the elutriation method (Figure 3.2) (Seinhorst, 1962). Counting was done under a dissecting microscope (magnification: x 40) with a De Grisse counting dish (ARC, 1997) and a series of hand counters. The plant-parasitic nematodes were identified to a species level. The free-living nematodes were counted but not identified. When specific identification was difficult, about 30 specimens of the genera concerned were extracted from the solution, fixed (Southey, 1986) and sent to the Plant Protection Research Institute (PPRI) in Pretoria, South Africa, for accurate identification. The abundance of nematodes was expressed as number of individuals per litre of moist soil.

3.2.3.3. Statistical analyses

The data collected were analysed in three steps. Firstly, General Linear Model (GLM) and Tukey's tests were used to compare nematode abundance in the different cropping systems. The ratio of free-living nematodes to plant-parasitic nematodes was also calculated.

Secondly, the diversity of plant-parasitic nematodes was estimated using the Shannon-Wiener index (Krebs, 1985):

$$H = \sum_{i=1}^{s} \log Pi$$

where s = number of species, Pi = proportion belonging to the i_{th} species, and H estimates the probability of correctly predicting the species of an individual randomly drawn from the population. H confounds the number of species and the evenness. A separate measure of the evenness is usually given:

$$J = \frac{H}{H\max} \quad \text{where } H\max = \log_2 s$$

Finally, given the multiplicity of the cropping systems and the environmental and nematological data, a multivariate approach was used to characterise the relationships between the different components. Two separate principal component analyses (PCA's) (Benzecri, 1979; Foucart, 1982) were used to find possible interrelationships between the nematode genera on one hand and between soil parameters on the other. The relationships between plant-parasitic nematodes and soil physico-chemical properties were investigated using co-inertia analysis (Doledec and Chessel, 1994). These multivariate analyses were carried out with the ADE4 statistical package (Thioulouse *et al*, 1997).

3.3. Results

3.3.1. The nematode communities in the different cropping systems

3.3.1.1. Total nematofauna

The abundance of plant parasitic and free-living nematodes varied significantly ($P < 0.001$) between cropping systems (Table 3.1). The long-term natural fallows had lower populations than all the improved fallows. The *Crotalaria/Tephrosia* mixed fallows had higher populations than the maize/beans cultivated fields and the natural fallows. Free-living nematodes were significantly more abundant in the fallows than in the plots under maize/beans cultivation.

The ratio of free-living nematodes to plant-parasitic nematodes (R) was calculated for the different cropping systems. In the cultivated plots, R was 0.50, translating a dominance of the parasitic group. A similar trend was observed in the *Sesbania* fallows (R = 0.62) and in the *Crotalaria/Tephrosia* mixed fallows (R = 0.63). There was also a dominance of the plant-parasitic nematodes in the *Crotalaria* (R = 0.72) and *Crotalaria/Sesbania* fallows. In contrast, the long-term natural fallows were characterised by a strong dominance of the non-parasitic group (R = 5.63). Communities in the *Tephrosia* fallows (R = 1.05) were more balanced between the two trophic groups.

3.3.1.2. Diversity of plant-parasitic nematode communities

The list of plant-parasitic nematode species identified in the different cropping systems is given in Table 3.2. The maize/beans cultivated plots had the highest number of species (18), followed by the long-term natural fallows, which yielded 16 species. The improved fallows and the short-term natural fallows had lower numbers of parasitic species.

Table 3.3 gives the number of species and the values of Shannon diversity index (H) and evenness (J) for the different cropping systems. The number of species was significantly ($P < 0.001$) higher in the maize/beans cultivated fields than in the improved fallows. The Shannon diversity index was significantly ($P = 0.0316$) higher in the *Sesbania* and short-term natural fallows than in the crotalaria fallows. There was no significant difference in evenness between the different cropping systems.

3.3.2. Distribution of plant-parasitic nematodes in the cropping systems

The eigenvalues of the Principal Component Analysis (Figure 3.3A) shows that the first factor takes into account 27% of the total inertia. On the correlation circle (Figure 3.3B), this factor is represented by the horizontal axis, which opposes the dorylaimids (*Paratrichodorus*, *Xiphinema*) and *Rotylenchulus*, with the highest positive coordinates, to the spiral nematodes (*Helicotylenchus* and *Scutellonema*), with the highest negative coordinates. *Meloidogyne* and *Pratylenchus* occupy an intermediate position. On the factorial map (Figure 3.3C), the different plots are intermingled indicating the heterogeneities within cropping systems. However, trends can be observed. The maize/beans plots (5) have the highest positive coordinates on the F1 axis and are clearly separated from the other cropping systems. The convergence of these cultivated plots to the right side of the graph is related to the presence of

Paratrichodorus and *Xiphinema*, and the low populations of *Scutellonema*, *Helicotylenchus* and *Meloidogyne* as shown on Figure 3.4. Conversely, the *Crotalaria* (1), *Crotalaria/Sesbania* (2), *Crotalaria/Tephrosia* (3) and *Tephrosia* (8) fallows yielded no dorylaimids and had fairly high populations of spiral nematodes. The second factor (F2 axis of the correlation circle) accounts for 22% of the inertia and mainly highlights the opposition between *Scutellonema* and *Pratylenchus* to *Meloidogyne*, *Rotylenchulus* and *Helicotylenchus*. The position of the *Sesbania* fallows (6) on the highest level of the factorial map is due to the high incidence of *Meloidogyne* and *Rotylenchulus* (Figures 3.3C & 3.4). This contrasts with the *Crotalaria* fallows (1) characterised by high populations of *Pratylenchus* and *Scutellonema*.

3.3.3. Soil physico-chemical characteristics

The results of the principal component analysis on the 8 soil parameters are summarised in Figure 3.5. The first two axes conserved 47% of the total inertia (Figure 3A). The F1 axis (26% of inertia) mainly opposes the cultivated fields (5), the short natural (7) and *Crotalaria* (1) fallows characterised by high bulk density, to the long-term natural and other improved fallows, which had higher values of magnesium, potassium and clay contents (Figures 3.5B, 3.5C, 3.6). The second axis (21% of the inertia) mainly isolates the long-term natural fallows associated with high values of clay and soil organic matter and the cultivated plots, which had higher values of bulk density and calcium.

3.3.4. Soil parameters-plant nematodes relationships

3.3.4.1. Description of nematodes

On the first axis, the opposition between *Scutellonema* and *Paratrichodorus* becomes stronger and gives a better discrimination between the cultivated plots (5) and those under fallows (Figures 3.7A & 3.7B). This consolidates the strong opposition between *Meloidogyne*, *Rotylenchulus* and *Helicotylenchus* on the one hand, and *Scutellonema, Xiphinema, Paratrichodorus* and *Pratylenchus* on the other.

3.3.4.2. Description of soil parameters

Calcium plays a more important role on the first axis since it has the highest positive coordinate, but is still linked to the cultivated plots (Figures 3.7C & 3.7D). Also, a positive correlation appears between exchangeable acidity, magnesium, potassium, pH (H_2O) and clay, which were related to the fallows. In the second axis, the opposition between organic carbon/clay and exchangeable acidity becomes more pronounced, increasing the distance between the long-term natural fallows and the cultivated fields.

3.3.4.3. Relationships between nematodes and soil parameters

The significance of the Monte Carlo test (the 1000 row permutations provided no inertia value higher than that obtained with the original, non-permuted, data) (Figure 3.8A) indicates the existence of correlations (co-structures) between nematodes and soil parameters (Figure 3.8B). Thus, *Pratylenchus* was positively correlated to bulk density, pH (H_2O) and exchangeable acidity. *Helicotylenchus* was strongly associated with pH (H_2O) and clay. *Scutellonema* was highly correlated to exchangeable acidity, magnesium, potassium and pH (H_2O). *Rotylenchulus* had common structures with soil organic matter, pH (H_2O) and calcium. *Meloidogyne* was more positively correlated to clay, potassium and organic carbon. *Paratrichodorus* and *Xiphinema* had common structures with calcium and soil bulk density.

3.4. Discussion

3.4.1. Impact of land management on nematodes

The variability in nematode abundance and trophic composition observed in the different agroecosystems of western Kenya is an indication that land management has a significant impact on nematode communities. The long-term natural fallows had lower nematode populations than the improved fallows. This nematode build-up following tree/shrub planting could be related to the important production of root biomass that triggers increased biological activity in the soil (Derouard and Lavelle, 1994). It was possible to monitor the successional trends in nematode communities by comparing the maize/beans plots and the different stages of natural fallows. In the cultivated plots, which constitute the first stage of the succession, plant-parasites composed 69% of the community; they then decreased to 41% in the short-term natural fallows to reach only 18% in the long-term natural fallows.

The role of fallowing for the control of plant-pathogenic nematodes is well known (Weaver *et al.*, 1995). The reduction of parasitic nematodes during the fallow period may be attributed to two major factors. When farmlands are 'rested' from cultivation, there is a natural succession of the vegetation from crops to weeds and then to maturity species (Donfack *et al.*, 1995). Even though most nematodes occurring in cultivated fields are polyphagous, their re-adaptation to new plant species may not be automatic, and in some cases they may require a transition period to feed on new resources (Baujard and Martiny, 1995). Elsewhere, the progressive accumulation of organic matter in the soil induces the emergence of antagonistic organisms that maintain the populations of plant-pathogenic nematodes below damaging levels (Hominick, 1999).

Thus, in natural or lightly managed areas, free-living nematodes compose a higher proportion of the total nematode population (Hillocks and Waller, 1997). That is why in the traditional farming systems such as shifting cultivation or fallow agriculture, where short cultivation phases are separated by long periods of bush regrowths, parasitic nematodes seldom constitute a problem unless introduced with the planting material (Brown and Kerry, 1987). However, when farmlands undergo permanent cultivation, important changes occur in the system and the balance reverses rapidly in favour of the pathogenic species. Free-living nematodes are known for their high sensitivity to perturbations. Their low populations in the cultivated plots often indicate the degradation of the soil properties and a loss of fertility (Bongers and Bongers, 1998). In such conditions, plant-parasitic nematodes rapidly become a yield limiting factor, especially when the same crops are continuously grown over the years (Hillocks and Waller, 1997).

In this study, the preponderance of the parasitic nematodes over the free-living nematodes observed in the maize/beans farms remained unaffected when trees were planted in the croplands. Improved fallows are therefore unlikely to reduce the populations of parasitic nematodes in the soil. Realistically, though, it would be hard to expect the sanitising effect of natural fallows to be achieved with improved fallows for two simple reasons. Firstly, the time the trees occupy the land (one or two seasons) may not be long enough to allow any significant changes in the trophic structure of the nematode communities. Secondly, nematode communities, especially in the tropics, are generally polyspecific and the component species have wide host ranges (Nickle, 1991). As a result, all improved fallow trees (shrubs) used in western Kenya are alternative hosts for the locally occurring nematode species. The increase in overall plant-parasitic nematodes in the soil following the planting of these improved fallow species is due to the massive production of root biomass that confers upon trees a greater capacity than found in crop species to support large nematode populations.

3.4.2. The phytoparasitic nematofauna of western Kenya

Nematode communities in western Kenya are dominated by the genera *Scutellonema*, *Pratylenchus* and *Meloidogyne*. Root-lesion nematodes (*Pratylenchus* spp.) are known to be cosmopolitan in maize fields (Luc *et al.*, 1990). Moreover, the two species identified in western Kenya, *P. zeae* and *P. brachyurus*, are the most common in subtropical and tropical regions. *Meloidogyne incognita* and *M. javanica* have also been reported worldwide to be associated with maize (Luc *et al.*, 1990). In East Africa, however, maize is believed to be resistant to root-knot nematodes (Whitehead, 1969; Desaeger and Rao, 1999), whereas beans, the main leguminous crop cultivated in association with maize in western Kenya, are affected by these nematodes. *Sesbania sesban* and *Tephrosia vogelii* are also good hosts for *Meloidogyne* spp. (Whitehead, 1969; Faridah & van der Maesen, 1997) and heavy root infestations have been observed in the area (Desaeger and Rao, 1999).

Scutellonema is a polyphagous genus associated with a wide range of plant species including maize (Bridge *et al.*, 1995).

In this survey, species richness was higher in the maize/beans cultivated plots than in the improved fallows. The natural fallows also yielded a relatively high number of species. It is generally accepted that undisturbed systems have more diverse communities of soil organisms. This was, for example, shown for earthworms (Fragoso *et al.*, 1997) and nematodes (Cadet, 1998). However, if in these two instances increased diversity was associated with the number of species recorded, it has not been the case in the present study since leaving lands to lie fallow did not result in any gain in nematode species. The equitability in the distribution of the different nematode species played a very important role in the diversity of the communities in the short natural fallows. However, if disturbance is associated with human activities (tillage, weeding, fertilisation, removal of farm products, etc.), a planted fallow would constitute a transitional stage between a cultivated plot and a natural fallow. Therefore, what explains the poor diversity of nematodes in the improved fallows compared with the cultivated fields? Since agricultural practices in the study area have been traditionally based on a succession of cropping and natural fallow, we hypothesise that the nematofauna must have adapted to this land use systems, hence the greater number of species in the maize/beans cultivated fields and in the natural fallows. Improved fallows, which by contrast are a newly introduced technology, are very likely to lead to a selection of nematodes and, as a result, reduce diversity. Certainly, the mere introduction of new crop species into established agricultural settings represents sufficient perturbation (Day and Murphy, 1998) to have a negative impact on organismal diversity. This is particularly true for nematodes (Nickle, 1991). Additionally, the choice of improved fallow trees (shrubs) is based on criteria including rapid growth, resource use efficiency and high biomass production. Improved fallows create a floral uniformity and a simplification of the agroecosystem by inhibiting weeds. Therefore, planting such trees (shrubs) in the fields only favours the nematode species to which they are alternative hosts and suppresses the other species that cannot find suitable hosts. The *Crotalaria* fallows where the combination *Pratylenchus/Scutellonema* made 90% of the total nematode community exemplified well this situation. Likewise, the nematofauna of the *Tephrosia* fallows had low diversity because of the overwhelming dominance of *Scutellonema* and *Meloidogyne*, which together, constituted 82% of the parasitic nematofauna.

3.4.3. Typology of cropping systems in relation to nematode communities

It was possible to characterise the different agroecosystems in relation to the species composition and the structure of the nematode communities. *Scutellonema*, albeit omnipresent, had its highest populations in the planted fallows, except for the pure plantations of *Sesbania sesban*. This genus can therefore be considered as the most descriptive of the improved fallows. The abundance of *Pratylenchus* in the *Crotalaria* and in the maize/beans plots is a clear confirmation of the host status of *Crotalaria grahamiana* and the two crop species for this nematode. On the other hand, the near-absence of

Meloidogyne spp. in the *Crotalaria* fallows indicates that this plant is not host to root knot nematodes as stated by Shepherd and Barker (1993). This is also consistent with the findings of Desaeger and Rao (1999). Also, this study confirms that *S. sesban* and *Tephrosia vogelii* are good hosts for root-knot nematodes. Such conclusions are, however, more difficult to make for the rare nematode species. For example, it is not easy to say whether the apparent land use-specificity of the dorylaimids (*Xiphinema* spp. and *Paratrichodorus* spp.) is due to a particular affinity between them and maize and/or beans or just to their scarcity. Either way, their association with the cultivated plots appeared very strong.

3.4.4. Nematodes and the soil properties

There is no doubt that the host plant plays a prime role in the structuring of the nematode communities, and this role can be direct (quantity and quality of the food resource) or indirect (changes in soil properties). In this study, there were differences between cropping systems regarding some physical and chemical properties. The multivariate analyses showed strong correlations between nematodes and soil characteristics. Such relationships were reported in previous studies (Robinson *et al.*, 1987; Zoon *et al.*, 1993). The ectoparasitic genus *Scutellonema* was positively correlated to the exchangeable bases (magnesium and potassium) and the exchangeable acidity. Although the nature of such a relationship is not known, the strong presence of *Scutellonema* in the improved fallows may be indicative of some improvement in the chemical characteristics of the soil. Increase in plant-pathogenic nematodes with increasing levels of potassium was reported earlier (Kincaid *et al*., 1970; Badra and Yousif, 1979). In another experiment, Francl (1993) found a positive correlation between the density of *Heterodera glycines* and the level of magnesium. The dorylaimids (*Xiphinema* spp. and *Paratrichodorus minor*) were associated with bulk density, which was higher in the cultivated plots. This agrees with the conclusions of Manlay *et al.* (2000), who found a close relationship between *Xiphinema* and soil bulk density in west Africa.

Table 3.1. Comparison of total plant-parasitic and free-living nematode populations for different cropping systems in western Kenya[a]

Cropping systems	Plant-parasitic nematodes[b]	Free-living nematodes[b]	Ratio free-living to parasites (R)[c]
Maize-beans farms	1349 (3.13 bc)	675 (2.83 b)	0.50
Short natural fallows	1478 (3.17 bc)	1994 (3.30 a)	1.35
Long natural fallows	561 (2.75 c)	3161 (3.50 a)	5.63
Crotalaria fallows	2883 (3.46 ab)	2088 (3.32 a)	0.72
Sesbania fallows	3466 (3.54 ab)	2131 (3.33 a)	0.62
Tephrosia fallows	3089 (3.49 ab)	3235 (3.51 a)	1.05
Crotalaria/Sesbania fallows	3235 (3.51 ab)	2511 (3.40 a)	0.78
Crotalaria/Tephrosia fallows	7412 (3.87 a)	4676 (3.67 a)	0.63
P	< .001	< .001	

[a] Means in the same column followed by different letters are significantly different by Tukey's test

[b] Numbers in brackets are log-transformed values used in statistical analysis

[c] The R ratio was calculated using the non-transformed means

Table 3.2. Major plant-parasitic nematode species and their distribution in the different cropping systems[a]

Nematode species	Cropping systems							
	1 (7)[b]	2 (8)	3 (6)	4 (5)	5 (7)	6 (5)	7 (7)	8 (6)
Pratylenchus brachyurus	6[c]	5	5	4	5	0	6	0
Pratylenchus zeae	7	8	6	5	7	3	7	4
Meloidogyne incognita	0	3	2	1	4	3	3	2
Meloidogyne javanica	3	5	6	5	5	5	7	6
Helicotylenchus dihystera	3	6	5	3	5	4	6	4
Helicotylenchus pseudorobustus	4	4	3	4	4	3	6	4
Scutellonema clathricaudatum	7	8	6	5	7	4	7	6
Scutellonema magniphasmum	7	8	6	4	6	4	5	6
Scutellonema brachyurum	7	6	4	5	6	3	6	3
Scutellonema unum	1	0	0	0	2	0	0	0
Hemicriconemoides snoecki	0	0	1	2	2	0	0	1
Rotylenchulus borealis	2	2	2	3	5	3	2	4
Xiphinema elongatum	1	2	0	1	3	1	2	0
Xiphinema pinoides	2	1	1	0	3	0	0	1
Xiphinema setariae	0	0	0	2	2	0	0	0
Paratrichodorus minor	0	3	0	1	3	0	0	0
Ditylenchus spp.	1	2	0	2	2	0	0	
Tylenchorhynchus spp.	0	0	0	3	3	0	0	0

[a] (1): *Crotalaria* fallows; (2): *Crotalaria/Sesbania* mixed fallows; (3): *Crotalaria/Tephrosia* mixed fallows; (4): long-term natural fallow; (5): maize/beans fields; (6): *Sesbania* fallows; (7): Short-term natural fallows; (8): *Tephrosia* fallows

[b] Numbers in parentheses represent the total number of fields sampled for each cropping system

[c] Numbers in the table represent the number of fields of each cropping system from which the different plant-parasitic nematodes species were recovered

Table 3.3. Diversity of plant-pathogenic nematode communities in different cropping systems in western Kenya

Cropping systems	Diversity parameters		
	Number of species	Shannon diversity Index (H)	Evenness (J)
Crotalaria fallows	8.00 cd	0.85 b	0.70
Crotalaria/Sesbania fallows	8.50 cd	1.27 ab	0.76
Crotalaria/Tephrosia fallows	9.67 cd	1.39 ab	0.73
Long natural fallows	12.20 abc	1.23 ab	0.77
Maize/beans fields	14.57 a	1.42 ab	0.62
Sesbania fallows	7.00 d	1.64 a	0.78
Short natural fallows	13.12 ab	1.69 a	0.82
Tephrosia fallows	10.33 bcd	1.18 ab	0.72
P	< .001	0.0316	0.7615

[a] Means in the same column followed by different letters are significantly different by Tukey's test

