SPATIAL DISTRIBUTION OF SOIL NEMATODES IN THE SUB-ARCTIC ENVIRONMENT OF CHURCHILL, MANITOBA

BY

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ABSTRACT

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The tundra ecosystem, with its frost-molded landscape and large peat reserves, is vulnerable to climate change. Thus, any increase in temperature due to global warming will cause changes in above-and belowground biota. Understanding the linkage between these biotas will help make prediction of the biodiversity and ecosystem functioning when global change phenomena occur, and consequently aid in making management strategies. The role of nematodes in nutrient cycling and decomposition, among many other attributes, make them useful organisms to study soil processes. Associations between plant and nematode communities, from six sites (Berm Face, Berm Crest, Tundra Heath, Polygon, Hummock and Forest) and from within a young, visually homogeneous tundra heath field site, were examined in the subarctic environment of Churchill, Manitoba. The study also provided nematofaunal information, which is very limited in this region. Multivariate analyses of nematode taxa abundance revealed four distinct groupings: Berm Face, Berm Crest, heaths (Tundra Heath, Polygon and Hummock) and Forest. The result showed a parallel relationship between nematode and vegetation assemblages, and thus, a seeming interdependency between above-ground and below-ground biota. Conversely, association between nematode and plant assemblages within a visually homogeneous tundra site was not as obvious. At this fine scale, the heterogeneous nature of edaphic factors and not plant assemblages is hypothesized to influence within-site nematode communities. The thesis also provided results to improve nematofaunal analysis to enhance their utility as bioindicators of soil food webs.

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LIST OF ABBREVIATIONS

α   -   Probability level
μm   -   Micrometer
ANOVA   -   Analysis of Variance
Ba   -   Bacterivore
BC   -   Berm crest site
BF   -   Berm face site
CV   -   Coefficient of variation
c- p   -   Colonizer -persister scale for nematodes
cp 1   -   Enrichment opportunist nematodes
cp 2   -   General opportunist nematodes
cp 3,4 & 5   -   Persister nematodes
EI   -   Enrichment Index
F   -   Fungal- feeding nematode
f:b   -   Fungal to bacterial feeding nematode ratio
Fig.   -   Figure
g   -   Gram
H'   -   Shannon diversity index
L   -   Liter
lb   -   Pound
m   -   Meter
MI   -   Maturity Index
ORF   -   Obligate root-feeder
OV   -   Omnivore
P   -   Probability level
PCA   -   Principal Component Analysis
r   -   Correlation coefficient
RA   -   Root-associated nematode
RDA   -   Redundancy Analysis
SI   -   Structure Index

1. GENERAL INTRODUCTION

Soil is home to magnificently diverse organisms whose spatial distribution varies across and within the earth's landscape. Unravelling the influential factors of such complex spatial patterns has been a major theme of community ecology (Huston, 1994). Biological diversity is a complex phenomenon and cannot be explained by a single process. A range of factors interplays in the patterns of diversity, such as productivity, predation, competition, dispersal and evolutionary history; and all these vary at different spatial and temporal scales (Ettema and Wardle, 2002). There are many studies on the patterns and determinants of biodiversity in above-ground organisms, but the below-ground communities have been oftentimes overlooked despite the fact that they constitute the majority of terrestrial species (Wardle, 2002). Diversity below-ground is several orders of magnitude greater than above-ground organisms (Heywood, 1995). Recognizing the major role of soil organisms in ecological processes in ecosystems, there has been a surge of interest in examining soil communities (Van der Putten et al., 2001; Bardgett and Wardle, 2003). Among soil organisms are the nematodes. Nematodes, being heterotrophs, are ultimately dependent on autotrophs such as plants for energy. Plant species, in turn, differ greatly ecologically, and this is reflected in the quantity and quality of resources that they produce which energize soil food webs (Wardle, 2002).

Plants are important determinants of decomposer function and community composition in soil (Wardle, 2005). Studies have shown microbial composition (Grayston et al., 1998; Bardgett et al., 1999; Marschner et al., 2001), nematodes (Porazinska et al., 2003; Wardle et al., 2003; De Deyn et al., 2004; Viketoft et al., 2005; Viketoft, 2007), collembolans (Salamon et al., 2004; Milcu et al., 2006) and mites (Badejo and Tian,

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1999) varies with the presence of different plant species. Even in the high arctic heath vegetation where growth of plants is limited, collembolans and mites were shown to be influenced by plant species (Coulson et al., 2003). Removal or introduction of plant species have been shown to affect soil biota. In an experimental study in New Zealand pastures, removal of a particular plant species affected the community structure of soil microbes, microbe-feeding and herbivorous nematodes, and arthropods (Wardle et al. 1999; Smith et al., 2003).

1.1. Biological attributes of nematodes

Nematodes as a group possess a number of biological characteristics that make them useful ecological indicators (Freckman, 1988). Nematodes have a permeable cuticle that allows them to respond to varying effects of pollutants and the soil ecosystems' restorative capacity (Wasilewska, 1989). Some nematode species have short generation times that allow them to respond quickly to changes in food supply (Bongers, 1990). Nematoda are found in all soils—even in heavily polluted soil, acidified forests, heavy clay, deep sea sediment, decomposing material and compost. The ubiquity of roundworms reflects change in ecological structure and function of soils in ways more predictable and efficient compared with other soil flora and fauna (Bongers and Ferris, 1999). Nematodes have the ability to enter cryptobiosis, a resistant stage that survived during unfavorable environmental conditions (Bongers, 1990).

Nematodes as a group have a wide trophic diversity that reflects the structure of soil food webs in response to changes in resource availability, as mirrored in shifts of trophic groups. In general, five major trophic groups are recognized: plant-feeders,

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bacterivores, fungivores, predators and omnivores (Yeates et al., 1993). Nematodes have key roles in nutrient cycling and decomposition. Bacterial and fungal feeders occupy a central position in the detritus food web (Moore and de Ruiter, 1991).