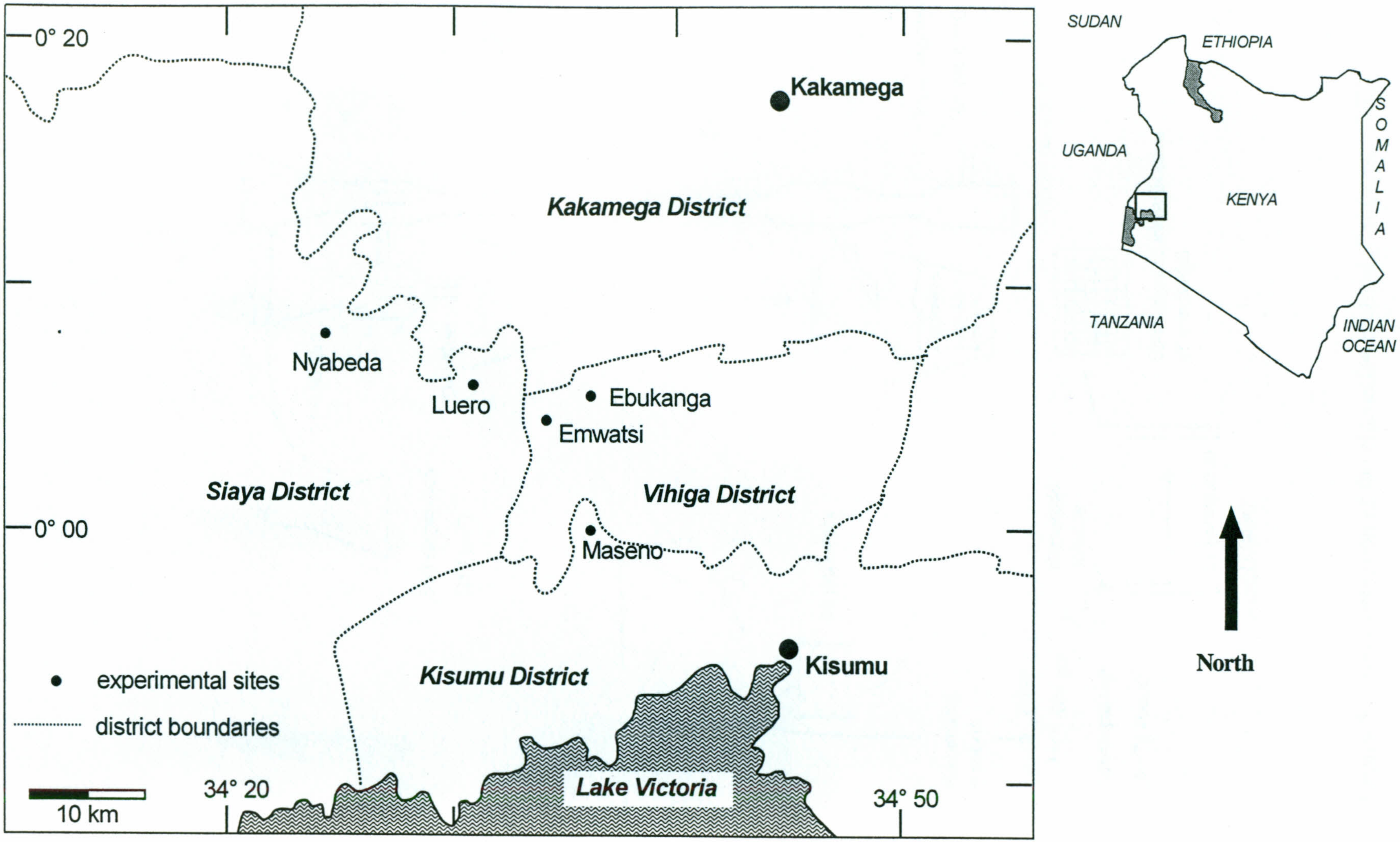


Figure 3.1. Location of the different sites sampled in the highlands of western Kenya

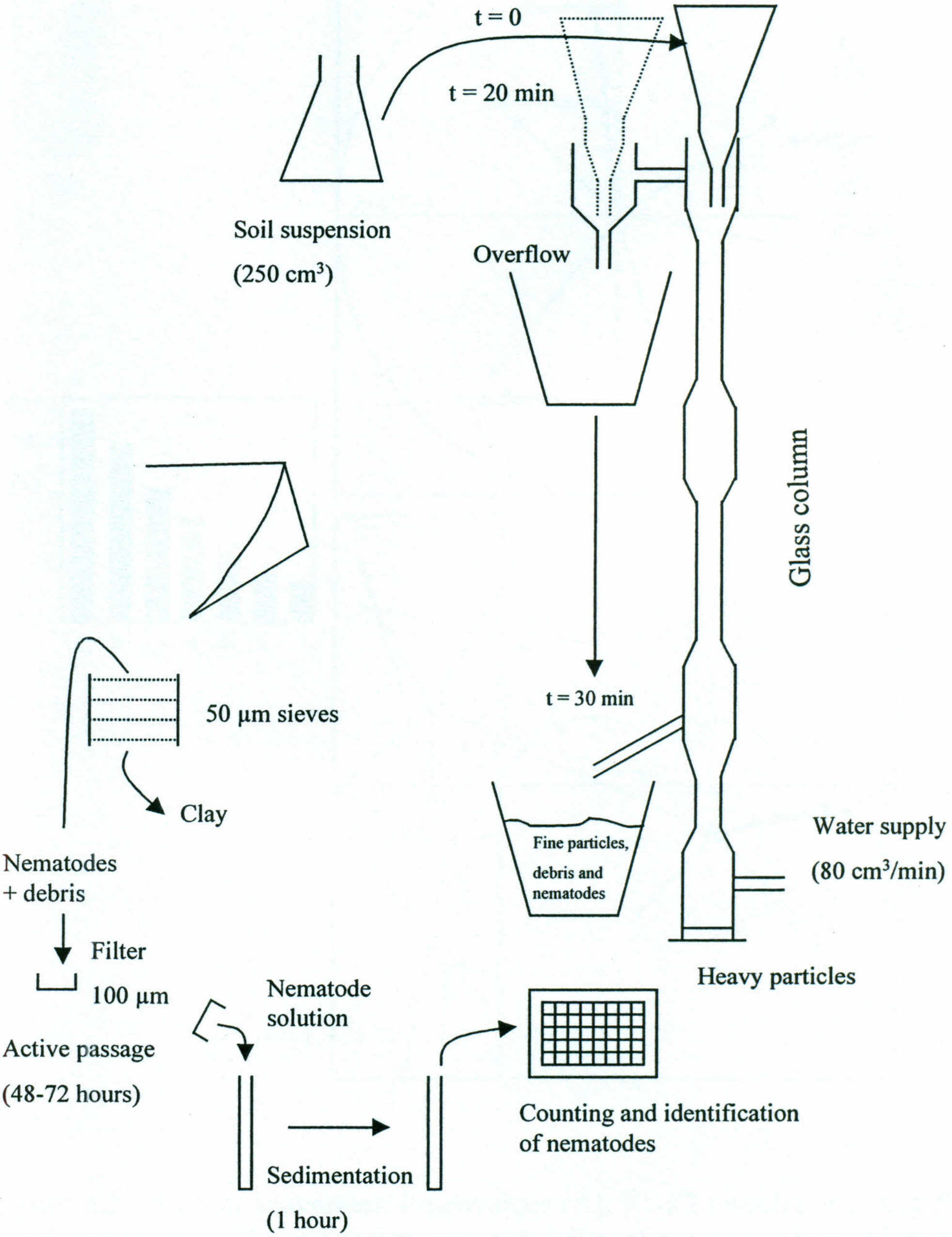


Figure 3.2. Representation of the elutriation method (Seinhorst, 1962)

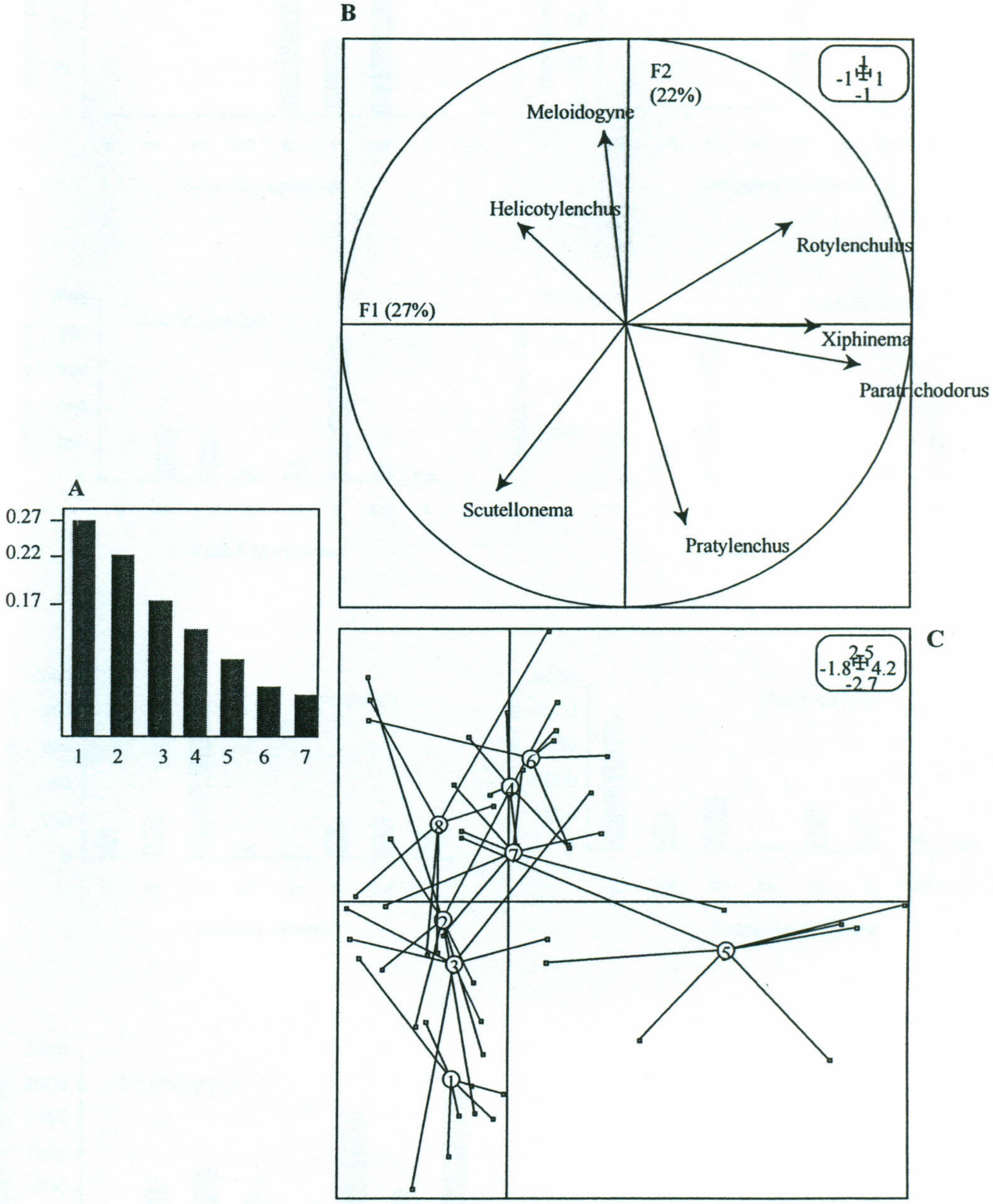


Figure 3.3. PCA on nematodes. Eigenvalues (A); F1-F2 correlation circle (B) and factor map (C). On the factor map, the different plots are projected to the gravity centre of the cropping system they belong to: (1) *Crotalaria* fallow; (2) *Crotalaria/Sesbania* fallow; (3) *Crotalaria/Tephrosia* fallow; (4) long-term (> 20 years) natural fallows; (5) maize/beans fields; (6) *Sesbania* fallow; (7) short-term (< 3 years) natural fallow; (8) *Tephrosia* fallow.

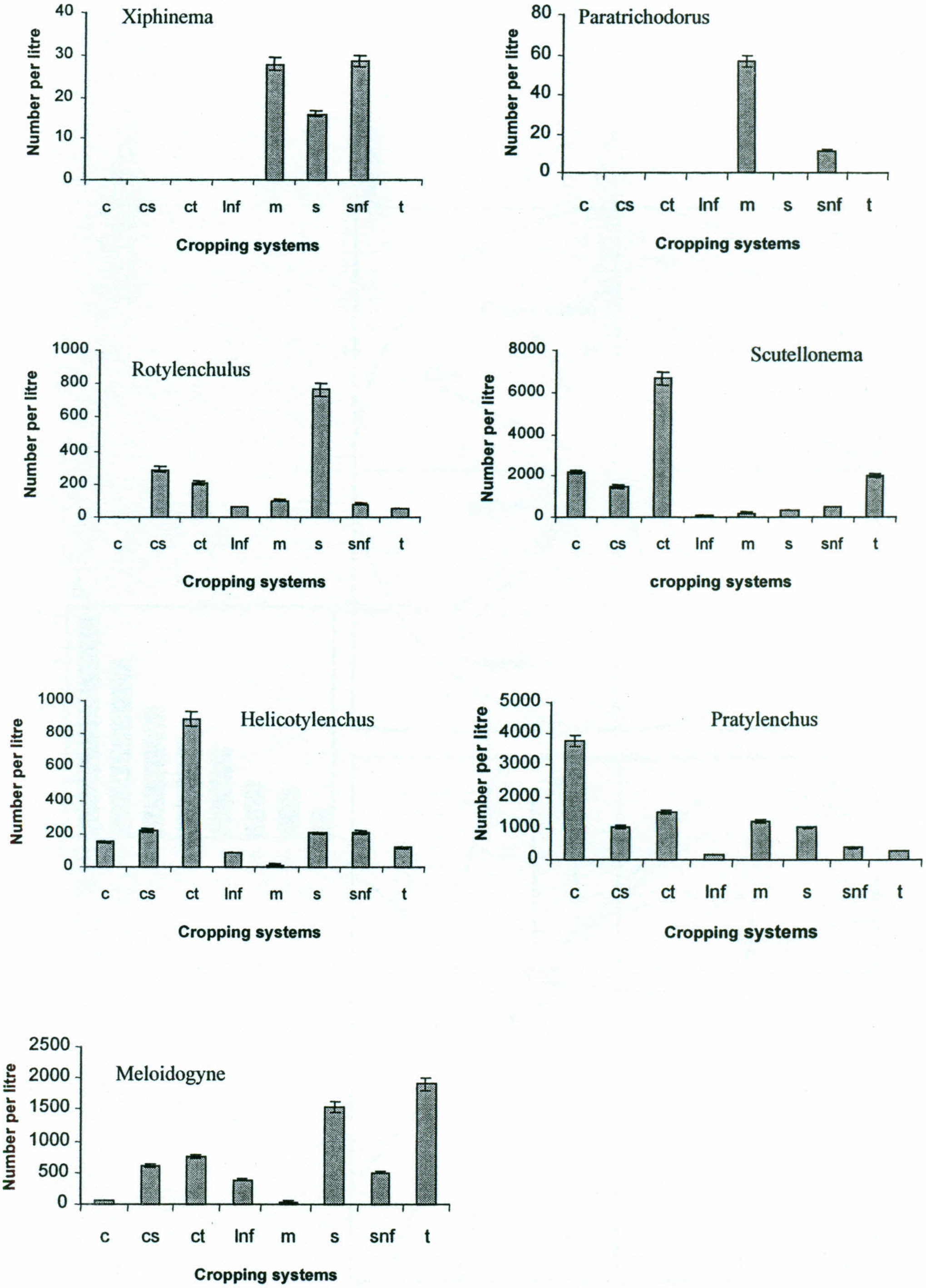


Figure 3.4. Abundance of plant-parasitic nematodes in different cropping systems. The cropping systems are the same as in Fig. 1. Bars represent standard errors

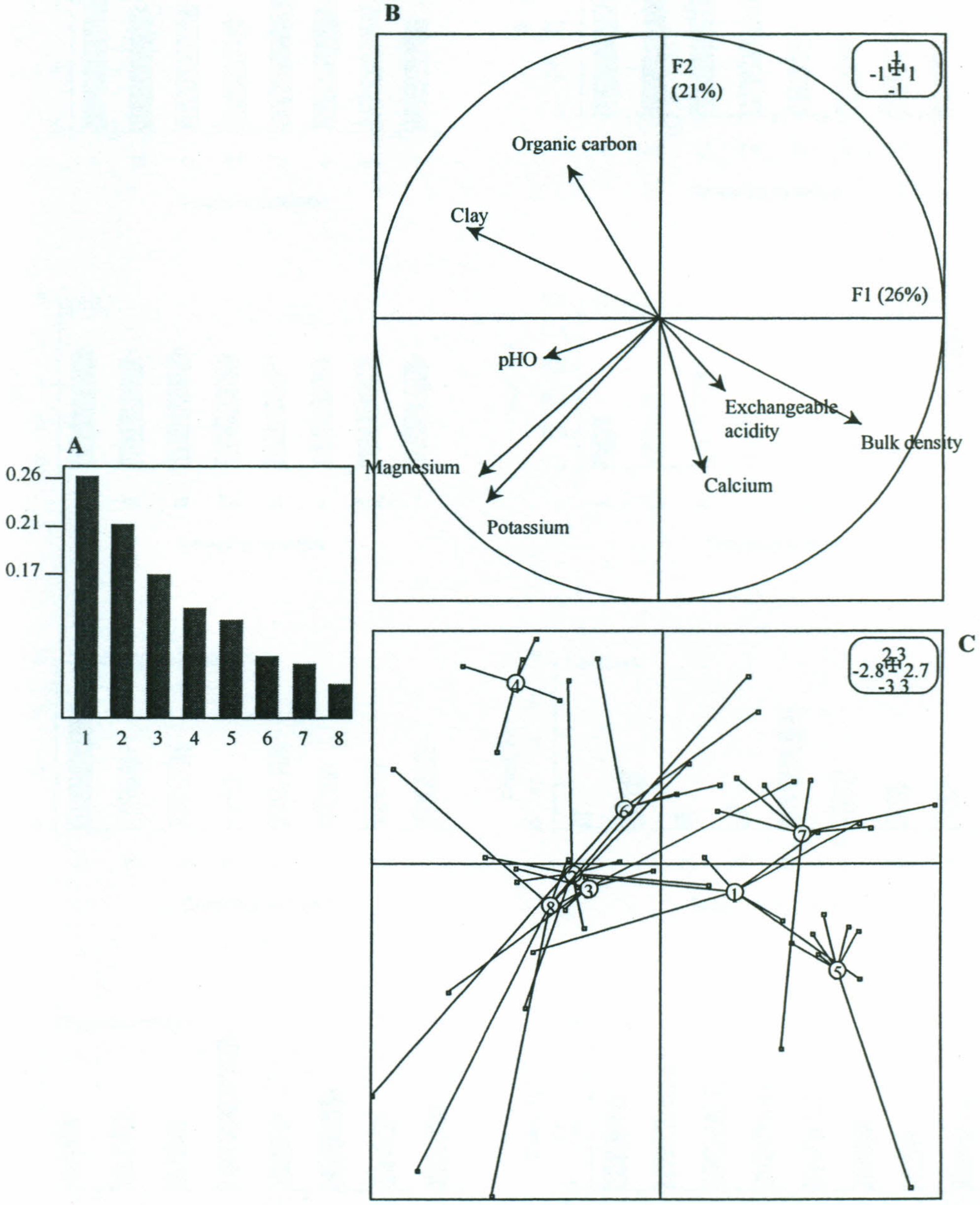


Figure 3.5. PCA on soil properties. Eigenvalues (A); F1-F2 correlation circle (B) and factor map (C). For more explanation, see Figure 3.3.

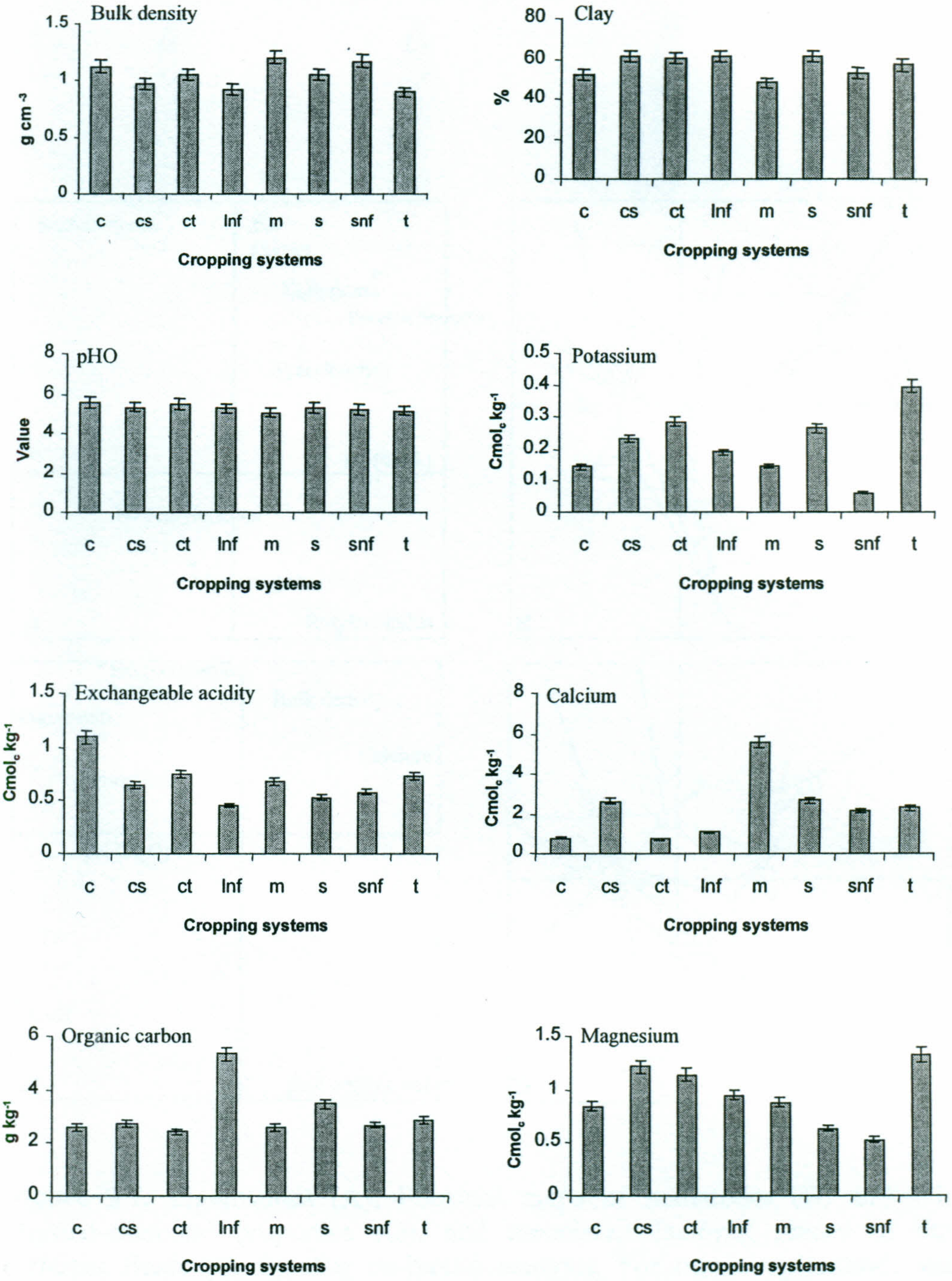


Figure 3.6. Measures of soil physico-chemical properties in different cropping systems. For more explanation, see Figure 3.4.

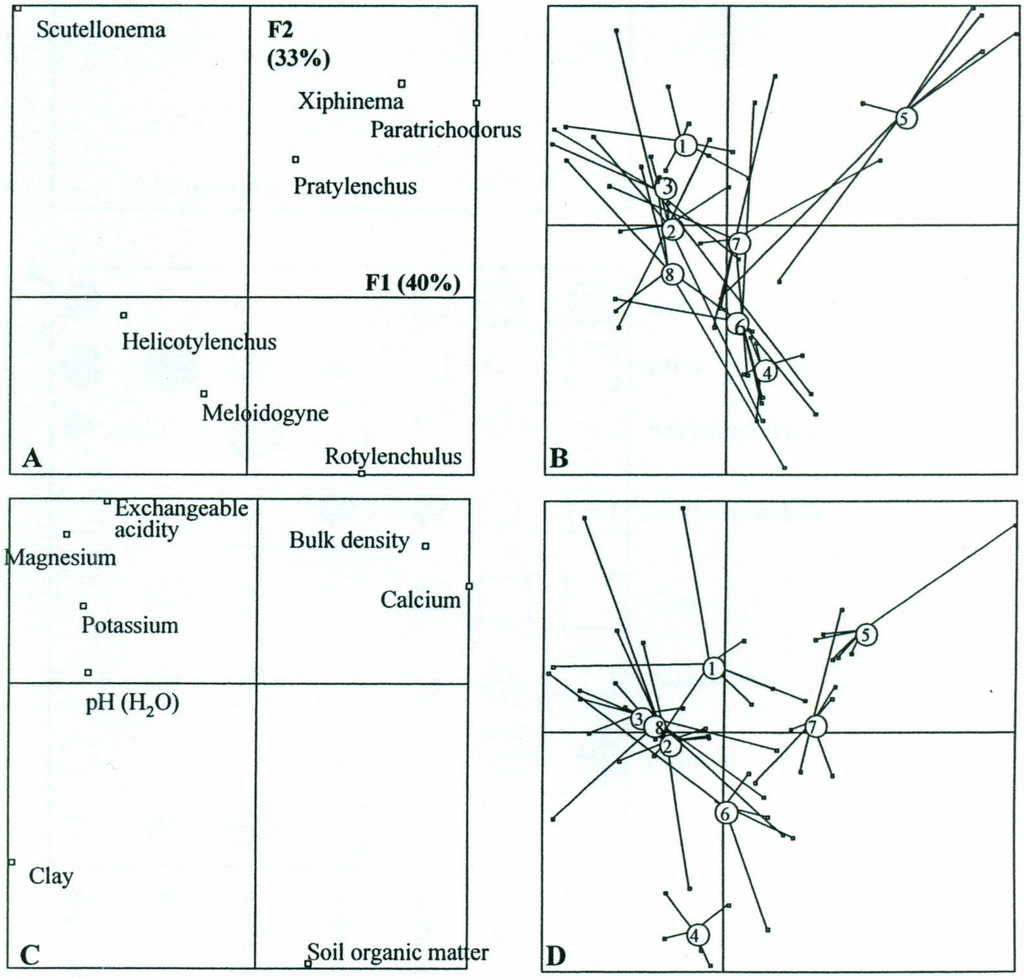
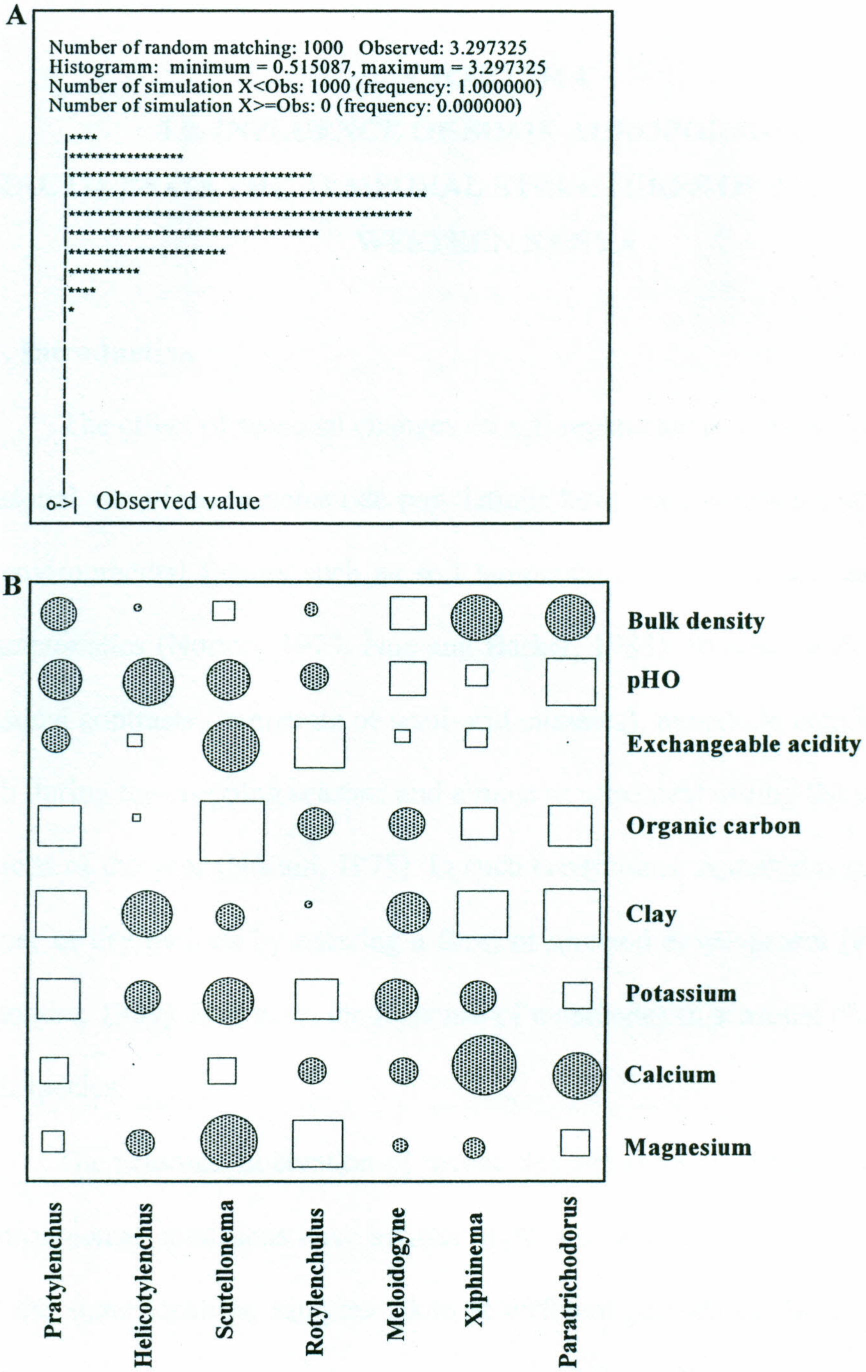