1.2. Measures of nematode community structure

In ecological studies, diversity indices such as species richness and species evenness are widely used to assess ecological changes and effects of disturbance and pollution in the ecosystem. These indices are also used in nematode ecological studies. However, this use of nematodes is potentially more informative than use of other groups, because the phylum Nematoda is a large group comprising different life-history strategies that make them respond differently to changes in the environment. A colonizer-persister (cp) scaling involving the ordination of nematode life history strategy based on the ability of taxa to colonize and persist in habitats had been formulated, resulting in the creation of the maturity index (MI; Bongers, 1990). Each nematode family is allocated to a cp scale (1-5) based on that closely related species show similarities with respect to life history traits due to relatedness in phylogenetic lineage, morphology, anatomy, physiology and genetics (Bongers, 1990).

The MI was first successfully developed using nematode data from river pollution studies (Zullini, 1976), an oil spill in Brittany, France (Boucher, 1980), heavy metal studies in the New York Bight Apex (Tietjen, 1980) and from the Clyde estuary (Lambshead, 1986). Presently, there are numerous reports using the MI of nematodes as an ecological indicator. Dr. Tom Bongers (Wageningen University, the Netherlands) has a listing of reports using the MI: http://www.nem.wur.nl/UK/Research/Maturity+index/

Below is a description of the cp continuum and corresponding nematode life history characters. The numbers 1-5 are the corresponding cp scores.

Description of the cp values (adapted from Bongers, 1990):

cp-1: Short generation time, small eggs, high fecundity, mainly bacterivores, feed continuously in enriched media, form dauerlavae as microbial blooms subside

cp-2: Longer generation time and lower fecundity than the cp-1 group, very tolerant of adverse conditions and may become cryptobiotic. Feed more deliberately and continue feeding as resources decline. Mainly, bacterivores and fungivores

cp-3: Longer generation time, greater sensitivity to adverse conditions. Fungivores, bacterivores and carnivores

cp-4: Longer generation time, lower fecundity, greater sensitivity to disturbance. Besides the other trophic roles, smaller omnivore species

cp-5: Longest generation time, largest body sizes, lowest fecundity, greatest sensitivity to disturbance. Predominantly carnivores and omnivores.

The MI is calculated as the weighted mean of the individual cp scores:

$$\text{MI} = \sum_{i=1} v(i).f(i)$$

where $v(i)$ is the *cp* value of taxon i and $f(i)$ is the frequency of that taxon in a sample.

Dr. Tom Bongers made an example that suppose we compare two sites, where site A has 10 species of Rhabditidae (cp-1) and 90 species of Dorylaimidae (cp-4), and where site B has 90 species of Rhabditidae and 10 species of Dorylaimidae. These two families

have different cp values and so result in different MIs in the two sites. However, if we merely use diversity indices, we conclude that the two sites are the same. The nematode ecologist will recognize that site B is a ruderal environment that has been disturbed. The development of the MI was a significant advancement in interpreting the relationship between the ecology of nematode communities and soil function, which made nematode communities widely used as indicators in biomonitoring (Neher, 2001).

An improvement of the MI was made through the creation of a conceptual framework by Ferris et al. (2001) which combined the cp scaling with feeding habits. Within this framework, weighted functional guilds of the nematodes give rise to an Enrichment Index (EI) and a Structure Index (SI) (Fig.1). Ferris et al. (2001) used a weighted system based on the structure and enrichment trajectories in the food web.
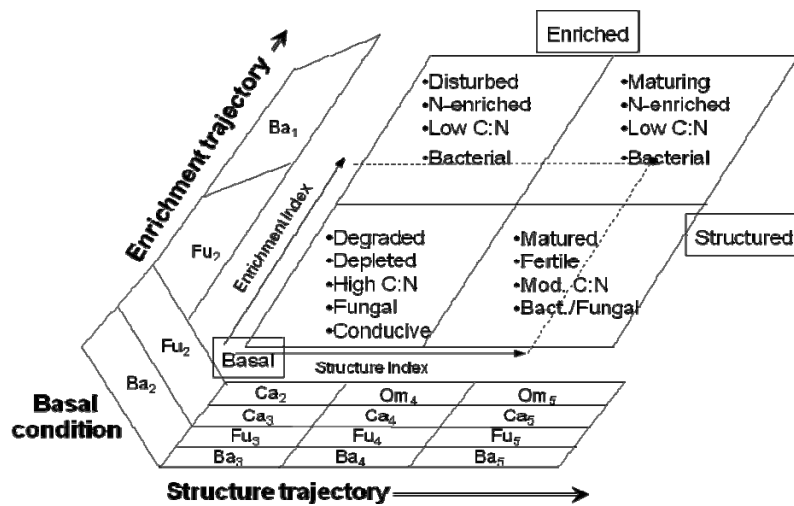
Fig.1.1. Functional guilds of soil nematodes characterized by trophic group- Bacterivore (Ba), Fungivore (Fu), Omnivore (Om) and Carnivore (Ca) and by life history characteristics expressed along a colonizer–persister (cp 1-5 written as subscripts of trophic group) scale (Bongers and Bongers, 1998). Indicator guilds of soil food web condition (basal, structure, enrichment) are designated and weightings of the guilds along the structure and enrichment trajectories are provided, for determination of the Enrichment Index (EI) and Structure Index (SI) of the food web (Adapted from Ferris, et al., 2001).

1.3. The use of nematodes—taxa composition and functional groupings

Nematodes possess several attributes that make them useful ecological indicators (Bongers and Ferris, 1999) and enable them to provide a holistic measure of the biotic and functional status of soils (Neher, 2001). Nematode species composition reflects substrate texture, climate, biogeography, and both natural and anthropogenic disturbances. Nematodes that feed on bacteria and fungi play important roles in influencing the turnover of the soil microbial biomass and thus in the availability of plant nutrients (Bardgett et al., 1999). Decomposition processes in the soil, although ultimately dependent on the plant resource base, are often allocated to either the bacterial-based energy channel, or pathway, or the slower fungal-based channel (Moore and Hunt, 1988). The relative use of bacteria and fungi by nematodes reflects differences in decomposition pathways or channels. Within the constraints of soil type, soil moisture and temperature, the nature of the food resource influences the species and dominance within each nematode trophic group (Yeates, 2003).