Figure 3.7. Eigenvalues (A); Factorial maps of nematodes (B) and soil physico-chemical properties (D), and associated factorial planes of the different fields (C, E) after co-inertia analysis. For more explanation, see Figure 3.3.



```
Number of random matching: 1000   Observed: 3.297325
Histogramm:  minimum = 0.515087, maximum = 3.297325
Number of simulation X<Obs: 1000 (frequency: 1.000000)
Number of simulation X>=Obs: 0 (frequency: 0.000000)

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Figure 3.8. Monte Carlo permutation test (A) and correlation matrix (B) showing relationships between nematodes and soil physico-chemical properties after co-inertia analysis. The size of the circles (positive correlations) and the squares (negative correlations) is proportional to the degree of correlations.

CHAPTER 4

4.0. INFLUENCE OF SOME AGROFORESTRY PRACTICES ON THE TEMPORAL STRUCTURES OF NEMATODES IN WESTERN KENYA

4.1. Introduction

The effect of seasonal changes on soil organisms is a known phenomenon. Seasonal variations in nematode populations have been correlated with variation in environmental factors such as soil temperature, soil moisture and other soil characteristics (Norton, 1979; Noe and Barker, 1983). In areas with pronounced seasonal contrasts (temperate or semi-arid climates), nematode activity is usually high during the cropping seasons and almost non-existent during the unfavourable periods of the year (Norton, 1978). In such ecosystems, nematodes survive either winter or dry periods by entering a form of arrested development (Evans, 1987; Antoniou, 1989). However, the response of nematodes to seasonal changes varies with species.

The seasonal fluctuation of nematodes and their differential sensitivity to environmental conditions have serious implications on their community ecology. For the same location, samples taken at different periods of the year may give different information as to the population densities and community structures of nematodes. The western part of Kenya experiences marked seasonal changes despite the high annual rainfall. The bimodal distribution of the rains allows two growing seasons during which crops occupy the land, separated by two shorter dry periods when farms are left bare or under natural regrowth shortly before land preparation. However, with the recent introduction of improved fallows, this pattern has been changing since after harvest, soil-improving, leguminous trees/shrubs replace the natural vegetation in many fields. The role of tree fallows in increasing crop yields is well documented. However, planting trees/shrubs alone may not be of much benefit if the soils are deficient in some nutrients like phosphorus (Jama *et al.*, 1998). In many parts of western Kenya, phosphorus deficiency (Plate 4.a) is a major yield limiting factor. Several methods have been proposed to overcome phosphorus deficiency in croplands, among which is the use of chemical fertilisers such as Triple Superphosphate (TSP). In western Kenya, however, application of rock phosphate has been identified as an inexpensive technology for local farmers to replenish soil phosphorus in their depleted lands (Mutuo *et al.*, 1999). It has been shown that improved fallow trees and the level of phosphorus in the soil, alone or combined, have some effects on nematodes (Kandji *et al.*, 2001), but whether the diversity of plant species in the field or the application of rock phosphate in the soil affects the temporal variations of nematodes is not known.

This paper reports on a study conducted during a one-year period to address a number of questions including:

(1) the effect of seasonal changes on the abundance of nematodes;

(2) the influence of the plant species and the application of rock phosphate on these seasonal changes;

(3) the effect of the season on the trophic structures of the nematode communities in the cultivated part of the plots and in the hedges;

(4) the changes in species composition, structure and diversity of plant-parasitic nematode communities as influenced by seasons and farming practices.

4.2. Material and methods

4.2.1. Experimental site

This study was conducted at Ochinga Farm in Vihiga district, western Kenya (0°06’ N, 34°34’ E and at 1420m elevation). The mean annual rainfall is 1800mm. The soil is an Oxisol (very fine, isohyperthermic Kandiudalfic Eutrodox) with the following properties in the first 15cm: air-dried pH (1: 2.5 soil water suspension) = 5.1, organic C = 15g kg^{-1}, bicarbonate-EDTA extractable P = 2mg kg^{-1}, clay = 46%, sand = 26% (Maroko *et al.*, 1999).

4.2.2. Experimental design and data collection

The experiment was carried out between September 1998 and September 1999. The annual rainfalls recorded in the study area were 2077mm and 1528mm in 1998 and 1999 respectively. The experiment was divided into two phases. There was a fallow phase with 5 following treatments: (1) maize/beans intercropping; (2) maize/beans intercropping with rock phosphate (P); (3) *Crotalaria* (*Crotalaria grahamiana*) fallow; (4) *Crotalaria* fallow with rock phosphate; (5) *Crotalaria* fallow with rock phosphate plus *Calliandra* (*Calliandra calothyrsus*) & napier *(Pennisetum americanum)* hedges.

Soil sampling during this phase commenced in early September 1998, when the *Crotalaria* seedlings were 3 months old. In the cultivated plots, maize (cultivar H614D) and beans (cultivar Roscoco GLP-24) were planted in alternating rows (Plate 4.b), in late September 1998. The planting distance was

90cm between rows and 25cm within rows. The beans and the maize were harvested 2 and 4 months after planting respectively. The rock phosphate used in this experiment originated from Minjingu, Tanzania, and was applied at a rate of 500 kg/ha in the long rains of 1998 (before the experiment), when all plots were planted with maize and beans. The different treatments were distributed into 4 blocks with complete randomisation in every block. The plot size was 15m x 12m. The hedges consisted of one row of napier grass and one row of *Calliandra* separated by a distance of 50cm and planted along the upper and lower limits of the protected plots following the slope (Plate 4.c). The hedges were 1 year old at the first sampling date. The second phase started with the long rainy season (May 1999), when the *Crotalaria* fallows were already slashed down and all plots planted with maize and beans, using the same cultivars and spacing as above. Soil sampling and nematode analysis were carried out every two months between September 1998 and September 1999. At every sampling date, a composite soil sample (mixture of 5 sub-samples or cores) was prepared from the different replicates of each treatment. Thus, the first 4 sampling dates fell in the fallow phase and the last 3 sampling dates in the cultivation phase. Nematodes were extracted, counted and identified as in Chapter 3.

4.2.3. Data analysis

To follow the population dynamics of plant parasitic and free-living nematodes, temporal curves were constructed with the averaged densities of nematodes on the 7 sampling dates. Then, the raw counts of plant-parasitic nematodes: number per litre of soil (x) were transformed into logarithm (x + 10) before any analysis was carried out. A two-way analysis of variance was performed and least significant differences of means (LSD) calculated to compare nematode abundance for the different treatments and different sampling dates, both in the fallow and cultivation phases. The diversity parameters (number of species, Shannon diversity index and evenness) of the different nematode communities (Krebs, 1985) were also compared using Anova.

4.3. Results

4.3.1. Nematode succession during the study period

Both plant-parasitic and free-living nematodes fluctuated during the experiment. For the free-living nematodes (Figure 4.1B), the lowest populations were recorded in January 1999, which fell in a dry period (Figure 4.1A). In all cropping systems, the highest nematode abundance was recorded in September 1999, which was the start of the short rains. The lowest populations of plant-parasitic nematodes occurred in July 1999, viz at the end of the long rains (Figure 4.1C). The highest populations were recorded either in September (beginning of short rains) or May (middle of the long rains).

4.3.2. The plant-parasitic nematode species

The nine genera of plant-parasitic nematodes identified in this study are given below with their respective species. The genus *Tylenchorhynchus* was not identified at species level due to its low populations.

- *Pratylenchus*: *P. zeae* and *P. brachyurus*
- *Scutellonema*: *S. magniphasmum*, *S. clathricaudatum* and *S. brachyurum*
- *Meloidogyne*: *M. javanica* and *M. incognita*
- *Helicotylenchus*: *H. dihystera* and *H. pseudorobustus*
- *Rotylenchulus*: *R. borealis*
- *Xiphinema*: *X. elongatum*, *X. setariae*, *X. pinoides*
- *Paratrichodorus*: *P. minor*

- ☐ *Tylenchorhynchus*: *T. spp.*
- ☐ *Hemicriconemoides*: *H. snoecki*

4.3.3. Comparison of the nematode communities in the two phases

4.3.3.1. The fallow phase

Table 4.1 shows the abundance of plant-parasitic nematodes in the different cropping systems. As indicated by the results of the Anova, the cropping system did not have any significant impact on the abundance of the different nematodes. The number of *Helicotylenchus* spp., *Paratrichodorus* spp. and *Scutellonema* spp. did not show any significant variations during the fallow phase. However, root knot nematodes, *Meloidogyne* spp., were significantly ($P < 0.001$) more abundant in September 1998 than in the other sampling dates. Root lesion nematodes, *Pratylenchus* spp., showed the same trend as they had significantly ($P < 0.001$) higher populations in September and November 1998. The population of reniform nematodes, *Rotylenchulus* spp., was significantly ($P = 0.05$) higher in January 1999 than in the other sampling dates while dagger nematodes, *Xiphinema* spp., were more abundant in March 1999. There was no significant interaction between the cropping systems and the sampling dates.

4.3.3.2. The cultivation phase

In the cultivation phase, the number of species reduced dramatically. Only 5 genera had sufficient densities to be used in the Anova (Table 4.2). The populations of *Helicotylenchus* spp., *Meloidogyne* spp. and *Paratrichodorus* spp. did not vary between cropping systems. The number of *Pratylenchus* spp. was statistically (P = 0.033) higher in the continuous maize/beans cropping + rock phosphate and in the *Crotalaria*-maize/beans rotation + rock phosphate. *Scutellonema* spp. had significantly (P = 0.002) higher populations in the *Crotalaria*-maize/beans rotation + rock phosphate (with or without hedges) than in the continuous maize/beans. The population of *Scutellonema* spp. in the *Crotalaria*-maize/beans rotation + rock phosphate + hedges was also significantly higher than the population in the continuous maize/beans + rock phosphate. *Helicotytlenchus* spp. had significantly (P = 002) higher populations in July than in May and September 1999. *Pratylenchus* spp. were more abundant ($P < 0.001$) in May and September than in July 1999. The same trend was observed with *Scutellonema* spp. ($P = 0.003$).

4.3.4. Diversity of plant-parasitic nematodes

Nematode diversity (number of species, Shannon diversity index and evenness) did not vary among cropping systems throughout the study period (Table 4.3). However, the number of species in the various cropping systems decreased significantly ($P = 0.006$) from the fallow phase to the cultivation phase. The Shannon diversity index did not change, but the evenness of the different communities increased significantly ($P = 0.003$) during the cultivation phase.

4.4. Discussion

This temporal study of nematodes was intentionally conducted on a single farm to minimise the variations related to the macroclimate and the soil type, and to give more weight to the farming practices. Nematodes showed very strong fluctuations during the study period. For the free-living nematodes, soil samples taken in January yielded the lowest populations while samples collected in September yielded the highest populations. The plant-parasitic nematodes, on the other hand, had their lowest populations in July. These results agree with those of other studies (Brown and Kerry, 1987; Delaville, 1995; Pate, 1997) that seasonal changes strongly affect nematode density in the soil. Also, a behavioural difference appeared quite clearly between free-living and plant-parasitic nematodes. The low populations of free-living nematodes in the driest period of the year (January) suggest that soil water is a crucial factor regulating the dynamics of these nematodes. The plant-parasitic nematodes had their lowest populations in July 1999 despite a relatively important rainfall. This could be explained by the fact that July corresponds to the end of the long rains, when the maize crop starts drying up in the fields. Those differences notwithstanding, nematode dynamics, both of free-living and plant-parasites, was strongly influenced by the rhythm of the rains. The hypothesis that nematode densities are at their highest in the middle of the rainy season (Richard and Barker, 1982) was, to a great extent, validated for the plant-parasitic nematodes since in most cropping systems, these nematodes had their largest populations in May (middle of the long rains). However, in a few cases, the resumption of the rains in September induced a rapid development of nematodes, resulting in high populations at planting. This phenomenon was also described earlier (Nickle, 1991).

The identification of plant-parasitic nematodes has corroborated the results of a previous survey conducted in western Kenya (Kandji *et al*., 2001). Beside *Scutellonema unum* and *Ditylenchus* spp., all other species identified in that survey have been recovered in this study. All nematodes were, to some extent, affected by the seasonal changes. However, an example of behaviour worth emphasising in this study was that of root knot nematodes, *Meloidogyne* spp., some of the numerically and economically most important nematodes in western Kenya. From relatively high populations in the beginning of the experiment, these endoparasites virtually disappeared in the second sampling date, to reappear only sporadically and in low densities throughout the rest of the experiment. The real cause of this disappearance is not clear, but inter-specific competition with root lesion nematodes (*Pratylenchus* spp.), as it was reported between *Meloidogyne chitwoodi* and *Pratylenchus neglectus* (Umesh *et al*., 1994), may have played a role in it. Long years of maize/beans cultivation in the experimental site have led to the selection of *Pratylenchus*-dominated nematode communities. The strong presence of these migratory endoparasites in the soil may stand as a constraint to the survival of root knot nematodes.

There have been several attempts to explain the organisation of nematode assemblages in the soil. While some authors consider the competitive relationships as a major determinant in the dynamics of a nematode community, others strongly believe that nematode survival and community dynamics depend more on natural cyclic patterns and inherent differences between species than on direct interspecific competition. Thus, temporal studies in agroecosystems often reveal sequential complementary distributions of different species of nematodes (Kraus-Schmidt and Lewis, 1979; Yeates *et al.*, 1985). In the present study, these behavioural differences were exemplified by the two dominant genera, *Pratylenchus* and *Scutellonema*. The first built up rapidly in favourable conditions but showed little resistance to the dry soil conditions, hence the marked fluctuations observed throughout the study period. Rapid multiplication and lack of stability like in the case of *Pratylenchus* is a typical feature of coloniser nematodes, which have a short lifespan but maintain their populations by leaving a substantial amount of eggs in the soil during dry periods. Conversely, the behaviour of *Scutellonema* spp. could be likened to that of persisters (Bongers and Bongers, 1998). Their densities varied little during the year due to their ability to survive in dry conditions (Demeure *et al.*, 1980). Resistance of this genus to drought was also reported from the groundnut-producing plains of Senegal. In those agroecosystems characterised by long and hot dry seasons, *Scutellonema cavenessi*, though a monovoltine species (one generation per year), constitutes the dominant nematode in the agricultural lands (Demeure, 1975; Germani *et al.*, 1984). The *Scutellonema* spp. of western Kenya represent other species but seem to have the same behaviour because apparently they multiplied in the first half of the long rainy season and maintained fairly constant populations outside that period.

The impact of the seasonal changes on the nematode communities was not only quantitative but also qualitative. There were more plant-parasitic species during the fallow phase than during the cultivation phase. Admittedly, the non-identification of a nematode species from a sample of field soil does not necessarily mean its absence from the field. Nematodes are normally difficult to detect when they occur at low populations in the soil (Jones, 1969). Of course, at this level, a nematode is unlikely to cause any damage unless the species involved is a virus-carrier like some parasitic Dorylaimids (Nickle, 1991). Diversity, as expressed by the Shannon index, did not change significantly from the fallow to the cultivation phase. However, the nematode communities in the cultivation phase had a significantly better eveness than those in the fallow phase.

Table 4.1. Abundance of different genera of plant-parasitic nematodes in different land use systems and different sampling dates during the fallow phase of the study

	Nematodes						
	Helicotylenchus[2]	*Meloidogyne*[2]	*Paratrichodorus*[2]	*Pratylenchus*[2]	*Rotylenchulus*[2]	*Scutellonema*[2]	*Xiphinema*[2]
Cropping systems[1]							
T1	25 (1.25)	100 (1.30)	25 (1.21)	3045 (3.25)	60 (1.27)	330 (2.03)	15 (1.09)
T2	20 (1.15)	85 (1.22)	0.6 (1.02)	4650 (3.45)	245 (1.49)	418 (2.22)	0 (1.00)
T3	160 (1.27)	65 (1.28)	10 (1.12)	2345 (3.14)	70 (1.28)	360 (2.15)	0 (1.00)
T4	10 (1.08)	45 (1.31)	20 (1.09)	2460 (3.24)	100 (1.23)	305 (2.17)	0 (1.00)
T5	1 (1.03)	0 (1.00)	10 (1.12)	2280 (3.18)	65 (1.33)	415 (2.23)	100 (1.20)
P	NS	NS	NS	NS	NS	NS	NS
LSD	0.30	0.31	0.22	0.28	0.44	0.46	0.20
Sampling dates							
September 1998	28 (1.23)	220 (1.76)	0 (1.00)	4332 (3.45)	204 (1.36)	432 (2.22)	0 (1.00)
November 1998	121 (1.14)	0 (1.00)	8.5 (1.11)	3824 (3.45)	80 (1.37)	304 (1.96)	0 (1.00)
January 1999	0 (1.00)	8 (1.06)	8.0 (1.09)	1648 (3.04)	148 (1.55)	272 (2.02)	0 (1.00)
March 1999	24 (1.25)	8 (1.06)	36.0 (1.12)	2020 (3.08)	0 (1.00)	455 (2.44)	92 (1.23)
P	NS	<.001	NS	<.001	0.05	NS	0.029
LSD	0.27	0.27	0.20	0.25	0.39	0.41	0.18
Interaction							
P	NS	NS	NS	NS	NS	NS	NS

[1] T1 = Maize/beans; T2 = Maize/beans + rock phosphate ; T3 = *Crotalaria*; T4 = *Crotalaria* + rock phosphate; T5 = *Crotalaria* + rock phosphate + hedges

[2] Numbers in brackets represent the log-transformed data used in the Anova.

NS = Not significant ($P > 0.05$)

LSD = Least significant difference of means

Table 4.2. Abundance of different genera of plant-parasitic nematodes in different land use systems and different sampling dates during the cultivation phase of the study

	Nematodes				
	Helicotylenchus[2]	*Meloidogyne*[2]	*Paratrichodorus*[2]	*Pratylenchus*[2]	*Scutellonema*[2]
Cropping systems[1]					
T1	13.3 (1.10)	0.0 (1.00)	0.0 (1.00)	3107 (3.04)	487.0 (2.29)
T2	0.0 (1.00)	0.0 (1.00)	0.0 (1.00)	4327 (3.27)	573.0 (2.42)
T3	20.0 (1.18)	0.0 (1.00)	0.0 (1.00)	1660 (2.96)	1047 (2.52)
T4	13.3 (1.10)	33.3 (1.13)	6.7 (1.08)	2973 (3.11)	960 (2.81)
T5	13.3 (1.16)	20.0 (1.12)	0.0 (1.00)	3460 (2.84)	1827 (3.10)
P	NS	NS	NS	0.033	0.002
LSD	0.25	0.22	0.10	0.27	0.41
Sampling dates					
May 1999	0.0 (1.00)	32.0 (1.15)	4.0 (1.05)	5060 (3.58)	992 (2.67)
July 1999	36.0 (1.33)	0.0 (1.00)	0.0 (1.00)	340 (2.09)	476 (2.31)
September 1999	0.0 (1.00)	0.0 (1.00)	0.0 (1.00)	3916 (3.48)	1468 (2.90)
P	0.002	NS	NS	<.001	0.003
LSD	0.20	0.17	0.08	0.21	0.32
Interaction					
P	NS	NS	NS	<.001	NS

[1] T1 = Continuous maize/beans; T2 = Continuous maize/beans + rock phosphate; T3 = *Crotalaria*-maize/beans rotation; T4 = *Crotalaria*-maize/beans rotation + rock phosphate; T5 = *Crotalaria*-maize/beans rotation + rock phosphate + hedges

[2] Numbers in brackets represent the log-transformed data used in the Anova.

NS = Not significant ($P > 0.05$)

LSD = Least significant difference of means

Table 4.3. Variation of diversity parameters of the nematode communities among cropping systems and sampling dates during the study period

	Diversity parameters		
	Number of species (N)	Shannon diversity index (H')	Shannon evenness (J)
Cropping systems[1]			
T1	7.29	0.24	0.50
T2	6.29	0.19	0.46
T3	7.29	0.29	0.62
T4	7.14	0.26	0.54
T5	6.29	0.26	0.56
P	NS	NS	NS
LSD	1.59	0.13	0.22
Phases			
Fallow phase	7.54	0.24	0.43
Cultivation phase	5.94	0.25	0.68
P	0.006	NS	0.003
LSD	1.08	0.09	0.15
Interaction			
P	NS	NS	NS

[1] T1 = Continuous maize/beans; T2 = Continuous maize/beans + rock phosphate; T3 = *Crotalaria*-maize/beans rotation; T4 = *Crotalaria*-maize/beans rotation + rock phosphate; T5 = *Crotalaria*-maize/beans rotation + rock phosphate + hedges

NS = Not significant ($P > 0.05$)

LSD = Least significant difference of means

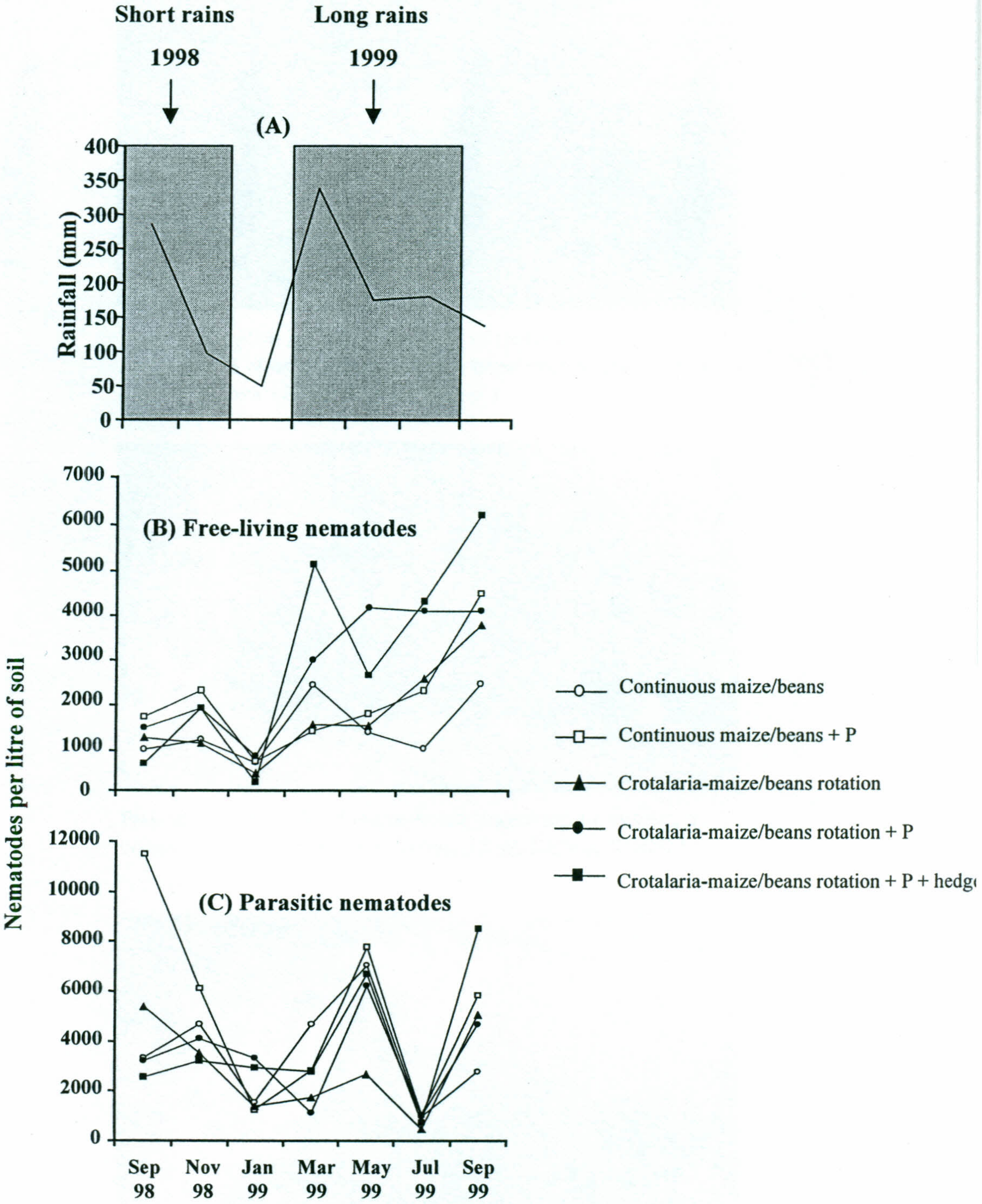


Figure 4.1. Fluctuation of rainfall (A), and abundance of free-living (B) and plant-parasitic (C) nematodes between September 1998 and September 1999 in the study site.

Plate 4a. Purplish stripes on the edge of maize leaves are indicators of phosphorus deficiency, phenomenon common in western Kenya (Photo Serigne Kandji)

Plate 4b. An example of maize-beans intercropping system, a common practice in western Kenya (Photo Serigne Kandji)

Plàte 4c. Calliandra and napier grass hedges planted at the lower end of the plot to reduce erosion (Photo Serigne Kandji)

CHAPTER 5

5.0. SPATIAL MICRO-DISTRIBUTION OF NEMATODES IN THE AGROFORESTRY SYSTEMS OF WESTERN KENYA

5.1. Introduction

The need to develop adequate sampling techniques is probably more acute for nematodes than for many other organisms because of their characteristically uneven distribution in the soil. Among the basic patterns of spatial distribution associated with nematodes, clustering is by far the most common (Marshall *et al.*, 1998). According to Nickle (1991), this tendency of nematodes to aggregate is explained by a number of factors including (1) occurrence of qualitative differences within hosts, resulting in some parts attracting and nourishing some nematodes more than others; (2) production of eggs in clumps by sedentary females; (3) production of several generations of nematodes with short life spans that flourish in some habitats and not in others; (4) competition among various fauna and microflora for nutrients or space; (5) inhibition by local environmental factors such as toxic substances; and (6) crop management practices in agroecosystems that may reduce numbers of some nematodes and increase others.

Quite often, the examination of samples taken from different parts of a field reveals a few spots with large populations while the majority of samples contain few nematodes. Because of this high degree of variability, frequency distributions of nematodes are often skewed making the estimation of their populations all the more difficult and imprecise (Noe and Barker, 1985). Yet, inadequate information on the size of a nematode population in the fields can have serious consequences. As Ferris (1984) pointed out, errors in the structure of the sampling plan can result in anything from a gross misinterpretation of the species and population levels present to increased variability in developing damage functions. Underestimating some species like root knot nematode can lead to agricultural disaster. Conversely, recommendations based on an overestimation of nematodes can also prove costly, as it can incur unnecessary expenses in nematode control and have long-term environmental drawbacks.

Nematode sampling is therefore a delicate process since there is no proven procedure generalisable to all situations. Sample size depends on several factors including the nematode species targeted, the size of the plot sampled and the objective of the sampling. It is generally agreed that sampling plans should be conceived so as to maximise the number of cores collected while minimising their size (Elliott, 1979), but the most difficult decision while sampling for nematodes is where to locate those cores. Systematic sampling is usually preferred to most of the other sampling patterns available, for the high- and low-density patches in the fields have the same likelihood of being sampled (Anscombe, 1950; Church *et al.*, 1959). The existence of obvious gradients in soil type, crop growth and slope can also guide the location of the sampling spots in the field (Smith and Wallace, 1976).

If in monocrop situations where there is uniformity of crop species the spatial distribution of nematodes is so intricate, how about the complex agroecosystems like the agroforestry systems in western Kenya? The purpose of this study was to contribute towards solving the problems associated with nematode sampling through a better understanding of the distribution patterns of nematodes in row crops. To establish the variability of nematode distribution in relation to nematode biology and some soil micro-heterogeneities, it seemed necessary to reduce the study scale from the plot to the plant rhizosphere. In addition, the use of a sampling grid (systematic sampling) was justified since it takes into account the aggregated distribution of nematodes and allows easier construction of spatial maps (Delaville, 1995; Marshall *et al*., 1998).

5.2. Materials and methods

5.2.1. Data collection

The plots sampled in this study were located at Ochinga's farm, Emwatsi (see map, Chapter 2) and are the same as those used in Chapter 4. To investigate the micro-distribution of nematodes in the rhizospheres of crops and planted tree fallows, a two-month old maize/bean crop and a five-month old *Crotalaria* fallow were sampled in November 1998 (short rains). Prior to the experiment, both plots were cultivated with maize and beans. Two consecutive rows of maize (with a bean row in the middle) and two consecutive *Crotalaria* rows were chosen in the middle of the experimental plots. The distance between rows was 90cm for both the crops and *Crotalaria.* Systematic sampling (Cochran, 1953; Freese, 1962; Chessel, 1978) was carried out by placing a small rectangular grid (135cm x 75cm) between those rows of crops or fallow tree species (Figures 5.1 & 5.2). The grid comprised of 6 lines and 10 columns. The external lines (line 1 and line 6) had a distance of 7.5cm from the maize or *Crotalaria* rows. The sampling points were separated by a distance of 15cm within row and within column. A small, 5cm-diameter, auger was used to remove a soil core in the 20 first cm from each sampling points. In total, 60 soil samples were collected from each grid and extracted separately according to the method of Seinhorst (1962) to determine the nematode populations. In March 1999 (long rainy season), part of the *Crotalaria* fallow was slashed and the plot planted with maize and beans. The other part of the fallow was left intact and another sampling was conducted in May 1999, when the *Crotalaria* was ten-month old.

5.2.2. Data analysis

After nematode identification, the logarithm-transformed nematode counts were separately subjected to analysis of variance (ANOVA) (PROC GLM, SAS Institute, 1985) to compare the densities of nematodes in the different lines of the grids. In addition, a cartography of nematodes in the sampling grids was carried out and maps drawn using the statistical package ADE-4 (Thioulouse *et al*, 1997). The outputs of the different analyses were presented in the form of tables and graphs.

5.3. Results

5.3.1. Characterisation of the nematofauna at rhizosphere scale

In the short rainy season of 1998, the nematofauna in the *Crotalaria* fallow was composed of 36% free-living nematodes and 64% plant parasites (Table 5.1). Among the parasites, *Scutellonema* was largely dominant, constituting 38% of the total nematofauna and 60% of the parasitic group. *Pratylenchus* was also fairly abundant with 17% and 26% of total and parasitic nematodes respectively. Compared to the maize/beans plot (2489 individuals/125cm^3 of soil), the total population of nematodes in the *Crotalaria* fallow (236 individuals/125cm^3 of soil) was low. The nematofauna of the cultivated plot was overwhelmingly dominated by the plant parasites, which made 93% of the total. In addition to the genera identified in the *Crotalaria* fallow, *Paratrichodorus minor* appeared (102 individuals/125cm^3). The commumity was however dominated by *Rotylenchulus borealis* (43% of total and 46% of parasites), *Scutellonema* (26%, 28%) and *Pratylenchus* (19%, 21%).

In the 1999 long rainy season, the nematode density in the *Crotalaria* fallow increased to reach 3883 individuals/125cm^3 of soil but only 3 genera of plant-parasitic nematodes were recovered (Table 5.2). The population of free-living nematodes was low (11%). The parasitic nematofauna was mainly composed of *Scutellonema* spp. (79%) while *Pratylenchus* spp. and *Helicotylenchus* spp. appeared in a similar proportion of 10%. In the cultivated plots, the free-living nematodes constituted a relatively higher proportion (33%).

Among the 4 parasitic genera recovered, *Pratylenchus* was by far the most abundant (89%).

5.3.2. Distribution of nematodes on the sampling lines

5.3.2.1. Short rains 98

The horizontal micro-distribution of nematodes in the 5 month-old *Crotalaria* fallow is shown on Figure 5.3. A general observation of the histograms reveals distribution gradients, nematode densities decreasing from the first to the sixth sampling lines due to a slope effect. However, high nematode densities were observed in the middle of the grids (4th line for most nematodes or 3rd line for *Helicotylenchus*), where a maize row of the preceding crop was located.

In the maize/beans plot, there were three major types of distribution (Figure 5.4). The free-living nematodes ($P = 0.008$), and the genera *Helicotylenchus* ($P = 0.001$), *Paratrichodorus* ($P = 0.008$) and *Pratylenchus* ($P = 0.002$) had significantly higher densities near the two maize rows. The sum total of nematodes ($P = 0.002$), the sum total of parasites ($P = 0.002$), and the genera *Rotylenchulus* ($P = 0.028$) and *Scutellonema* ($P < 0.001$) were more abundant in the right half of the grid. The few juveniles of *Meloidogne* spp. observed were concentrated between the 4th and 5th lines delimiting the bean intercrop.

5.3.2.2. Long rains 99

The distribution patterns of nematodes in the 10 month-old *Crotalaria* fallow are summarised in Figure 5.5. Practically, all nematodes had higher populations near the two rows of *Crotalaria* delimiting the sampling grid. In the maize/beans plot (Figure 5.6), a row effect (concave histogram) was observed for total parasites ($P = 0.003$) and the genus *Pratylenchus* ($P < 0.001$). A slope effect appeared with the free-living nematodes ($P = 0.004$) since they showed declining densities from the first to the last lines. *Helicotylenchus* and *Meloidogyne* had relatively high populations in the middle of the grid, where the bean intercrop was located. The convex-shaped histogram of *Scutellonema* ($P < 0.001$) shows that this nematode was concentrated in the middle of the grid, where a *Crotalaria* row of the preceding fallow must have been located.

5.3.3. Description of the nematode maps