1.4. Horizontal pattern of nematodes

Martinus Beijerinck, a famous Dutch microbiologist, suggested that "everything is everywhere, the milieu selects" (De Wit and Bouvier, 2006). This quote means that wherever the environment is favorable for growth, particular microbial organisms are found. This statement is true, not only for microbes, but for other soil biotas that are influenced by the heterogeneous nature of soil. Different groups of organisms have varying spatial pattern as they react differently to soil conditions and resources, and their abundance and activity vary both horizontally and vertically through the soil profile. This

spatial heterogeneity which is observable at the scale of millimeters to hundreds of

meters has been found to be influenced by site gradients and soil properties such as bulk

density, oxygen concentration, moisture etc. (Paul, 2007). However, a dominant role of

soil conditions may not always be the case, as Robertson and Freckman (1995) point out

that they found soil characteristics have a relatively minor influence on spatial variation

of soil organisms. In addition, spatial heterogeneity can be high even in soils considered

relatively homogenous at the plot or field scale (Franklin and Mills, 2003). Heterogeneity

may be even higher in a less disturbed system, because even in a field which was subject

to monoculture cropping and had undergone years of tillage, nematode communities were

still strongly patterned (Robertson and Freckman, 1995).

There is little information about spatial distribution of soil biota. Studies of spatial

heterogeneity have mostly been concerned with the vertical pattern, and not much has

been done on the horizontal pattern, especially on nematodes. Most studies on horizontal

pattern of nematodes were done on agricultural fields and were focused on selected plant-

parasitic species. In addition, there is very limited information about arctic and sub-arctic

nematofauna, let alone their spatial pattern. Among all the terrestrial regions, the tundra

ecosystem is the farthest north that supports terrestrial life. Tundra is also the ecosystem

most vulnerable to climate change (Grogan and Jonasson, 2005). The lower layer of the

tundra soil is permanently frozen and dead organic matter remains undecomposed as

peat: only the upper few centimeters of tundra soil supports the majority of life. Any

increase in temperature due to global warming will increase belowground activities such

as decomposition and precipitate rapid changes in the soil food web and soil community

structure (Coulson et al., 1996). In turn, because of the linkage between belowground and

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aboveground systems, it is expected that this will result to changes in vegetation, which again will cause changes in the soil, and so on.

Hence, this thesis examined spatial variation of nematodes at the ecosystem level (Chapter 2), at the within-site scale (Chapter 3), and the extent of the influence of vegetation composition on this spatial variation. The nematode communities from six sites at the ecosystem level were examined. For within-site scale variation, 93 sample positions in a visually homogeneous field site were used to examine associations of nematode and plant taxa. I looked at the influence of plant species coverage on the nematode assemblages in soil. Chapter 4 is the over-all synthesis discussing the general findings, conclusions and future prospects.

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2. SOIL NEMATODE COMMUNITIES AS INDICATORS OF THE INTER-DEPENDENCY OF ABOVE- AND BELOWGROUND BIOTA IN SUB-ARCTIC TERRESTRIAL SYSTEMS OF CHURCHILL, MANITOBA

2.1. Abstract

Nematodes, because of their attributes and varied key roles in the soil food web and soil nutrient recycling, are ideal organisms for studying the linkage of above- and below-ground processes and biota in terrestrial systems. Information on arctic and sub-arctic terrestrial nematodes is very limited, particularly on the association of nematode and plant communities in natural ecosystems. Thus, this study focused on describing the soil nematode taxa in six sites of a sub-arctic natural ecosystem at Churchill, Manitoba, so as to obtain nematofaunal information and examine associations of nematode and plant taxa. The six sites were chosen from the coast of Hudson Bay going inland. Coastal Sand Dune of contiguous pure stand mat of *Honckenya peploides* (L.) Ehrh. was located at the seaward side (Berm Face), *Leymus arenarius* (L.) Hochst. Next inland (Berm Crest), heaths composed of Tundra Heath, Polygonized Peat Plateau and Hummocky-Eutrophic Fen, and a Spruce-Lichen Forest. A total of 36 nematode taxa identified as 34 genera and 2 families and covering a total of 27 families, were observed at the sites. *Plectus* spp. and *Teratocephalus* sp. were observed to be ubiquitous. Heaths had the lowest total nematode abundance. Berm sites, in contrast to the Forest, had the lowest Shannon diversity index, MI and fungal to bacterial ratio. As revealed by Principle Components Analysis (PCA) and Discriminant analyses, four distinct sites exhibited associations between vegetation and nematode assemblages: Berm Face, Berm Crest, Heaths and Forest. The study showed a parallel relationship between nematode and vegetation taxa, and thus, a seeming interdependency between above-ground and below-ground biota.

2.2. Introduction

The complementary work of above- and below-ground processes in ecosystems makes these processes key drivers of both community- and ecosystem-level functioning for the maintenance of ecosystem properties. As such, understanding this linkage is essential to better understand the ecological consequences over time and space of the interdependent biotic and abiotic processes (Bardgett, 2002). This linkage of above- and below-ground subsystems at the local scale is mainly via plants (Wardle, 2002). Ecologically, plant species differ greatly and this is reflected in the quantity and quality of resources that they produce which affects the decomposer subsystem and the root associated organisms such as root herbivores, pathogens, and symbiotic mutualists (Wardle et al., 2004). The decomposer subsystem in turn affects plants through litter breakdown and soil nutrient cycling, which indirectly regulate plant growth. Plant-feeding organisms directly affect plants as they influence the quality and flow of energy and nutrients between plants and decomposers. Studies of above- and below-ground linkages point out the need for more research on this area (Hooper et al. 2000; Wardle et al., 2004; Bardgett et al. 2005; De Deyn and Van der Putten, 2005).There has been growing interest in understanding the linkage of above-and below-ground feedback, owing to this important ecological process (Wardle, 2005; Van der Putten, 2005).