The spatial maps give additional information on the distribution of nematodes in addition to the row and slope effects shown by the histograms. In the 5-month old *Crotalaria* fallow, three patterns of distribution could be observed (Figure 5.7). *Meloidogyne* and *Helicotylenchus* had a fairly regular distribution on the lines where they appeared. *Rotylenchulus* had the most irregular type of distribution because, while appearing on the first 4 sampling lines, it was strongly scattered and recovered only from 10 spots out of 40. *Pratylenchus*, *Scutellonema* and the free-living nematodes were more spread in the grid, but presented different levels of populations in the sampling spots. In the maize/beans plot of the short rains 98, *Meloidogyne* showed an aggregated type of distribution in the lower right quarter of the map (Figure 5.8). This was similar to *Scutellonema*, which was clustered in the upper right quarter of the map.

In the 10-month old *Crotalaria* fallow, no clear pattern of nematode distribution could be described beside the row and slope effects (Figure 5.9). In the maize/beans crop of the long rains 99, *Meloidogyne* and *Helicotylenchus* were strongly aggregated (Figure 5.10).

5.4. Discussion

5.4.1. Effect of the row-planted crops on the spatial distribution of nematodes

Because nematodes are mainly found in the rhizospheres of plants, the way crops or fallow trees are arranged in a field can have a major impact on the spatial organisation of nematodes. To understand the various patterns of nematode distribution in the *Crotalaria*-maize/beans improved fallow systems of western Kenya, a certain number of factors should be considered: (1) the host plant: three different species (two crops and a fallow tree), are present in the fields and their disposition in space and time follows a certain pattern (intercropping of maize and beans, then relay intercropping of maize and *Crotalaria*). The three plant species are not necessarily hosts to the same nematodes; (2) the spatial distribution of the food resources and other soil parameters as influenced by the expansion of the different root systems and (3) the interspecific competion between nematodes for space and resources

In this study, nematode distribution was investigated with a sampling grid spread between adjacent rows of crops and fallow trees. In the 5 months old fallow, the row effect of *Crotalaria* was not visible because of the strong influence of the slope. However, there were high populations of nematodes in the middle of the sampling grid as an effect of the preceding maize crop. This clearly shows that in no-till conditions, row cropping can have lasting effects on the spatial distribution of nematodes. In the cultivated plot, the major parasites of maize, *Pratylenchus* and *Paratrichodorus*, were highly concentrated along the maize rows. Mehta *et al.* (1992) observed a similar pattern with *Pratylenchus* on sugar cane in India. This is also in accordance with other observations made by Delaville (1995) in some sugar cane fields of Martinique (French West Indies). According to Ferris (1978), this behaviour of *Pratylenchus* is mainly due to its propensity to attack fresh roots, which are mostly found near the plant rows. Similarly, the distribution of *Meloidogyne* followed that of the bean plants, which confirms the strong association between root knot nematodes and the crop (Desaeger and Rao, 1999; Kandji *et al.*, 2001). The free-living nematodes were also aggregated near the plant rows probably because of higher microbial activity.

5.4.2. Effect of the slope on the spatial distribution of nematodes

The effect of the slope was particularly visible in the 5 months old *Crotalaria* fallow, where nematode populations decreased from the first to the last line of the sampling grid. Although the effect of the slope on soil organisms at a centimetre scale is not well documented, these results confirm that topography is a major determining factor in the horizontal distribution of nematodes (Barker and Nusbaum, 1971). The asymmetrical distribution of nematodes between the 5 months old *Crotalaria* rows could be ascribed to two major causes: (1) when erosion occurs, clay particles and nutrients are transferred from the upper to the lower parts of the plot. This translates into better plant growth in the lower rows of the plots, ultimately resulting in increased populations of nematodes; (2) nematodes are as easily carried away by runoff waters as the light particles of the soil (Cadet and Floret, 1999). The detection of nematodes in the runoff waters collected from the experimental plots (personal observation) provides evidence that physical transport through water runoff must have contributed to the concentration of nematodes in the lower part of the studied area.

5.4.3. Effect of other soil heterogeneities

One major advantage of systematic grid-sampling is that it facilitates spatial representation of the spots sampled and their associated nematode populations (Chessel, 1978). This was particularly useful in this study since it showed other aspects of nematode distribution in addition to the influence of the slope and the plant rows. The distribution of nematodes in the soil is the result of several processes. The occurrence of high-density spots for some species such as *Meloidogyne* spp. has a rather biological origin. Females of root-knot nematodes, like many other sedentary species, are known to lay eggs in batches (egg masses), favouring a distribution in clusters (Siddiqi, 1986) as shown by these results. On the other hand, if scavenging ectoparasites like *Scutellonema* and *Helicotylenchus* are clustered as observed in this study, other causes such as the existence of micro-heterogeneities in the soil (Delaville, 1995) must be considered. Those heterogeneities can originate from various sources including the intrinsic differences between plants and the distribution of some soil physico-chemical parameters, which are known to influence nematodes (chapter 2). However, clustering was mainly observed in the cultivated plots, which compared to the crotalaria fallows, constitute a more heterogeneous habitat owing to presence of the two intercrops (maize and beans) and the various crop management practices.

5.4.4. Effect of fallow age

Plant phenology is known to have effects on the populations of nematodes (Mehta *et al.*, 1992). Queneherve (1989) reported that seasonal fluctuations in nematode populations depend more on some physiological aspects of the plant rather than on the climatic changes. This hypothesis seems to have been corroborated in the present study. The exponential multiplication of *Scutellonema* in the 10 months old fallow had probably little to do with the season since the two samplings were conducted in the middle of the two rainy seasons. This was certainly related to the increased availability of root biomass resulting from the better growth of *Crotalaria*. In addition, the slope effect disappeared in favour of a more symmetrical distribution showing a strong row effect. Explanation to this phenomenon probably resides in some intrinsic characteristics pertaining to the physiology of *Crotalaria grahamiana.* Due to the growth pattern of this shrub (Godefroy, 1988), the heterogeneity created by the slope in the early stage of the fallow subsided when *Crotalaria* developed into a dense thicket, limiting water runoff and soil erosion.

Table 5.1. Abundance of free-living and plant-parasitic nematodes in a 5 month-old *Crotalaria* fallow and 2 month-old maize/bean field (short rains 1998)

a. *Crotalaria* fallow

Nematode taxa	Abundance ($125 cm^3$ soil)	Relative abundance (%)	Relative abundance within parasites (%)
Free-living nematodes	84	36	
Parasites	152	64	100
Pratylenchus	39	17	26
Rotylenchulus	2	1	1
Meloidogyne	14	6	9
Scutellonema	91	38	60
Helicotylenchus	6	2	4
Total	236	100	

b. Maize/beans field

	Abundance ($125 cm^3$ soil)	Relative abundance (%)	Relative abundance within parasites (%)
Free-living nematodes	177	7	
Parasites	2312	93	100
Pratylenchus	477	19	21
Rotylenchulus	1063	43	46
Meloidogyne	4	-	-
Scutellonema	643	26	28
Helicotylenchus	23	1	1
Paratrichodorus	102	4	4
Total	2489	100	

Table 5.2. Abundance of free-living and plant-parasitic nematodes in a 10 month-old *Crotalaria* fallow and a 2-month old maize/bean crop (long rains 1999)

a. *Crotalaria* fallow

Nematode taxa	Abundance (125cm^3 soil)	Relative abundance (%)	Relative abundance within parasites (%)
Free-living nematodes	440	11	
Parasites	3443	89	100
Pratylenchus	330	9	10
Scutellonema	2775	71	80
Helicotylenchus	338	9	10
Total	3883	100	

b. Maize/beans field

	Abundance (125cm^3 soil)	Relative abundance (%)	Relative abundance within parasites (%)
Free-living nematodes	418	33	
Parasites	862	67	100
Pratylenchus	769	59	89
Meloidogyne	13	1	2
Scutellonema	72	6	8
Helicotylenchus	8	1	1
Total	1280	100	

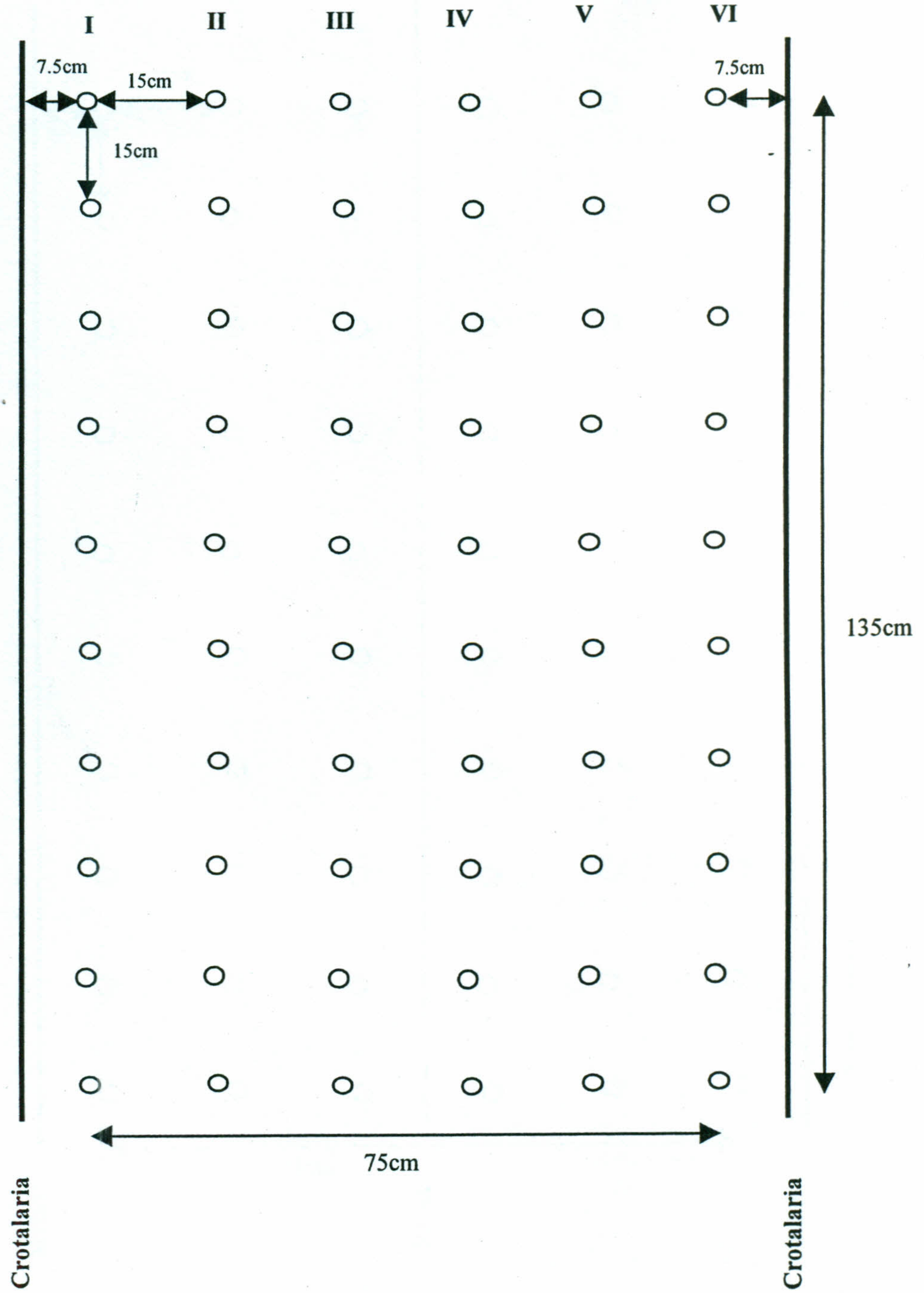


Figure 5.1. Sampling pattern for the study of the spatial micro-distribution of nematodes in a *Crotalaria* fallow

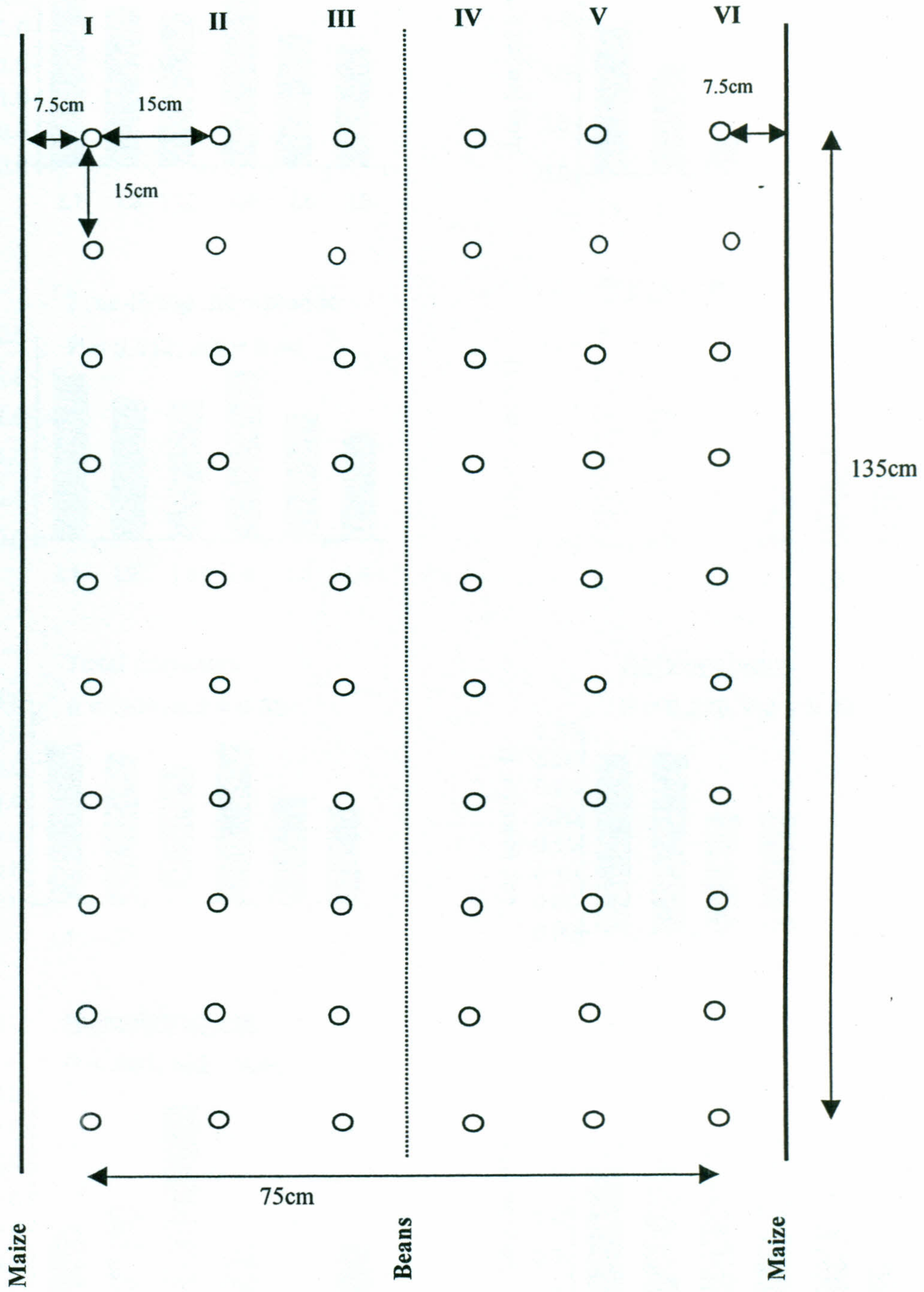


Figure 5.2. Sampling pattern for the study of the spatial micro-distribution of nematodes in a maize/beans intercropping system

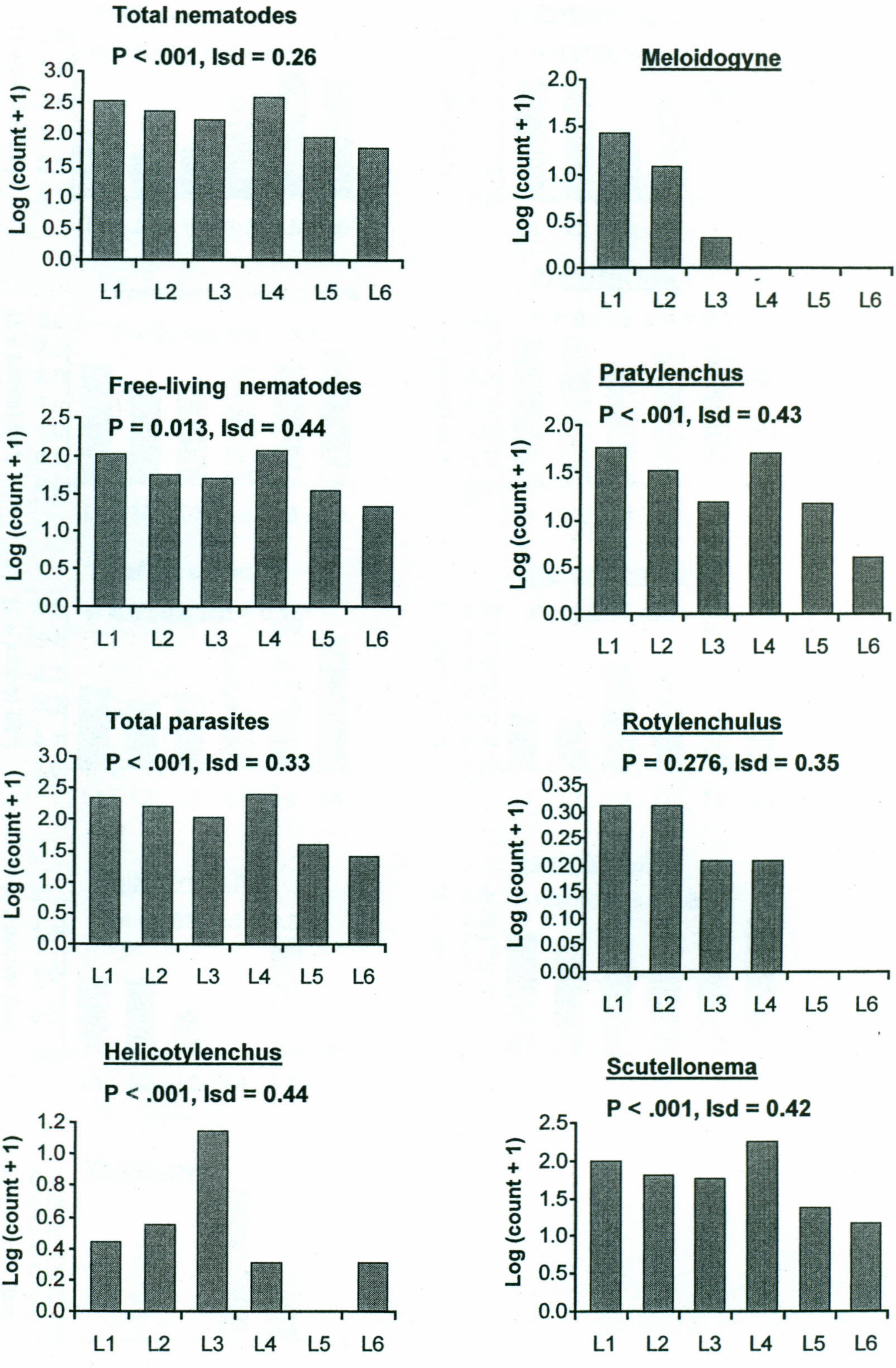


Figure 5.3. Number of nematodes on the sampling lines between two rows of *Crotalaria* in the 5 month-old fallow (short rains 1998)

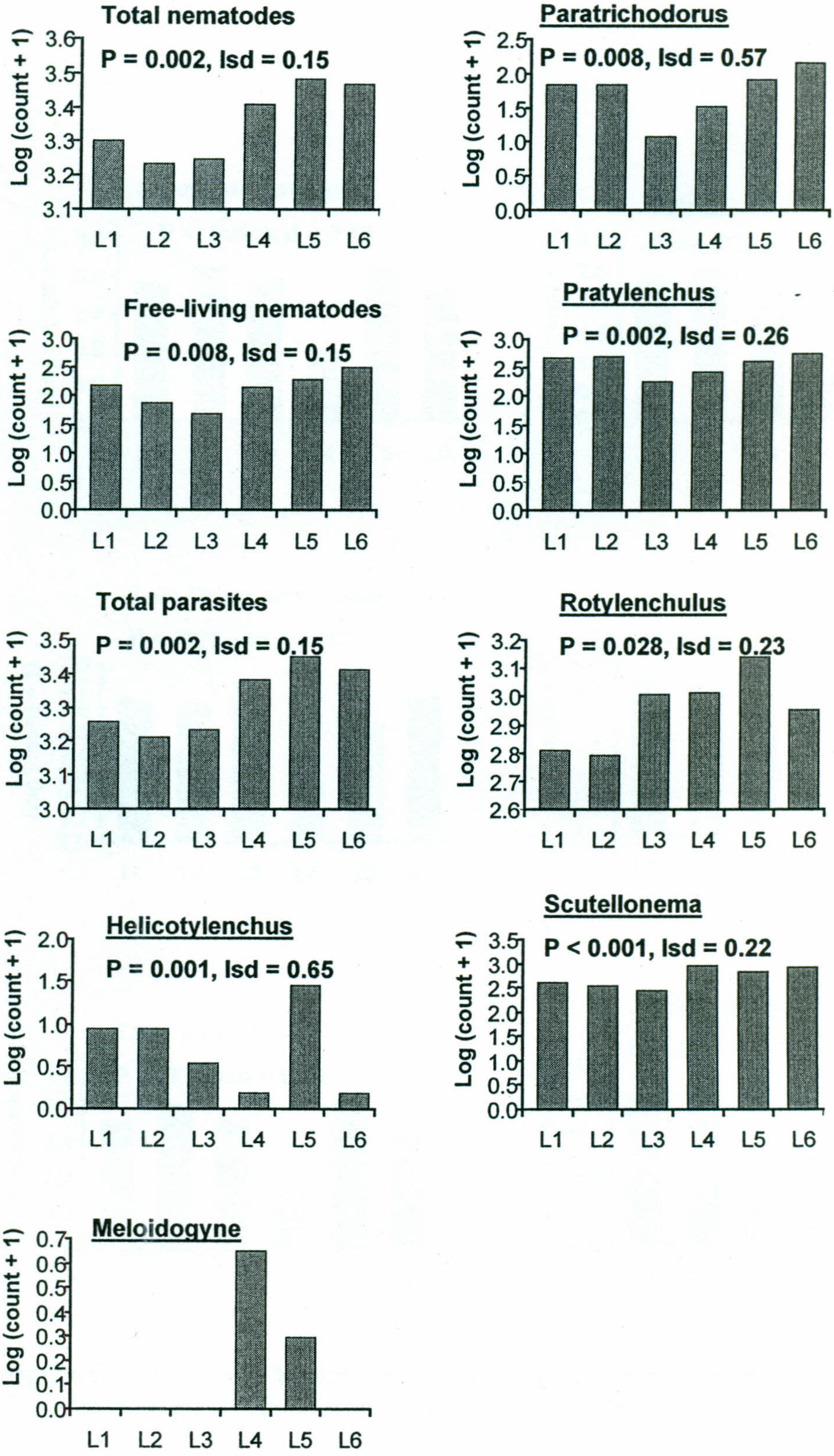
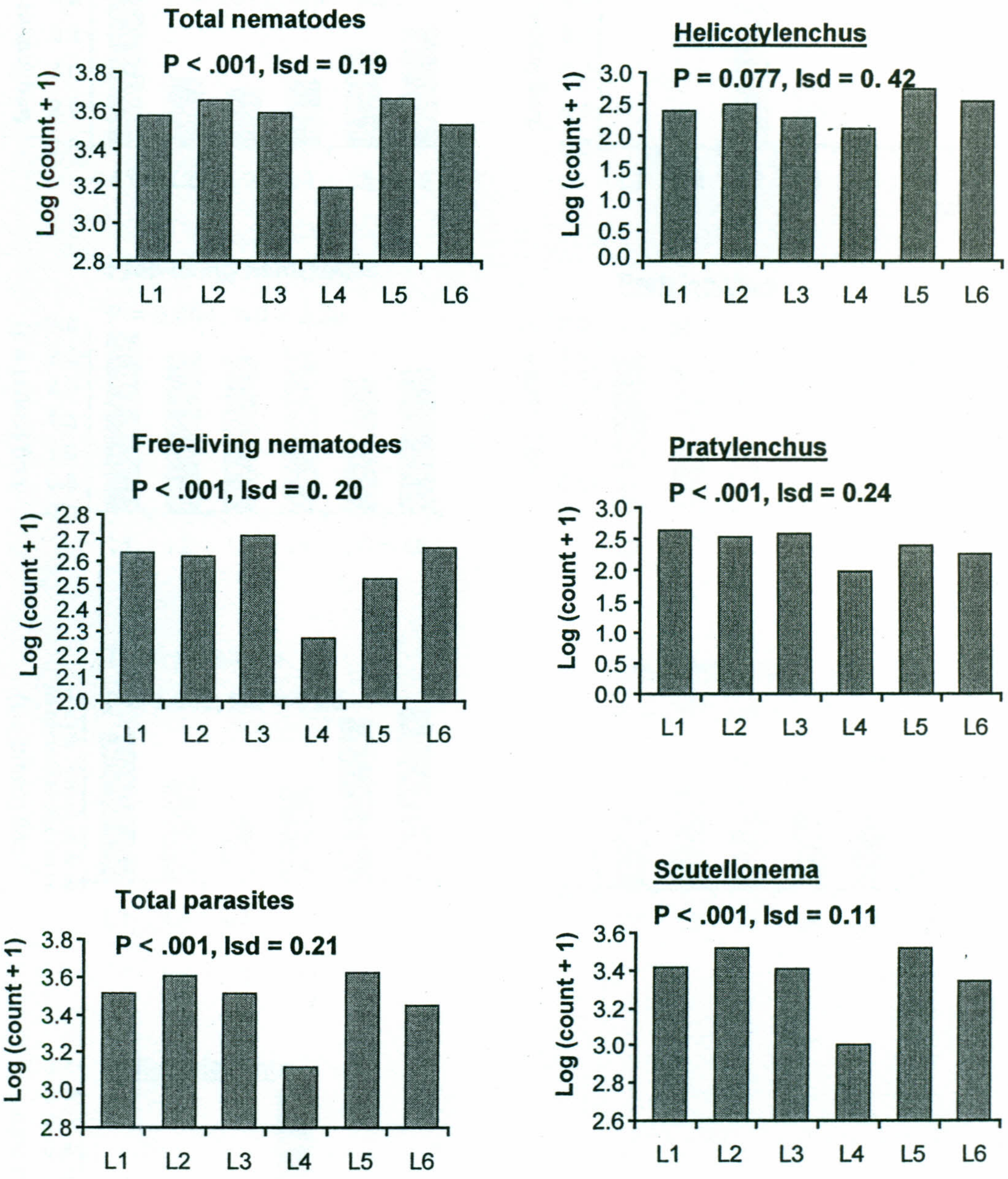


Figure 5.4. Number of nematodes on the sampling lines between two rows of maize in the 2 month-old maize/beans intercropping system (short rains 1998)



Total nematodes
P < .001, lsd = 0.19

Helicotylenchus
P = 0.077, lsd = 0. 42

Free-living nematodes
P < .001, lsd = 0. 20

Pratylenchus
P < .001, lsd = 0.24

Total parasites
P < .001, lsd = 0.21

Scutellonema
P < .001, lsd = 0.11

Figure 5.5. Number of nematodes on the sampling lines between two rows of *Crotalaria* in the 10 month-old fallow (long rains 1999)

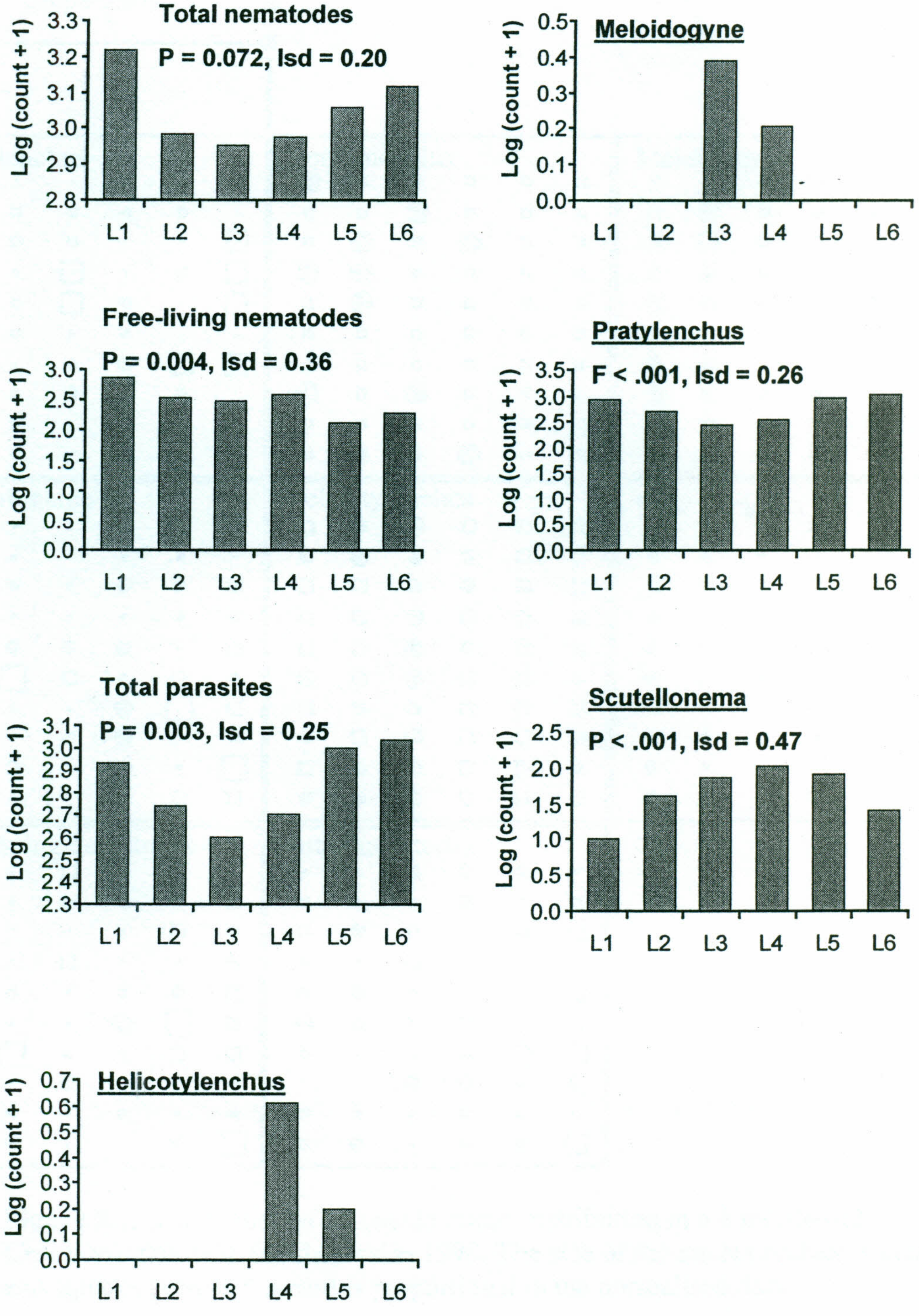


Figure 5.6. Number of nematodes on the sampling lines between two rows of maize in the 2 month-old maize/beans intercropping system (long rains 1999)

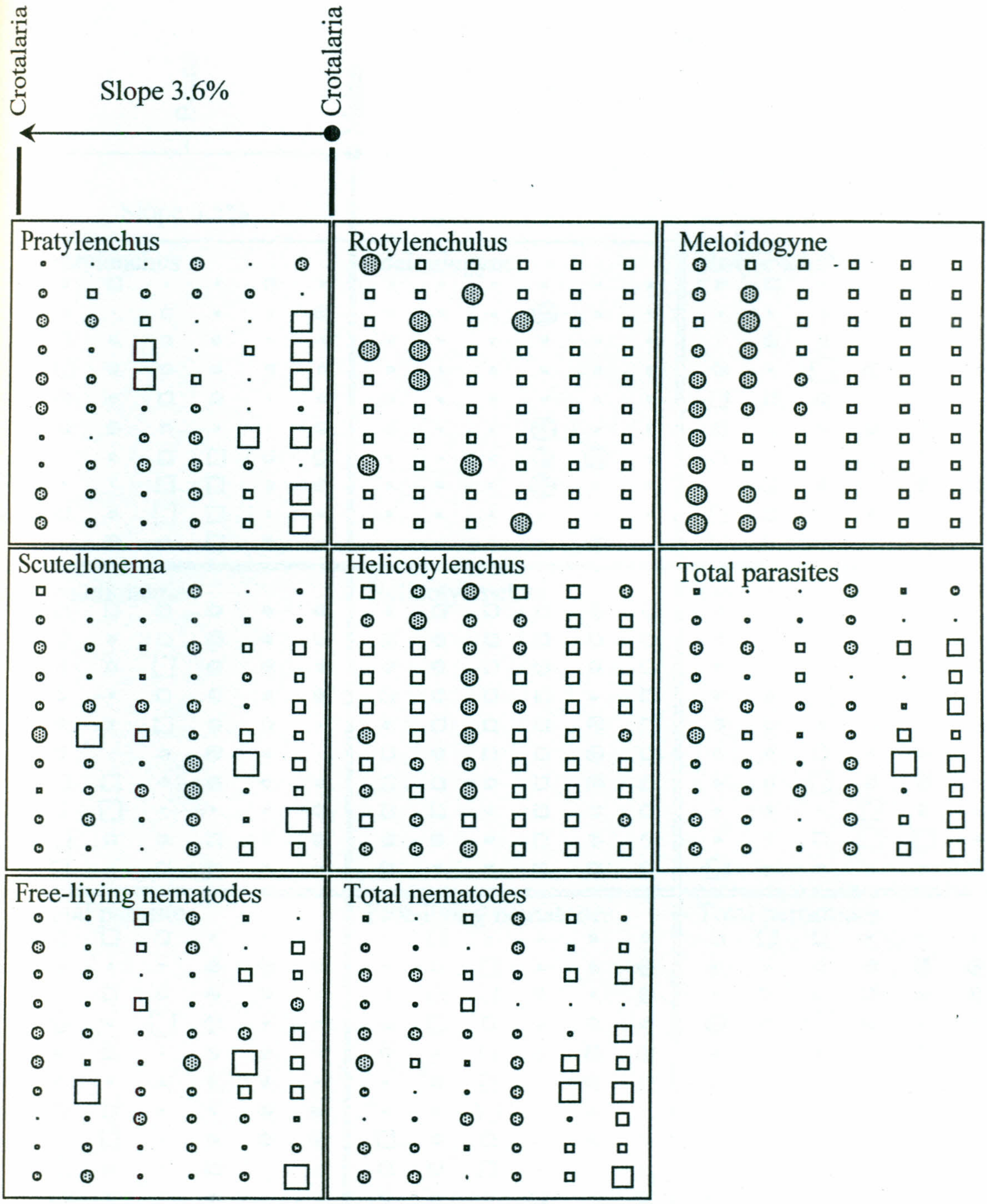


Figure 5.7. Spatial map of nematode micro-distribution in a 5 month-old *Crotalaria* fallow in the short rains 1998. The size of the circles (values > mean) and squares (values < mean) is proportional to the normalised data

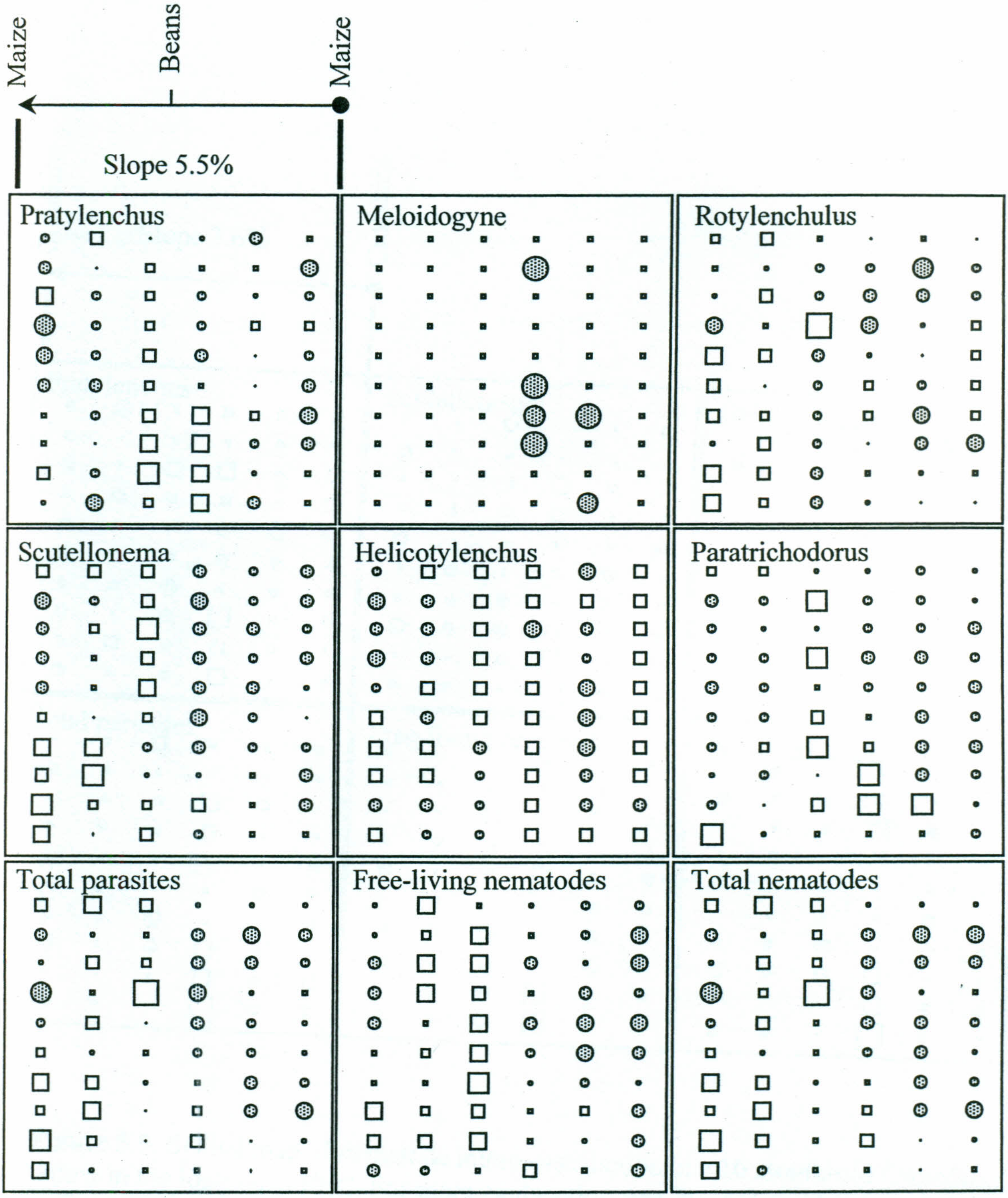


Figure 5.8. Spatial map of nematode micro-distribution in a 2 month-old maize/beans crop in the short rains 1998. For more explanation, see Fig. 5.7.

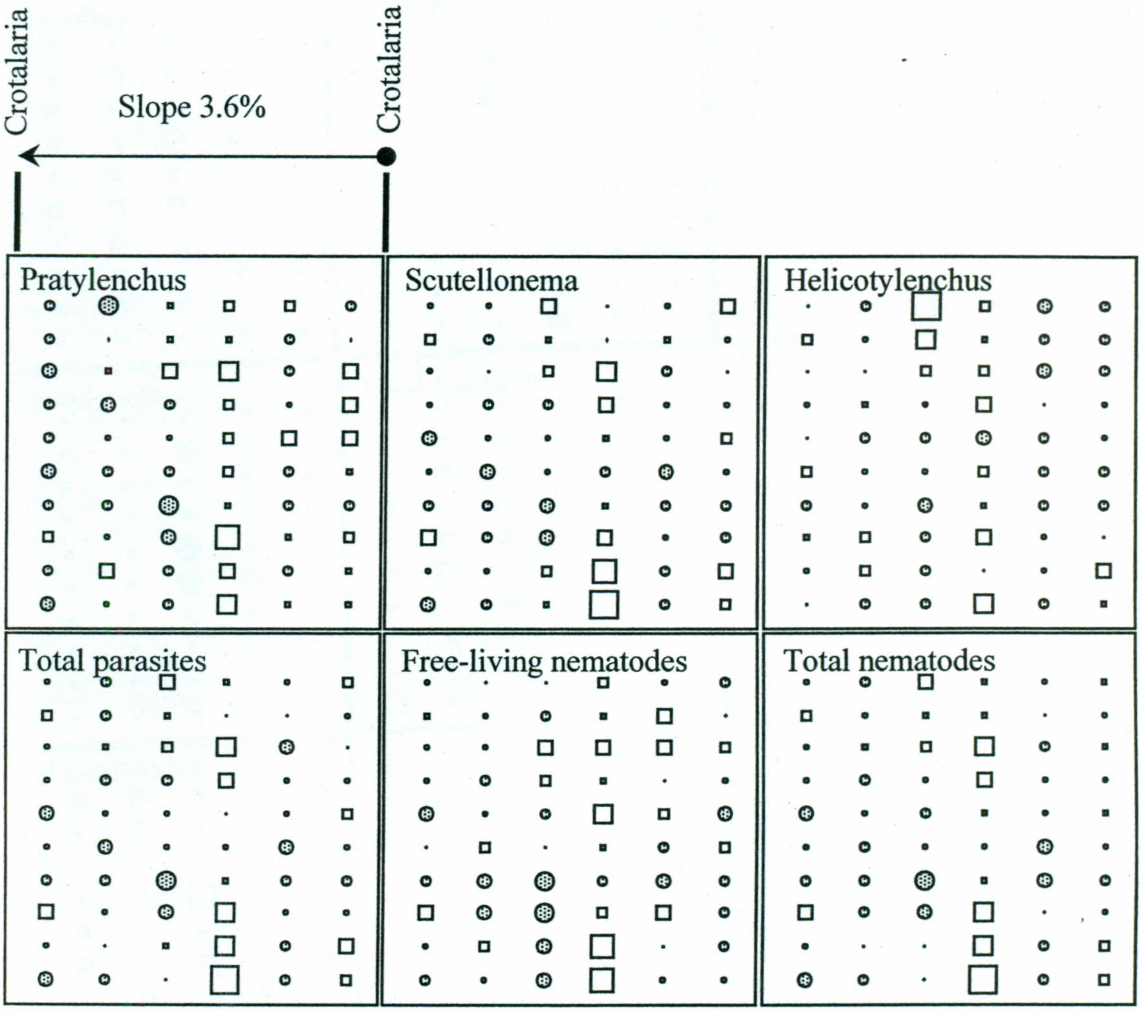


Figure 5.9. Spatial map of nematode micro-distribution in a 10 month-old *Crotalaria* fallow in the long rains 1999. For more explanation, see Fig. 5.7.

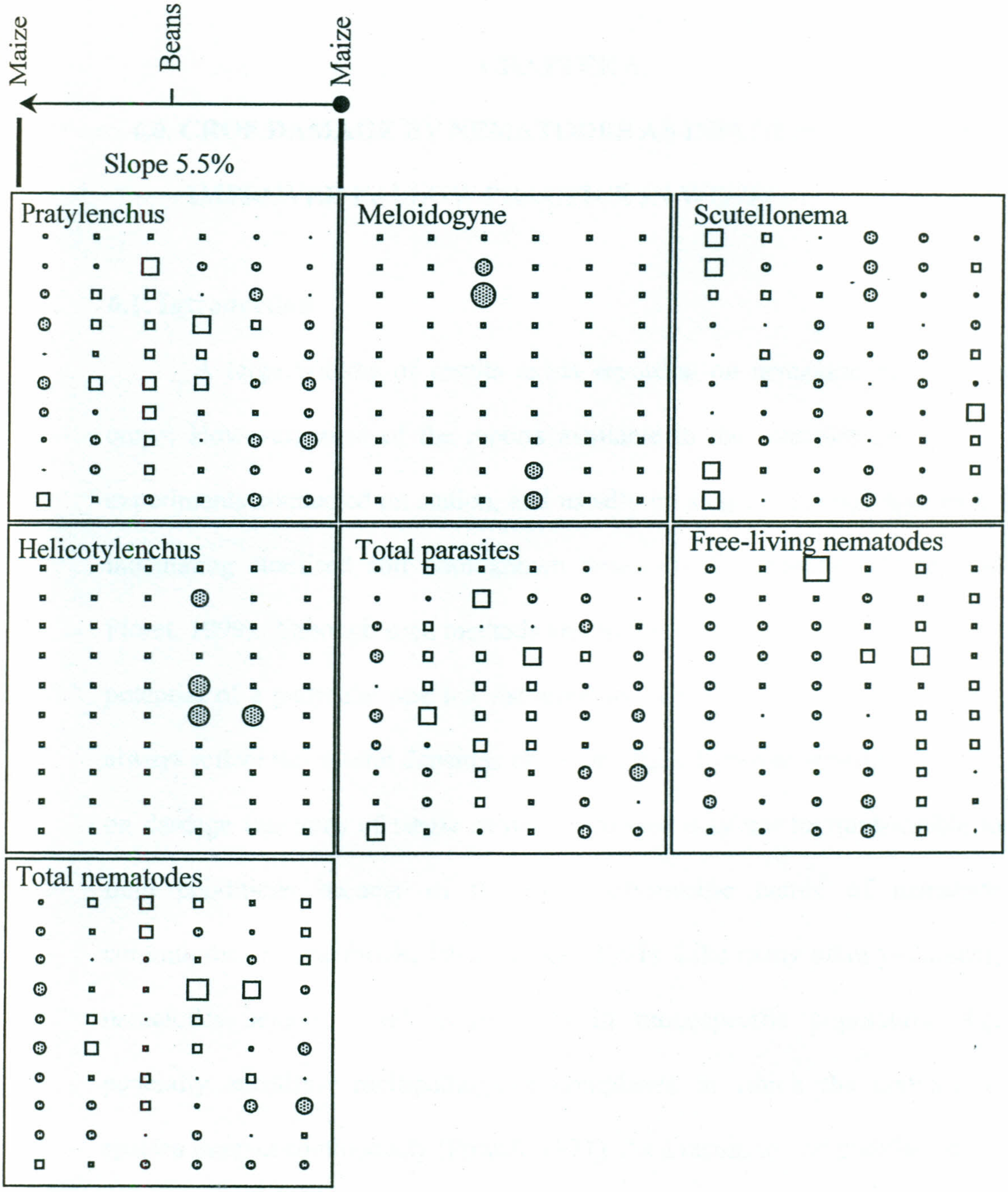


Figure 5.10. Spatial map of nematode micro-distribution in a 2 month-old maize/beans crop in the long rains 1999. For more explanation, see Fig. 5.7.

CHAPTER 6

6.0. CROP DAMAGE BY NEMATODES AS INFLUENCED BY THE IMPROVED FALLOW PRACTICE IN WESTERN KENYA

6.1. Introduction

A large volume of results exists reporting on nematode damage on crops. However, most of the reports available in the literature come from experiments conducted on station, and usually on single nematode species by inoculating sterilised soil with known densities of nematodes (Cadet and Floret, 1999). Although such methods are useful to have an insight on damage potential of a particular species, the amounts of inoculum involved may not always reflect the natural densities of nematodes. Moreover, information built on damage functions of single nematode species may not be transposable to field conditions because of the often-polyspecific nature of nematode communities (Oostenbrink, 1972; Nickle, 1991). Like many other pathogens, nematodes seldom attack plant roots in monospecific populations but generally constitute multipathogenic complexes in which the component species interact continuously (Powell, 1971). As a result, mixed populations of nematode species or of races/pathotypes of the same species may result in synergistic interactions that can diminish crop yields faster than do the individual pathogens (McKenry and Ferris, 1983).

Maize and beans constitute the major food crops in the highlands of western Kenya. Investigations conducted in various parts of the world showed that these two crops are prone to nematode attacks and can undergo severe yield losses when attacked by highly damaging species such as root knot and root lesion nematodes (Luc *et al.*, 1990). Improved fallows are known to improve soil fertility and enhance maize and bean production in western Kenya. At the same time, they increase considerably the number of plant-parasitic nematodes, including species that parasitise maize and beans (see Chapter 3). Therefore, to optimise the benefits of improved fallows with respect to sustained crop production, the potential impact of nematodes on maize and bean yields must be thoroughly understood.

As nematode communities undergo perpetual changes over time, an appropriate understanding of the dynamics of nematode pathogenicity in croplands may require *in situ* observations for several years (Cadet and Floret, 1999). However, the use of field data to determine nematode-induced crop losses is not always practical, due to the difficulty to isolate main effects from confounding factors. That is why in the recent past, greenhouse crop simulations have been largely used in nematological studies (Cadet and Floret, 1999; Desaeger and Rao, 2000a). The objective of this study was to evaluate the impact of plant-parasitic nematodes on crop growth and to monitor changes in the community structure and pathogenicity of nematodes under continuous cropping. Thus, I proposed to model the process of crop production by transferring naturally nematode-infested field soils to pots and conducting successive cycles of crops. Fertilisers were applied to offset the differences of fertility between soils.

6.2. Material and methods

6.2.1. Experimental protocol

The trial was conducted in the Maseno Agroforestry Research Centre. The soils used in the experiment were collected from Luero village (see map, chapter 3) and on 5 different cropping systems: maize/beans plot, natural fallow, *Crotalaria* fallow, *Tephrosia* fallow and *Crotalaria*/*Tephrosia* mixed fallow. In each plot, about 60 litres of fresh soil were collected from the top 20cm, covering the plot more or less evenly. The soil from each field was then mixed homogeneously and a sample of 250cc taken to estimate the initial populations of nematodes. The rest of the soil was used to fill 12 plastic pots of 8 litres. A composite formula of fertilisers (5.5g urea, 12.5g triple superphosphate and 5.5g potash) was added to half the pots (6) before planting. Two maize seeds (cv. H614D) and two bean seeds (cv. Roscoco GLP-24) were then sowed in these pots. One week after germination, both maize and beans were thinned to leave only a plant of each crop in the pot. Watering was done on a daily basis by supplying about 500ml water per pot, taking in consideration the field capacity of each soil.

The experimental design was a split-plot where the 5 cropping systems represented the plots and the 2 levels of fertilisers represented the sub-plots. The 60 pots were distributed into 6 raised beds to avoid contact with the soil. These beds were considered as completely randomised blocks and placed under a shed with a transparent roof. At each watering, the position of the pots on the same bed was changed to minimise positional effects within blocks (Desaeger and Rao, 2000a). After 6 weeks for beans and 2 months for maize, the plants were uprooted and aerial and root biomass measured. Height measurements were also taken for maize before uprooting.

After removal of the maize, the pots were left to rest for one week before starting another cycle. In total, 3 successive cycles were conducted between June 1999 and December 2000. The same formula of fertilisers was applied in the beginning of each cycle.

6.2.2. Nematode extraction

In each cycle, a 125 cc soil sample was taken from each single pot before planting, at bean harvest, and at maize harvest, to estimate nematode populations. Nematode extraction was conducted with a modification of the sieving and decanting technique (Marshall *et al.*, 1998). Nematodes were also extracted from roots of both plants, using the modified Baermann-funnel method (Desaeger and Rao, 2000b).