Recent studies have shown above- and belowground associations, specifically between plant and soil microbial compositions (Grayston et al., 1998; Bardgett et al., 1999; Marschner et al., 2001), nematodes (Porazinska et al., 2003; Wardle et al., 2003; De Deyn et al., 2004; Viketoft et al., 2005; Viketoft et al., 2009), collembolans (Salamon et al., 2004; Milcu et al., 2006) and mites (Badejo and Tian, 1999). Understanding the

ecological roles and interactions among the component species in communities will help us make accurate prediction of the biodiversity and ecosystem functioning when changes caused by anthropogenic and natural disturbances occur (Johnson et al. 1996). Many important attributes of nematodes make them informative organisms to indicate soil ecological processes. Nematodes are not only the most abundant multi-cellular organism on earth, they are diverse and ubiquitous as well. Nematodes do not just have a key role in soil nutrient recycling, but they also occupy most trophic levels in the soil food web, thereby making them useful organisms for soil community and food web studies (Bongers and Ferris, 1999).

The Canadian arctic region has a tundra biome, which is the coldest of all the biomes. The tundra is known for its extremely low temperatures, poor nutrients and frost-molded landscapes. Presence of deep root systems in the vegetation is restricted by ice, and decomposition is slow, thereby resulting in large accumulations of peat. The Hudson Bay Lowland is the second largest peatland system in the world (Rouse et al., 2002). Due to this large carbon storage and presence of permafrost, the arctic region is known to be most vulnerable to climate change (Chapin et al., 1992; Chapin and Korner, 1995). An increase in temperature facilitates rise in decomposition rates due to an increase in soil microbial activity, thus, leading to changes in soil biota and plant community compositions (Nadelhoffer et al., 1992). These characteristics make the arctic region a very interesting site for soil ecological studies.

The nematode communities in different terrestrial habitats and in almost all parts of the world have been widely studied. Yet, information on arctic and subarctic terrestrial nematodes is very limited (Boag and Yeates 1998), particularly in regards to the

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association of nematode and plant communities. Most studies that have examined the influence of plants on soil communities have been done in experimental plots of arable fields and grasslands. The research reported here was done in a natural ecosystem in the sub-arctic environment at the Hudson Bay Lowland in Churchill, Manitoba.

The Hudson Bay Lowland is a complex mosaic of different vegetation and habitats interspersed with small ponds and lakes. Subsequent isostatic rebound resulted in age gradient, which increased in age with distance from the Hudson bay coast, with coastal sand dune being the youngest habitat that emerged from the Hudson bay (Ritchie, 1957). Permafrost and peatland formation coupled with hydrological dynamics resulted in the creation of tundra heath, polygonized peat plateau, fen hummocks and spruce forest, among others (Ritchie, 1956). This area, which is vulnerable to climate change, is an ideal location to study associations of soil food web and vegetation. Six sites were chosen ranging from the coast of Hudson Bay to more inland locations.

The study specifically aimed to:

(1) Provide nematofauna information in this region.
(2) Determine if nematode taxa associate with particular plant communities.
(3) Determine if habitats with similar plant communities but differing origin of soil formation have similar nematode taxa.
(4) Investigate whether nematode taxa from two adjacent patches of differing plant species differ.
(5) Examine associations between nematode taxa.

2.3. Materials and methods

2.3.1. Site description

The study was conducted in the sub-arctic coastal environment located at Churchill, Manitoba, Canada. In July 2008, six sites were chosen from the coast of Hudson Bay going inland: Coastal Sand Dune with contiguous pure stands of *Honckenya peploides* L. Ehrh. intermingled with wave-deposited brown seaweeds of the Phaeophyceae located at the seaward side (Berm Face), *Leymus mollis* (Trin.) Pilg. at the beach berm crest (Berm Crest), Tundra (Heath), Polygonized-Peat Plateau (Polygon), hummocks of a Hummocky-Eutrophic Fen (Hummock) and Spruce-Lichen Forest (Forest). Heath, Polygon and Hummock sites are heathlands or referred to here as heaths dominated by ericaceous plant communities with patches of *Carex* sp. and with a cover of lichens and mosses. Common ericaceous plants in the sites were *Rhododendron lapponicum* (L.) Wahlenb. and *Rhododendron subarcticum* Harmaja, *Empetrum nigrum* L., *Vaccinium vitis-idaea* L. ssp. *minus* (Lodd.) Hultén, *Dryas integrifolia* Vahl., *Arctostaphylos rubra* (Rehder & Wilson) Fernald and *Rubus chamaemorus* L. The Spruce Forest was located more inland from the Hudson Bay and was dominated by *Picea glauca* (Moench) Voss (white spruce) and ericaceous vegetation, with lichen and moss in the understory. The heaths and spruce forest were underlain by different mosses; dense mosses such as *Dicranum* for heaths and mainly loose mosses, like *Sphagnum* for spruce forest. This will give the organic layer being sampled different characteristics such as density, aeration, pore diameter and water holding capacity, among others, which will be affecting the soil food web. Identification of plant communities was done using Johnson (1987).

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2.3.2. Sampling

Sampling was done in July 2008. There were four replicate plots in each site. Each plot had a dimension of 10 m x 10 m wide except for sites Hummock and Coastal sand dune. Since Coastal sand dune sites were not wide enough, each plot could only have a dimension of 10 m x 1 m. The four coastal sand dune plots were at least 150 m away from each other. At the heath site, plots 1 and 2 were 4 m away, and these two plots were separated by a pond about 50 m away from plot 3; plot 4 was about 20 m away from plot 3. For polygonized peat plateau, the first two plots were about 10 m distant from each other and these first two plots were at least 200 m away from plots 3 and 4, which were 30 m away from each other. The four fen hummock plots were at least 100 m away from each other. In the case of the four forest plots, they were at least 150 m distant from each other.

In each replicate plot, 10 soil blocks of 10 cm x 10 cm and 20 cm depth were taken with the use of a flat spade in a zigzag pattern. The ten blocks were bulked and mixed. For Hummock site, each plot consisted of four hummocks of 0.5 m to 1 m high from the water table. In each hummock, with the use of a flat spade, 8 soil blocks of 10 cm x 10 cm and 20 cm depth were randomly taken covering the whole mound. The soil blocks taken from four hummocks in each plot were bulked and mixed. For six sample sites, there were a total of 24 nematode samples. Coastal sand dune sites were entirely mineral, while heaths and Forest were entirely peat soils. A subsample of 500 g was placed in a polyethylene bag and transported to the laboratory in an ice chest, stored at 4ºC, and extracted for nematodes within one week.

2.3.3. Extraction and identification of nematodes

An examination was done to determine the nematode extraction technique that gave maximum nematode recovery for the organic-rich soil of Churchill. A subsample of 50 g soil (wet weight) was used for extraction. From the preliminary investigation (see Appendix 5.1), I found that the best method was to use a combination of Cobb's sieving and decanting using USA Standard Test Sieve 45 and 400 mesh, followed by sugar flotation at a concentration of 1 lb sugar per 1 L of distilled water (Ingham, 1994) and the Baermann pan technique (Townshend, 1963). A Baermann pan was used to extract nematodes from the debris excluded during Cobb's sieving and decanting. Recovered nematodes for a sample were combined from the two techniques to ensure maximum recovery. Total numbers of nematodes were immediately counted using a stereo microscope at 40x magnification and preserved with 4% hot formaldehyde. Temporary mounts of the nematode suspension were made and the first 100 nematode individuals were identified, using a compound microscope at 400 x magnification, to the genus level except for individuals belonging to families Rhabditidae and Tylenchidae following Bongers (1994). Nematodes were then assigned to functional guilds as a combination of feeding habit following Yeates et al. (1993) and cp scaling (1-5) according to Bongers (1990). The guilds identified were: bacterivores-cp1 (Ba_1), bacterivores-cp2 (Ba_2), bacterivores-cp3 (Ba_3), bacterivores-cp4 (Ba_4); fungivores-cp2 (F_2), fungivores-cp4 (F_4); predators-cp4 (PRD_4), omnivores-cp4 (OV_4), omnivores-cp5 (OV_5), obligate root-feeders-cp3 (ORF_3) and root-associated-cp2 (RA_2). Obligate root-feeders are those that are directly feeding on plant roots, while root-associated are from the family Tylenchidae whose feeding habit is still uncertain but are known to be associated and hence thought to

feed on plant roots, algae, moss and fungi. Taxa that were not detected in a site were given an abundance of zero during the analysis. All nematode counts were adjusted for soil moisture to give number of nematodes 100 g^{-1} dry soil.

2.3.4. Data analysis

Nematode fauna in the different sites were characterized using several ecological indices: number of taxa (S); Shannon's diversity index (H' = $-\Sigma p_i$ x $\ln p_i$, where p_i is the proportion of each taxa in a sample) (Magurran, 2004), taxa here refers to genera and two families which may compromise the results; fungal to bacterial feeder ratio (f:b), based on the ratio of number of individuals in each group, which assesses the relative flow of energy and nutrients through the fungal and bacterial channels (Wasilewska, 1979) and Maturity Index (MI). The Maturity Index is based on placing free-living nematode families into a colonizer-persister scale based on life strategies and histories, ranging from 1 to 5 where low values are assigned to families that have a short life span, high tolerance to disturbances and high colonization ability (Bongers, 1990). This life strategy concept was extended by Ferris et al. (2001) with an incorporation of feeding habits, hence the creation of functional guilds. Functional guild analysis provides an indicator of food web condition, structure, functionality and resource availability. To calculate the nematode faunal ecological indices, all genera were assigned weights for indices, according to their classification into functional guilds. An ordination was generated showing structure and enrichment trajectories. The structure trajectory provides an index of competition for resources, stability of environmental conditions resulting in a complex soil food web. The

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enrichment trajectory indicates when there's a flush of resources (energy and nutrients) caused by disturbances and changes in the environment (Ferris et al., 2001).

Enrichment (EI) and Structural (SI) indices were calculated as follows:

$$(1)\ \mathrm{EI} = 100 \times \left(\frac{k_e e}{k_e e + k_b b} \right) \qquad (2)\ \mathrm{SI} = 100 \times \left(\frac{k_s s}{k_b b + k_s s} \right)$$

where e is the abundance of individuals in guilds in the enrichment component weighted by their respective k_e values, b is the abundance of individuals in the basal component (these are ubiquitous nematodes) weighted by their k_b values, and s is the abundance of individuals in the structural component weighted by their k_s values (Ferris et al., 2001; Please refer to Fig. 1.1). The enrichment trajectory thus is a weighted abundance of opportunistic Ba_1 and F_2 nematode taxa that respond rapidly to flushes of microbial activity. The structure trajectory is a weighted abundance of K-strategists and high cp-valued nematodes: Ba_3-Ba_5, F_3-F_5, OV_3-OV_5, PRD_2-PRD_5.

To determine differences in index values for sites, one-way ANOVA was used. Data were examined for homoscedacity using Levene's test prior to analysis. Log (x+1) transformation and arcsine transformation (for proportion and percentages) were performed when necessary. The statistical difference between groups was determined by Tukey's multiple-range test, with $P < 0.05$ indicating significance. Spearman rank correlation analysis was used to determine associations between nematode taxa. The purpose of determining associations was to indicate possible relationships for populations of certain taxa. Principal components analysis (PCA) was used to determine if nematode taxa differed among sites. Discriminant analysis was performed to classify the sites using eight variables comprising all six trophic groups, H' and MI. The program PC-ORD v.5

(MjM Software Design, Gleneden Beach, OR) was used for PCA and STATISTICA v.8

(StatSoft Inc., Tulsa, OK) was used for all other analyses.