6.2.3. Data analyses

The different agronomic parameters measured for crops were subjected to a two-way analysis of variance in randomised blocks to test whether statistically significant differences existed between the different treatments of each factor. If so, least significant differences (LSD) were calculated to separate means. Then, regressions were fitted to relate the agronomic parameters of crops considered as dependent variables (y) and the density of a particular nematode group considered as independent variable (x). In addition, the Seinhorst's equation $y = (y_m)m + (y_m)(1 - m)z^{Pi-T}$ (where y = a ratio of yield at nematode density Pi and that in the absence of nematodes, y_m = average yield for $Pi < T$, T = nematode population density below which no detectable loss in yield occurs, m = minimum yield, z = a constant reflecting nematode damage, Pi = initial population density) was fitted to detect damage threshold for different nematodes.

6.3. Results

Results of the three cycles are presented separately. Root extractions conducted throughout the study confirmed the presence of the endoparasites, *Meloidogyne* spp. and *Pratylenchus* spp. in the roots of both crops. However, root nematode populations were not included in the analyses because of the often- low root biomass of beans and the difficulty to separate the maize and bean roots in the pots.

6.3.1. First cycle

6.3.1.1. The parasitic nematode communities at planting

The size, composition and structure of the initial parasitic nematofauna in the different soils are shown in Table 6.1. Soils from the improved fallows had higher nematode populations than the soil from the cultivated plot and the natural fallow. Community structure varied with the different cropping systems. The cultivated plot and the crotalaria fallow were dominated by the spiral nematodes, *Scutellonema* spp. while root knot nematodes, *Meloidogyne* spp., were dominant in the *Tephrosia* and *Crotalaria*/*Tephrosia* fallows. In the natural fallow, only root lesion nematodes, *Pratylenchus* spp., were recovered.

6.3.1.2. Crop growth

The origin of the soil had a significant impact on the growth of beans (Table 6.2). With or without fertilisers, bean aerial biomass ($P < .001$) and root biomass ($P = 0.004$) were lower in the *Tephrosia* and *Crotalaria*/*Tephrosia* fallow soils. Maize growth was not affected by the previous cropping systems since the different parameters measured did not show any significant variation within soils.

Both crops responded well to fertilisers independent of the agricultural background. Aerial biomass significantly increased for maize ($P < .001$) and beans ($P < .001$) when fertilisers were added to the soil. The height of the maize plants also increased with the use of fertilisers ($P < .001$). However, response to fertilisers varied slightly with the treatments for both crops as indicated by the significance of the interaction: $P = 0.024$ for bean aerial biomass and $P = 0.044$ for maize height. Bean growth was negatively correlated with the population of root knot nematodes in the soil (Figure 6.1).

6.3.2. Second cycle

6.3.2.1. The parasitic nematode communities at planting

At the end of the first cycle and before planting the second crop, the parasitic nematode communities in the different treatments were characterised (Table 6.3). Nematode populations decreased considerably in the improved fallow soils. *Scutellonema* spp. became dominant in all soils and composed between 39 and 89% of the communities. There was also an appearance of other parasitic genera in the natural fallow soil beside the root lesion nematodes.

6.3.2.2. Crop growth

Crop growth was significantly different in the 5 soils and for both crops (Table 6.4). Bean biomass was lower in the improved fallow soils compared to the maize/beans and natural fallow soils. Maize root biomass and plant height were also significantly reduced in the *Crotalaria* and *Crotalaria*/*Tephrosia* mixed fallows. Response to fertilisers was positive for both maize and beans regardless of the soil. However, the additional root growth of maize and beans due to fertilisers varied slightly from one soil to another (see interaction). Bean root biomass and maize plant height reduced with increasing populations of *Scutellonema* spp.(Figure 6.2).

6.3.3. Third cycle

6.3.3.1. The nematode communities at planting

The parasitic nematofauna in the beginning of the third cycle was mainly composed of root lesion nematodes, root knot nematodes and spiral nematodes, *Scutellonema* spp. (Table 6.5). The densities of root lesion nematodes were similar to those in the beginning of the second cycle. Root knot nematodes reduced considerably while *Scutellonema* spp. increased substantially in the *Crotalaria* fallow soil. The relative abundance of *Scutellonema* spp. increased in the different soils since it composed between 57 and 97 percent of the nematode communities.

6.3.3.2. Crop growth

Due to poor growth, the bean roots were not taken into consideration in the analysis. The bean aerial biomass did not show any variability between soils (Table 6.6). On the contrary, maize growth was different on the different soils. Better growth was recorded in the maize/bean and natural fallow soils compared to the improved fallow soils. The fertilisers did not have any significant impact on maize growth. The latter was negatively correlated with the population of *Scutellonema* spp. (Figure 6.3)

6.3.3.3. Nematode communities at the end of the experiment

At the end of the third cropping cycle, root lesion, root knot and spiral nematodes were the main components of the nematode communities (Table 6.7). The density of *Scutellonema* spp. increased considerably in the natural fallow soil to be in the same order as in the other soils. The nematode communities had almost the same structures in all the 5 soil groups.

6.3.4. Tolerance limit of crops to nematodes

Table 6.8 summarises the Seinhorst equations fitted to different nematode-crop combinations in the three crop cycles. In the first crop, beans were highly sensitive to root knot nematodes and reduction in aerial biomass occurred in low *Meloidogyne* populations, as shown by the low tolerance limit (T = 0). However, root biomass was generally low and significant reductions could only be observed at relatively high populations (T = 5040). In the second crop, damage on both maize and beans was mainly associated with *Scutellonema* spp. and significant losses were noticeable when these nematodes reached a density of 1010 individuals per litre of soil. Tolerance of maize to *Scutellonema* spp. declined in the third crop, as significant growth loss could be observed at a density of 295 individuals per litre of soil.

6.4. Discussion

6.4.1. Impact of plant-pathogenic nematodes on crops

This study confirmed the detrimental effect of nematodes, on maize and beans, the two most widely cultivated food crops in western Kenya. In the first cycle of the experiment, bean growth was severely hampered by root-knot nematodes, *Meloidogyne* spp., even where soil fertility was adequate. The sensitivity of beans to root-knot nematodes is well known. Experimental work in Kenya (Ngundo and Taylor, 1974) and in Columbia (Mullin *et al*., 1991) established that these nematodes were responsible of up to 60% loss. Maize did not suffer from nematodes in the first cycle but substantial losses in maize growth were observed in the second and third crops. The negative correlation between maize biomass and the populations of spiral nematodes, *Scutellonema* spp., suggests that these nematodes played a prime role in the poor growth of the crop. Beans were also affected by spiral nematodes in the last two cycles of the pot experiment.

The devastating nature of root-knot nematodes (Plate 6) is known worldwide. Root galling and hypertrophy are the main features of the root knot nematode attack on plants, which constitute a diversion of plant biomass and production (Sharma *et al*., 1997). Damage by these nematodes is often exacerbated by secondary infections by other pathogens. Root knot nematodes are known to interact with fungal diseases such as *Fusarium* wilt or *Rhizoctonia solani* Kühn, constituting synergistic complexes, which may have a more damaging effect than the sum of the independent effects (Powell, 1979; Wallace, 1983). The spiral nematodes are comparatively little known.

Although *Scutellonema* is a polyphagous genus common in tropical agroecosystems, reports on extensive crop loss due to this nematode are few. About 120 species of plant-parasitic nematodes including *Scutellonema* spp. have been found associated with maize (Bridge *et al.*, 1995; Sharma *et al.*, 1997). However, the most common nematodes known to damage maize are root-lesion nematodes, *Pratylenchus* spp. In western Kenya, these nematodes are abundant in the maize/beans fields and in the crotalaria fallows, and cause sizable yield losses to maize (Desaeger and Rao, 2000b). In this study, however, no relationship was observed between root lesion nematodes and maize or beans. Curiously, the poor growth of maize was related to the strong presence of *Scutellonema* spp. The effect of these spiral nematodes on crops is still controversial but this study showed clearly that they can occasionally be a serious yield limiting factor. For example, in the rain-fed agroecosystems of West Africa, crop loss due to nematodes is mainly attributed to *Scutellonema cavenessi*, which dominates the parasitic nematofauna (Germani *et al.*, 1984; Baujard and Martiny, 1995).

6.4.2. Nematodes and plant nutrients

In the present study, fertilisers substantially improved growth of beans and maize resulting in increased aerial and root biomass. However, the results showed that the response of both crops to fertilisers was sometimes less effective in the presence of some species of pathogenic nematodes. The interactions between nematodes and plant nutrients have been widely studied. It is known that improved plant nutrition can buffer crops from pest attack or mitigate their damage (Norton, 1978; Simon and Rovira, 1985; Melakeberhan *et al*., 1988). Although the role of plant nutrients on individual nematode species is still a subject of controversy, application of fertilisers often allows crops to better withstand nematode pressure, and the resulting expansion of the root system can increase the number of nematodes in the soil. On the other hand, nematodes can interfere with nutrient uptake by plants because of the damage they inflict to the root systems (Taha, 1993; Desaeger and Rao, 2000b). This probably explains the poor performance of beans in the soil with a high infestation of root knot nematodes.

6.4.3. Changes in the nematodes communities

Tremendous changes occurred from the beginning to the end of the experiment. First, there was a dramatic reduction in plant-parasitic nematodes from the initial field populations to the first cycle. Such a decrease can be explained by two main factors. On one hand, cultivation of lands results in declining nematode populations owing to the perturbation of the habitat, the degradation of the soil physico-chemical properties and the erosion of the food resources (Bongers and Bongers, 1998). On the other hand, the experiment was conducted in pots, which represent microcosms that can support much lower populations of nematodes than the natural fields. However, there was an exception since in the maize/beans soil, nematode counts augmented instead of reducing. In the natural fallow soil, there was a decrease in the total number of nematodes, but the number of parasitic species increased. Since there was no contact between pots and therefore contamination was ruled out, these nematodes were obviously present in the field soil either in inactive forms or at populations too low to be recovered in the extraction (Seinhorst, 1962; Jones, 1969). Such low populations may not cause any harm to the first crop, but can multiply and constitute pathogenic populations when susceptible crops are planted in successive cycles.

The nematodes that decreased most during the experiment were the endoparasites, especially *Meloidogyne* spp., which were predominant in the *Tephrosia* and *Crotalaria/Tephrosia* fallow soils. This drastic reduction was probably due to the high sensitivity of beans to these nematodes. An early assault of *Meloidogyne* spp. on the bean seedlings triggered an intraspecific competion, which resulted in the destruction of the root system of the plant and a self-starvation of nematodes. This was aggravated by the fact that maize is not a suitable host for root knot nematodes in East Africa (Whitehead, 1969; Desaeger and Rao, 1999). The progressive dominance of *Scutellonema* spp. over the nematode communities was certainly favoured by their polyphagous nature and their ability to resist adverse conditions better than the other nematodes. In the end of the experiment, there was a stabilisation of the nematode communities with a tendency to a monogeneric structure. The total number of nematodes was almost the same in the different soils and *Scutellonema* became largely dominant in all the communities.

6.4.4. Changes in nematode pathogenicity

Crop damage was observed in the 3 cycles of the pot experiment as a result of nematode attack. In the first cycle, beans suffered substantial losses, and regressions showed that these losses were mainly due to *Meloidogyne* spp. Because of the high sensitivity of beans, adequate soil fertility did not prevent root knot nematodes from damaging the crop. This was evidenced by the low tolerance limit. The spiral nematodes, despite their high populations in some soils, did not have any negative impact on beans. Maize did not suffer any losses in the first cycle.

In the last two cycles, beans as well as maize, showed some sensitivity to *Scutellonema* spp. Maize became even more sensitive in the third cycle, when probably because of an advanced state of soil degradation, the crop was no longer responsive to fertilisers. It is known that the sensitivity of crops to nematodes increases as the soil gets exhausted, which makes understanding the role of nematodes with regards to yield reduction so difficult (Cadet and Floret, 1999). Nevertheless, this study showed that if plant-pathogenic nematodes are controlled, significant yield increases can be obtained in supposedly exhausted soils. Therefore, the significance of plant-parasitic nematodes in land productivity should by no means be underrated.

Simulating crop production in pots has its own limitations (Cadet and Floret, 1999). In this experiment, attempt was made to minimise those shortcomings by using natural field soils and intercropping maize and beans, the most popular food crop association in western Kenya. In the last few years, substantial nematological work has been conducted in the area and the nematofauna of the maize-based cropping systems and their damage potential is fairly well known (Desaeger and Rao, 2000b). However, while comprehensive knowledge exists on the role of root knot and root lesion nematodes in reducing yields, little is known on the damage function of the spiral nematodes. Root knot and root lesion nematodes comprise aggressive species, which can damage crops even when soil fertility is high (Luc *et al.*, 1990). On the other hand, spiral nematodes are less pathogenic and may not have a major impact in good soil conditions. This difference of pathogenicity could be explained by the nutritional behaviour of the nematodes. While root lesion and root knot nematodes are endoparasites whose mode of association with plants severely disturbs the nutritional function of the root system, the activity of ectoparasites such as spiral nematodes usually results in isolated single cell damage (Siddiqi, 1986). However, despite their high pathogenicity, root knot and root lesion nematodes may be relatively easier to manage through crop rotation because of their relative selectiveness towards the crops and fallow trees/shrubs cultivated in western Kenya. In the long term, the spiral nematodes could be more problematic owing to their indiscriminate abundance in the improved fallows, their polyphagous nature and their ability to maintain high populations in the soil.