2.4. Results

2.4.1. Nematode taxonomic composition, abundance and indices

A total of 36 taxa (from 34 genera and two families) covering a total of 27 families were

observed at the sites. The dominant taxa with ≥90% occurrence across all sites, were

Tylenchidae (comprised of at least 6 genera and 16 morphospecies), *Plectus* spp. and

Teratocephalus sp. Morphospecies referred to here are taxa which appeared to be

markedly different at the morphological level. Table 2.1 lists the nematode taxa found in

the study and the mean abundance of each taxon at each site. The Berm Face (BF) was

highly dominated (~50%) by the r-strategist bacterial-feeder, *Panagrolaimus* sp. This

taxon was followed in much less abundance by the fungal-feeder *Aphelenchoides* sp.,

another r-strategist bacterial-feeder from family Rhabditidae, and the cp-2 bacterial-

feeder, *Heterocephalobus* sp. Berm Crest (BC) was dominated by the obligate plant-

feeder, *Pratylenchus* sp. (~60%), which was absent in BF. Other abundant taxa in the BC

were the same as that of the BF except that BC site lacked *Aphelenchoides* sp. and

Panagrolaimus sp. was rare. Heath (H), Polygon (P) and Hummock (Hk) (inclusively

referred to as Heaths) had about equal abundance of the dominant taxa, namely, root-

associated Tylenchidae, the obligate plant-feeder *Criconemoides* sp., and bacterial-

feeders *Plectus* spp. and *Teratocephalus* sp. The Forest had the highest abundance of

Tylenchidae, which was comprised mainly by the genus *Filenchus*, consisting of ≥eight

morphospecies. The cosmopolitan genus, *Plectus* had highest abundance in the Forest

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and this genus had at least four morphospecies at these sites. Other taxa which dominated

in the Forest were the fungal-feeding *Aphelenchoides* sp., the bacterial-feeding

Teratocephalus sp. and the omnivore *Eudorylaimus* sp.

Table 2.1. Abundance and frequency of nematode taxa and their guild found in each of the six sites.

Guild	Taxon	Frequency (%)	Mean abundance per site (100 g^{-1} soil), n=4					
			Berm Face	Berm Crest	Heath	Polygon	Hummock	Forest
Ba$_1$	*Bunonema* sp.	25	-	159	-	-	13	11
Ba$_1$	*Diploscapter* sp.	21	-	88	-	-	-	40
Ba$_1$	*Panagrolaimus* sp.	29	1561	43	-	-	-	-
Ba$_1$	Rhabditidae	38	363	267	-	-	-	10
Ba$_2$	*Acurobeloides* sp.	67	182	187	34	8	2	71
Ba$_2$	*Anaplectus* sp.	42	74	97	7	-	-	49
Ba$_2$	*Cervidellus* sp.	25	-	-	62	-	3	39
Ba$_2$	*Eucephalobus* sp.	46	214	66	5	3	-	30
Ba$_2$	*Eumonhystera* spp.	71	-	25	27	39	39	58
Ba$_2$	*Heterocephalobus* sp.	46	403	427	-	3	3	-
Ba$_2$	*Plectus* spp.	96	206	193	122	164	130	292
Ba$_2$	*Wilsonema* sp.	25	-	-	-	6	11	64
Ba$_3$	*Achromadora* sp.	25	-	-	14	8	6	-
Ba$_3$	*Bastiania* sp.	21	-	-	66	-	1	48
Ba$_3$	*Metateratocephalus* sp.	42	-	-	13	10	45	220
Ba$_3$	*Odontolaimus* sp.	4	-	-	10	-	-	-
Ba$_3$	*Prismatolaimus* sp.	38	-	-	7	8	123	75
Ba$_3$	*Prodesmodora* sp.	46	-	-	13	28	5	29
Ba$_3$	*Rhabdolaimus* sp.	58	-	-	128	38	40	45
Ba$_3$	*Teratocephalus* sp.	92	62	175	99	73	94	377
Ba$_3$	*Achromadora* sp.	25	-	-	14	8	6	-
Ba$_4$	*Alaimus* sp.	8	-	-	5	-	3	-
Fu$_2$	*Aphelenchoides* sp.	75	509	-	31	102	51	309
Fu$_4$	*Tylencholaimus* sp.	33	-	-	213	-	67	94
PRD$_4$	*Clarkus* sp.	13	-	-	-	7	-	8
PRD$_4$	*Coomansus* sp.	4	-	-	26	-	-	-
PRD$_4$	*Prionchulus* sp.	29	-	-	1	2	43	44
OV$_4$	*Enchodelus* sp.	29	31	-	52	21	-	-
OV$_4$	*Eudorylaimus* spp.	88	78	120	24	18	10	278
OV$_4$	*Mesodorylaimus* sp.	21	-	149	-	-	12	-
ORF$_3$	*Criconemoides* sp.	50	-	-	366	191	209	-
ORF$_3$	*Ditylenchus* sp.	13	-	-	34	5	-	19
ORF$_3$	*Pratylenchus* sp.	17	-	3517	-	-	-	-
ORF$_3$	*Trophonema* sp.	8	-	-	-	16	-	-
ORF$_3$	*Tylenchorynchus* sp.	8	-	-	-	-	253	-
RA$_2$	Tylenchidae	92	147	82	541	231	307	1133

Ba= Bacterivore; Fu= Fungivore; PRD= Predator; OV= Omnivore; ORF= Obligate root-feeder; RA= Root-associated

- is not detected. Nematodes with cp value of five were not detected.

There were great differences in total abundance of nematode numbers among the six sites. Mean total abundance ranged from 900-5000 100 g^{-1} soil, with the BC having the greatest abundance followed by the BF and Forest. The heath sites showed the lowest abundance. Mean abundance of the heaths was significantly different from that of the berms and the Forest sites. There was no significant difference between berm sites and Forest sites. Mean numbers of taxa ranged from 11-16 with the berm sites being the lowest and the Forest the highest, these two showing a significant difference. The Shannon diversity index (H') using number of taxa but not morphospecies was lowest in the berms which were significantly different to that of the heaths and Forest (Table 2.2). The highly abundant sites- berm face, berm crest and Forest were due to dominance of a single taxon and therefore the berms had an expected lower diversity. In the case of the Forest, despite the dominance of one taxon, the Forest had the highest Shannon diversity index because of its higher number of taxa.

Maturity Index values ranged from 1.6 to 2.8. Berm sites had significantly lower MI than the inland sites- Heath, Polygon, Hummock and Forest. Within Berm sites, the BF had a lower mean MI value at 1.58 than 2.05 for the BC. BF was dominated by the cp-1 nematode, *Panagrolaimus*. Furthermore, berm sites did not have predatory nematodes which have high cp values.

In these sites studied, decomposition was predominantly driven by bacteria as manifested by a higher proportion of bacterial:fungal feeders and measured by the f:b ratio. Importance of fungal-feeders in the Forest increased. Due to its high proportion of bacterial-feeders, the BF had the lowest f:b ratio. The f:b ratio in the BC was zero due to

the absence of fungal-feeders. The Forest showed a high ratio of fungal:bacterial feeding

nematodes (Table 2.2).

Table 2.2. Total abundance, diversity and community indices for each of the six sites examined (based on individuals 100^{-1} g soil). Shown are the mean (n=4) and ±1 standard error of the mean in parentheses. Different letters within a column indicate differences between means using Tukey's multiple comparison test.

Habitat	Abundance	# of taxa	H'	MI	f:b
Berm Face	3777 (1432)ab	11 (0.4) a	1.89 (0.10) ab	1.58 (0.04) a	0.14 (0.03) b
Berm Crest	5432 (998) c	12 (0.4) a	1.44 (0.06) a	2.05 (0.10) b	0.00 (0.00) a
Heath	1747 (456) a	15 (1.7) a	1.96 (0.19) ab	2.85 (0.10) d	0.19 (0.07) b
Polygon	978 (723) a	13 (1.0) a	2.10 (0.09) b	2.51 (0.06) c	0.24 (0.10) b
Hummock	1193 (462) a	14 (1.1) a	2.02 (0.15) ab	2.72 (0.04) cd	0.18 (0.09) b
Forest	3343 (404) ab	16 (1.2) a	2.19 (0.16) b	2.74 (0.07) cd	0.31 (0.06) b
			Probability		
ANOVA	0.0001	ns	0.001	<0.00001	0.01
Contrasts					
berms vs. heaths[1]	0.0005	ns	0.05	0.0001	ns
berms vs. Forest[1]	ns	0.03	0.04	0.0002	0.04
heaths vs. Forest[1]	0.03	ns	ns	ns	ns

[1] using unequal n honest significant difference (HSD) which is a modification of Tukey when n is not equal; berms being Berm Face and Berm Crest (n=8), heaths being Heath, Polygon and Hummock (n=12) and Forest (n=4)
H'- Shannon diversity index, MI- Maturity index, f:b- fungal to bacterial ratio

2.4.2. Nematode trophic groupings and community composition

Trophic group of nematodes also varied with sites (Table 2.3). Marked differences were

found in the adjacent berm sites having mats of *H. peploides* (BF) and *L. arenarius* (BC).

Bacterial-feeders predominated up to 80% of the trophic composition in BF, of which

60% was made up by *Panagrolaimus* sp. Berm Crest was dominated by obligate root-

feeder (~60%), *Pratylenchus* sp., followed by ~30% of bacterial-feeders. It is interesting

to note that the berm sites did not have k-strategist predatory nematodes. These sites also

had a very low proportion of root-associated feeders which are taxa in the family

Tylenchidae. The heaths (Heath, Polygon and Hummock) had a similar proportion of

trophic composition, although root-associated feeders in heath were slightly higher than bacterial-feeders. The Hummock and Polygon sites had the highest proportion of bacterial-feeders followed by root-associated feeders. The heaths also had a high proportion of obligate root feeders which consisted mainly of *Criconemoides* sp. Conversely, the Forest almost had an absence of obligate root feeders; it had a higher proportion of root-associated and bacterial-feeders. Among all the sites, the Forest had higher proportion of fungivores, omnivores (cp-4) and predators (cp-4).

Table 2.3. Percent relative abundance of nematode trophic groups for each of the six sites studied (based on individuals 100^{-1} g soil). Shown are the mean (n=4) and ±1 standard error in parenthesis. Different letters within a column indicate differences between means using Tukey's multiple comparison test.

Habitat	Obligate Root Feeder	Root Associated	Fungivore	Bacterivore	Predator	Omnivore
			relative abundance (%)			
Berm Face	0 (0) a	5 (2) a	11 (2) b	80 (1) b	0 (0) a	4 (1) ab
Berm Crest	64 (3) c	1 (1) a	0 (0) a	31 (3) a	0 (0) a	4 (2) ab
Heath	23 (12) b	33 (5) b	7 (3) a	33 (6) a	1 (1) a	4 (1) ab
Polygon	22 (2) b	25 (5) b	10 (4) b	39 (2) a	1 (1) a	4 (1) ab
Hummock	25 (10) b	27 (3) b	7 (4) a	39 (9) a	1 (1) a	2 (1) a
Forest	1 (1) a	34 (7) b	13 (2) b	43 (6) a	2 (1) a	8 (1) b
			Probability			
ANOVA	<0.0001	<0.00001	0.003	<0.0001	ns	0.02
Contrasts						
berms vs. heaths[1]	ns	0.0001	ns	ns	ns	ns
berms vs. Forest[1]	ns	0.0002	ns	ns	0.03	ns
heaths vs. Forest[1]	ns	ns	ns	ns	ns	0.03

[1] using unequal n honestly significant difference (HSD) which is a modification of Tukey when n is not equal; berms (n=8) heaths (n=12) Forest (n=4)