Table 6.1. Structure of the field plant-parasitic nematode communities in different cropping systems

Nematodes	Maize/beans field	Natural fallow	*Crotalaria* fallow	*Tephrosia* fallow	*Crotalaria*/*Tephrosia* fallow
Pratylenchus					
Abundance (litre of soil)	560	800	1840	0	1200
Relative abundance (%)	17	100	10	-	12
Meloidogyne					
Abundance (litre of soil)	160	0	320	5600	5200
Relative abundance (%)	6	-	2	67	52
Scutellonema					
Abundance (litre of soil)	1840	0	14560	2480	3680
Relative abundance (%)	57	-	76	29	36
Helicotylenchus					
Abundance (litre of soil)	0	0	720	0	0
Relative abundance (%)	-	-	4	-	-
Rotylenchulus					
Abundance (litre of soil)	640	0	1520	320	0
Relative abundance (%)	20	-	8	4	-
Total	3200	800	18960	8400	10080

Table 6.2. Comparison of some agronomic parameters of maize and beans grown on soils with different nematode communities in the first cycle

	Aerial biomass (g)		Root biomass (g)		Plant height (cm)[1]
	Beans	Maize	Beans	Maize	
Cropping system					
Maize/beans	1.64	2.93	0.47	2.07	7.33
Natural fallow	2.18	4.00	0.53	1.04	7.65
Crotalaria fallow	1.25	3.85	0.47	0.68	7.64
Tephrosia fallow	0.70	4.02	0.24	0.98	7.89
Crotalaria/Tephrosia	0.80	4.25	0.41	0.79	7.45
P	< .001	0.409	0.004	0.544	0.578
LSD	0.39	1.45	0.15	1.79	0.71
Fertiliser					
With	1.71	5.81	0.438	1.59	8.68
Without	0.91	1.82	0.407	0.63	6.51
P	< .001	< .001	0.492	0.094	< .001
LSD	0.25	0.92	0.09	1.13	0.45
Interaction					
P	0.024	0.332	0.339	0.577	0.044

The data used for the ANOVA are the square roots of the initial data

LSD = Least significant differences of means

[1] Was only measured for maize

Table 6.3. Community structure of plant-parasitic nematodes in the different soils in the beginning of the second cycle

Nematodes	Maize/beans	Natural fallow	*Crotalaria* fallow	*Tephrosia* fallow	*Crotalaria/Tephrosia* fallow
Pratylenchus					
Abundance (litre of soil)	108	183	150	75	192
Relative abundance (%)	3	32	5	5	7
Meloidogyne					
Abundance (litre of soil)	708	108	117	375	342
Relative abundance (%)	20	19	4	23	12
Scutellonema					
Abundance (litre of soil)	2667	225	2842	1133	2225
Relative abundance (%)	74	39	89	69	78
Helicotylenchus					92
Abundance (litre of soil)	108	58	67	42	3
Relative abundance (%)	3	10	2	3	
Total	3591	574	3176	1625	2851

Table 6.4. Comparison of some agronomic parameters of maize and beans grown on soils with different nematode communities in the second cycle

	Aerial biomass (g)		Root biomass (g)		Plant height (cm)[1]
	Beans	Maize	Beans	Maize	
Cropping system					
Maize/beans	1.44	3.54	0.26	1.55	8.78
Natural fallow	1.89	4.76	0.40	1.85	9.19
Crotalaria fallow	1.15	4.17	0.19	1.64	8.21
Tephrosia fallow	1.12	4.03	0.24	2.08	8.80
Crotalaria/*Tephrosia*	0.82	3.02	0.21	1.31	8.18
P	< .001	0.322	0.007	0.007	0.032
LSD	0.36	1.71	0.12	0.42	0.72
Fertiliser					
With	1.16	5.81	0.22	2.04	9.59
Without	1.41	1.82	0.29	1.33	7.67
P	0.033	< .001	0.066	< .001	< .001
LSD	0.23	1.08	0.07	0.26	0.46
Interaction					
P	0.240	0.312	0.023	0.005	0.604

The data used for the ANOVA are the square roots of the initial data

LSD = Least significant differences of means

[1] Was only measured for maize

Table 6.5. Community structure of plant-parasitic nematodes in the different soils in the beginning of the third cycle

Nematodes	Maize/beans	Natural fallows	*Crotalaria* fallows	*Tephrosia* fallows	*Crotalaria/Tephrosia* fallows
Pratylenchus					
Abundance (litre of soil)	147	128	187	40	220
Relative abundance (%)	4	25	3	3	12
Meloidogyne					
Abundance (litre of soil)	380	94	13	327	60
Relative abundance (%)	12	18	-	24	3
Scutellonema					
Abundance (litre of soil)	2760	295	6633	1000	1553
Relative abundance (%)	84	57	97	73	85
Total	3287	517	6833	1367	1833

Table 6.6. Comparison of some agronomic parameters of maize and beans grown on soils with different nematode communities in the third cycle

	Aerial biomass (g)		Root biomass (g)	Plant height (cm)
	Beans	Maize		
Cropping system				
Maize/beans	0.55	1.753	0.79	7.45
Natural fallow	0.74	2.212	0.92	8.43
Crotalaria fallow	0.48	1.211	0.56	6.92
Tephrosia fallow	0.42	1.739	0.64	7.48
Crotalaria/Tephrosia	0.62	1.679	0.63	7.45
P	0.519	< .001	0.012	0.001
LSD	0.38	0.40	0.22	0.66
Fertiliser				
With	0.34	1.755	0.68	7.64
Without	0.78	1.712	0.73	7.46
P	< .001	0.919	0.512	0.398
LSD	0.24	0.25	0.14	0.42
Interaction				
P	0.719	0.372	0.016	0.132

The data use for the ANOVA are the square roots of the initial data

LSD = Least significant differences of means

Root biomass and plant height were only measured for maize

Table 6.7. Community structure of plant-parasitic nematodes in the different soils in the end of the third cycle

Nematodes	Maize/beans	Natural fallows	Crotalaria fallows	*Tephrosia* fallows	*Crotalaria/Tephrosia* fallows
Pratylenchus					
Abundance (litre of soil)	93	120	173	87	87
Relative abundance (%)	4	9	9	5	4
Meloidogyne					
Abundance (litre of soil)	7	100	33	160	100
Relative abundance (%)	-	8	2	8	4
Scutellonema					
Abundance (litre of soil)	2180	1073	1667	1707	2153
Relative abundance (%)	96	83	89	87	92
Total	2280	1293	1873	1954	2340

Table 6.8. Seinhorst regression model $y = y_m(m) + y_m(1\text{-}m)z^{(Pi\text{-}T)}$ relating nematodes and some agronomic parameters of maize and beans in the three cycles

	Fitted equation	m	y_m	R^2
First cycle:				
Meloidogyne/bean aerial biomass	$y = 0.74 + 1.44 \times 0.997^{(Pi\text{-}0)}$	0.34	2.18	0.99
Meloidogyne/bean root biomass	$y = 0.00 + 0.49 \times 0.999^{(Pi\text{-}5040)}$	0.00	0.49	0.95
Second cycle:				
Scutellonema/maize height	$y = 8.39 + 0.80 \times 0.995^{(Pi\text{-}1010)}$	0.91	9.19	0.69
Scutellonema/bean root biomass	$y = 0.22 + 0.18 \times 0.982^{(Pi\text{-}1010)}$	0.55	0.40	0.90
Third cycle:				
Scutellonema/maize aerial biomass	$y = 1.45 + 0.76 \times 0.999^{(Pi\text{-}295)}$	0.65	2.21	0.75
Scutellonema/maize height	$y = 7.22 + 1.21 \times 0.998^{(Pi\text{-}295)}$	0.86	8.43	0.87

y = yield, m = minimum yield, T = tolerance limit, y_m = average yield for Pi < T, z = a constant reflecting nematode damage, Pi = initial nematode density

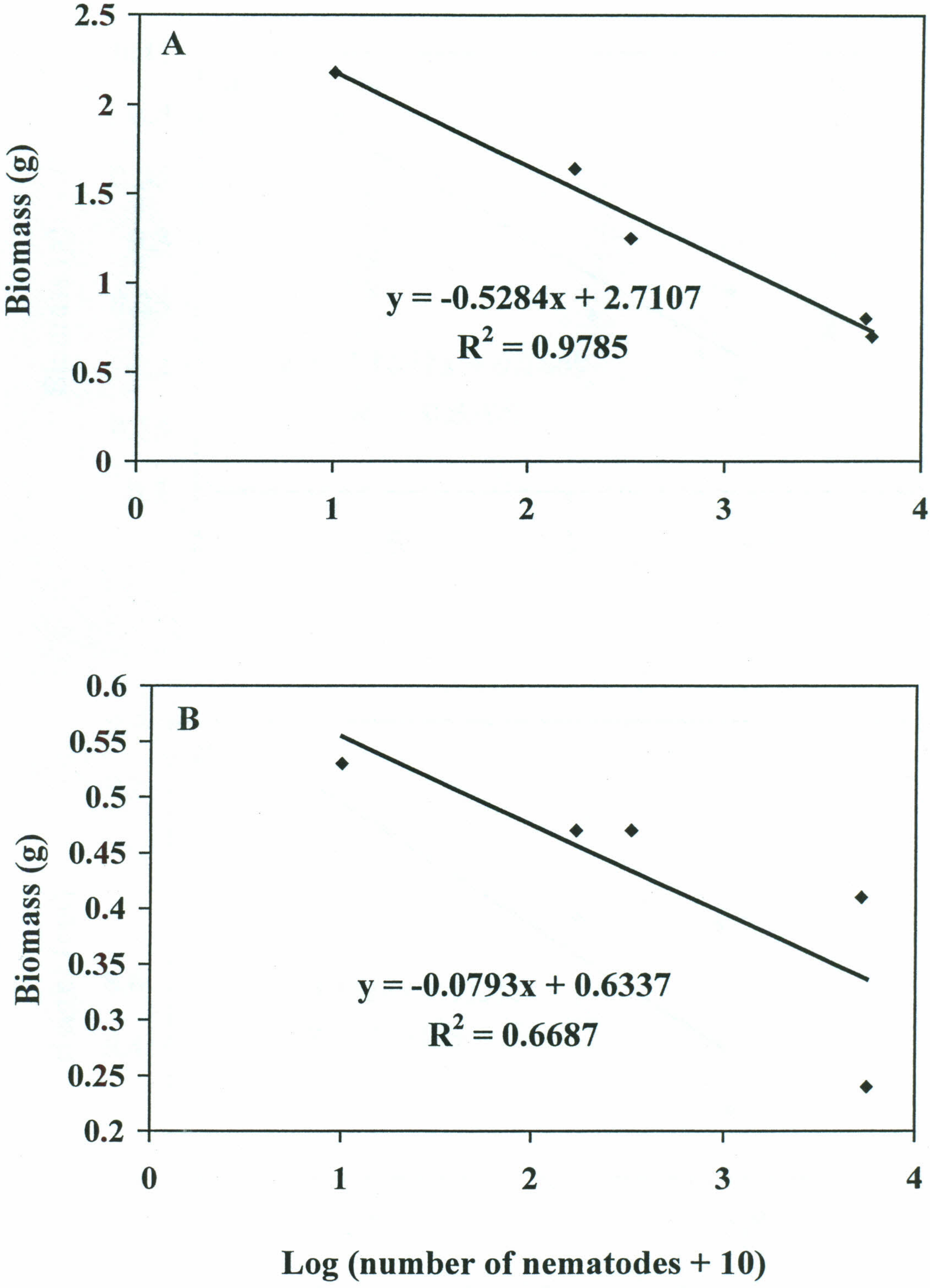


Figure 6.1. Relationship between root-knot nematodes, *Meloidogyne* spp., and bean aerial (A) and root (B) biomass in the first cycle.

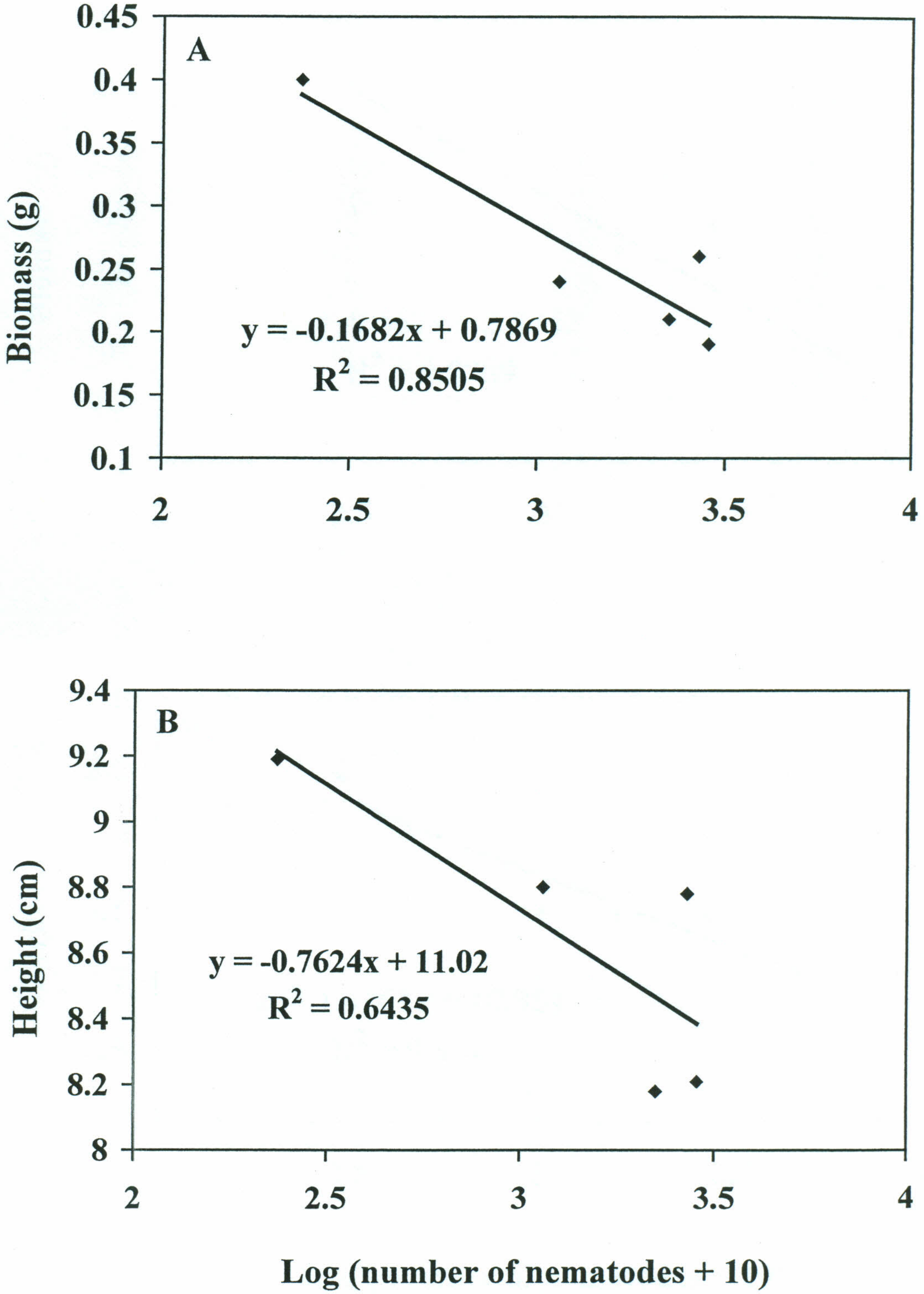


Figure 6.2. Relationship between spiral nematodes, *Scutellonema* spp., and bean root biomass (A) and maize height (B) in the second cycle.

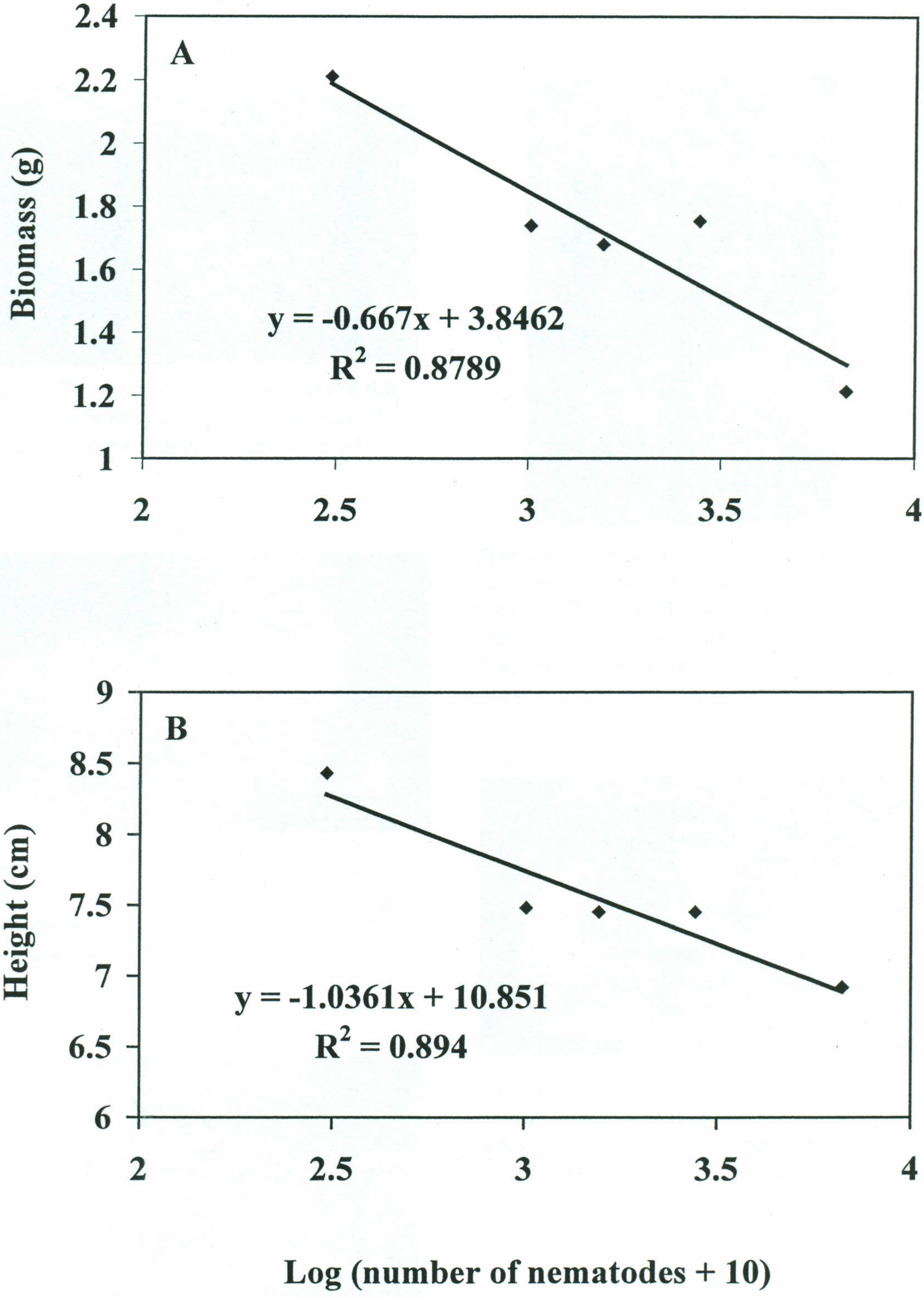


Figure 6.3. Relationship between spiral nematodes, *Scutellonema* spp., and maize aerial biomass (A) and height (B) in the third cycle

Plate 6.a. Pot experiment on the study of the community pathogenicity of nematodes on maize and beans (Photo Serigne Kandji).

Plate 6.b. Nematode damage on *Sesbania sesban*: the seedling on the right side was grown on root-knot nematode infested soil (Photo Serigne Kandji).

Plate 6.c. Yellowing and early maturing of beans (left) due to root knot nematodes compared to control (right) (Photo Serigne Kandji).

Plate 6.d. Early stunting of beans on tephrosia soil (right) as compared to healthy beans on natural fallow soil (left). Root knot nematodes multiply in tephrosia fallows and destroy the following bean crop (Photo Serigne Kandji).

Plate 6.e. Reduction of aerial and root biomass of beans (right) as a result of root knot nematode attack compared to non infested beans (left) (Photo Serigne Kandji).

CHAPTER 7

7.0. GENERAL DISCUSSION AND CONCLUSIONS

7.1. Discussion and conclusions

This study showed that land management had a great influence on the abundance and diversity of plant-parasitic nematodes (Chapter 3). Nematode populations, both parasitic and free-living, more than doubled in the improved fallows compared to the maize/beans fields. The high incidence of plant-parasitic nematodes in the improved fallows is an indication that the woody plant species used are alternative hosts for the nematodes occurring in the croplands (Desaeger and Rao, 1999; Kandji *et al*., 2001). However, this increase in nematode numbers was accompanied by a significant reduction in the number of species constituting the communities. This is due to the fact that the improved fallow trees used are not suitable hosts for all the nematodes found in the fields. For example, while the more polyphagous species like the spiral nematodes infested all improved fallows, the endoparasites were more selective in their parasitism. Root-knot nematodes, *Meloidogyne* spp., parasitised *Sesbania sesban* and *Tephrosia vogelii* but not *Crotalaria grahamiana* while root lesion nematodes, *Pratylenchus* spp., attacked *Crotalaria grahamiana* but not the two other fallow trees (Kandji *et al*., 2001).

There were strong fluctuations in the nematode populations regardless of the plant species (Chapter 4). As observed before (Brown and Kerry, 1987; Nickle, 1991), the peaks of nematode abundance appeared at the onset or in the middle of the rainy seasons while the lowest densities were recorded during dry periods. This study also confirmed the inherent differences associated with the biology of nematodes, which were exemplified by the two dominant genera in the study site. The spiral genus, *Scutellonema*, dominated in the communities at the end of the study because of its intrinsic ability to maintain its populations throughout the year. This agrees with observations made in the Sahelian agroecosystems of West Africa, where *Scutellonema cavenessi* developed mechanisms to resist long dry periods and became the dominant nematode species (Demeure, 1975; Germani *et al.*, 1984). This contrasted with the behaviour of root lesion nematodes, *Pratylenchus* spp., which fluctuated heavily with the seasons. Knowledge of this differential behaviour between species and the general fluctuations of nematodes in relation with the seasons is important in community studies. It appears that soil samples taken in humid periods are more likely to give reliable information than samples taken when the soil is dry. Pre-plant sampling immediately at the onset of the rains is advisable since it can help predict nematode damage and concurrent yield losses with the use of mathematical models. This is the best option if nematode control is the major objective. But if a follow-up is needed for any particular reason, sampling at mid-season or before harvest can provide additional information.

Several mathematical functions have been used to describe the spatial distribution of nematodes in the soil. Almost invariably, nematodes have been recognised as having an uneven distribution and because of that, systematic sampling is among the best sampling patterns recommendable in nematological work. In chapter 5, I was testing grid-sampling, a variant of systematic sampling more and more used in nematology (Delaville, 1995). This method allowed the detection of variabilities in the distribution patterns of the nematodes associated with the agroforestry systems in western Kenya. Most species were concentrated near the plant rows. This phenomenon of aggregation is a particularity of row crops and was observed in other areas such as India (Mehta *et al.*, 1992) and Martinique (French West Indies) (Delaville, 1995). This study also showed a gradual increase of nematode populations following the direction of the slope. Clumping was observed for root-knot nematodes, *Meloidogyne* spp., and the spiral nematodes, *Scutellonema* spp. and *Helicotylenchus* spp. From a practical point of view, these results indicated that systematic sampling could provide a reliable tool if accurate information is needed on the size and species composition of nematode communities. This can be particularly relevant for complex agroecosystems such as the maize/beans-improved fallow rotations of western Kenya, where various plant species are grown in the fields, following precise spatial and temporal patterns.

Finally, I found it relevant to evaluate the effects of the nematode communities that develop during improved fallows on food crops (Chapter 6). Three cycles of pot experiment allowed me to have a better insight on the dynamics of nematode damage on crops. In the first cycle, bean growth was poor on *Tephrosia* soil because of the high incidence of root-knot nematodes. Similar observations were made by Ngundo and Taylor (1974), Mullin *et al.* (1991) and Desaeger and Rao (1999). Maize, on the contrary, did not suffer from nematode attack in the first cycle, which supports the suggestions of

Whitehead (1969) and Desaeger and Rao (1999) that maize is resistant to root knot nematode in East Africa. The fact that the field density of nematodes declined drastically after the first crop of the pot experiment was not surprising. What was more difficult to anticipate, however, was the final dominance of *Scutellonema* spp. in all soils and their damage on maize and beans. The declining tolerance of maize to these spiral nematodes over time validates the hypothesis that crops become more sensitive to nematodes as the soil gets exhausted (Sharma *et al.*, 1997). This is a proof that low yields in degraded soils are not the only result of physical and chemical constraints. Clearly, soil-borne pests such as nematodes play an important role in that.

7.2. Suggestions for further studies

The results of this study have been very informative and add value to the nematological literature that has been gathered over the last few years in western Kenya. But obviously, the nematode issue in the improved fallows of western Kenya is way too complex to be covered in two and half years. Therefore, this study should only be viewed as a stepping stone for further research. The amount and scope of the work to be conducted in the future is certainly open to debate, but I just want to emphasise a few points that could complement this work:

(1) The development of a medium-term program for monitoring nematodes in the improved fallow systems and other agroforestry systems. This will provide much needed information on the inter-annual variations of nematode populations and the dynamics of nematode communities over a

longer period of time. Only then, shall we be able to confidently draw conclusions on the implications of nematodes for the viability of agroforestry in western Kenya.

(2) The study of the role of runoff waters in the field-to-field dissemination of nematodes. I carried out analyses of runoff water samples in which I detected some nematode species. I dropped the experiment because of time pressure, but still believed that such analyses were worth conducting in the future. This will allow for example a better understanding of the mechanisms through which nematodes are spread along a watershed and to see the scope of agroforestry in mitigating this field-to-field contamination. The ORSTOM rain simulator recently introduced at ICRAF can be used even in the absence of natural rainfall.

(3) The elaboration of quantitative tools for the adequate measure of nematode-induced yield losses. This is crucial since there are many (biotic and abiotic) factors in the fields that confound the real effects of nematodes on crops. Also, since nematode communities change over time and crop sensitivity to plant-parasitic nematodes increase with declining soil fertility, assessing the contribution of nematodes in the loss of land productivity can help decide on how many seasons the land should be cultivated after an improved fallow.

(4) The exploration of the potential of nematodes as biological indicators of soil conditions. Although in this study, plant-parasitic nematodes could be related to some soil physical and chemical characteristics, the breakdown of nematodes into trophic groups (plant-parasites, fungivores, bacterivores, predators and omnivores) will be more relevant in ecological studies. Nematode-based descriptors such as Maturity Indices (MI) are more and more used to describe soils and to predict changes in ecosystems.

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