A scatterplot representation of enrichment and structure indices, as a nematode faunal profile (Fig. 2.1), illustrates distinct differences between sites. The berm sites were positioned distinctly away from the other sites. This separation was due to higher

abundance of r-strategist nematodes (cp-1) resulting in higher enrichment values than other sites. Generally, the inland sites had more nematodes with high cp values (≥ 2.5) resulting in higher Structure Index values.
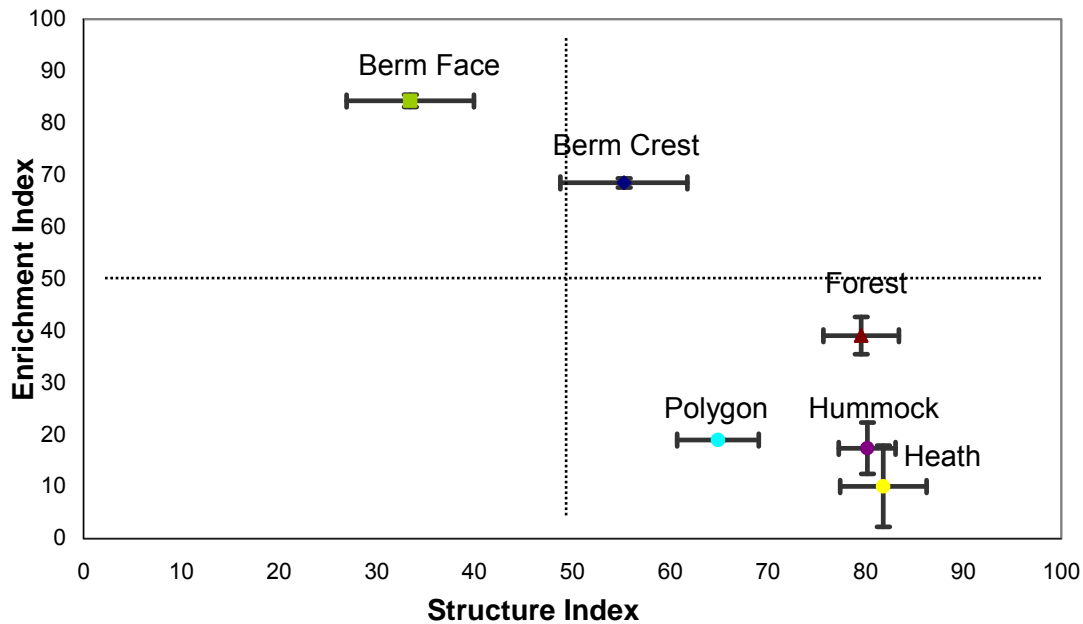
Fig.2.1. Faunal profile showing Structure and Enrichment index values of the soil food web using nematode taxa from the six sites sampled. Shown are the mean (n=4) $\pm$ SE

Multivariate analysis of nematode taxa abundance at the sites clearly showed four groupings; Berm Face, Berm Crest, heaths and Forest (Fig. 2.2 and Fig.2.3). This was shown in PCA analysis on log-transformed nematode taxa abundance (Fig.2.2). The total variation of the first two principal component axes accounted for 56% of the variation in the dataset. Similar result was also shown in Multiple Discriminant analysis (Fig.2.3). Of the eight variables that were subjected to Stepwise Discriminant analysis, only four variables showed to be discriminatory and were MI ($F = 46.3$, $P < 0.001$), RA ($F = 29.1$, $P < 0.001$), ORF ($F = 20.7$ $P < 0.001$) and OV ($F = 15.3$, $P < 0.001$). Fig.2.3 shows the ordination of Discriminant analysis canonical variates 1 and 2 which were statistically

significant at P < 0.001, and accounted for 69% and 22% of the variation in the dataset, respectively. Maturity Index and root-associated taxa were discriminatory in both axes, while obligate root-feeder was only discriminatory in axis 2. Omnivores showed to be discriminating in axis 3 (not shown).
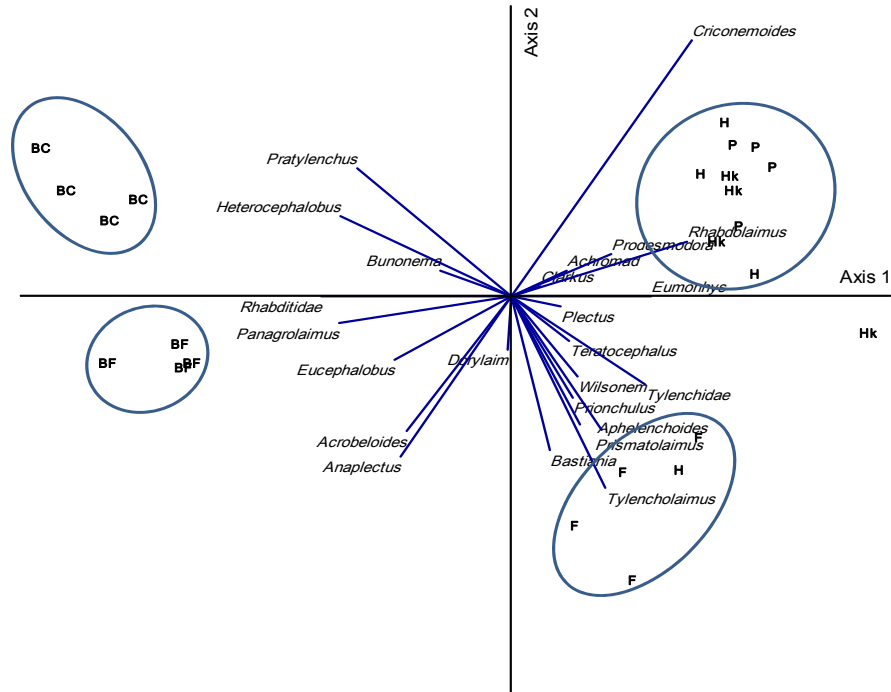
Fig.2.2. Principal Component Analysis of nematode taxa abundance (shown as vectors that correspond to taxa weighting) gave four distinct sites (scores); namely, Berm Face (BF), Berm Crest (BC), heaths (H=Heath, P=Polygon, Hk=Hummock) and Forest (F). Principal Component axes 1 and 2 explained 44% and 12 % of variation, respectively.
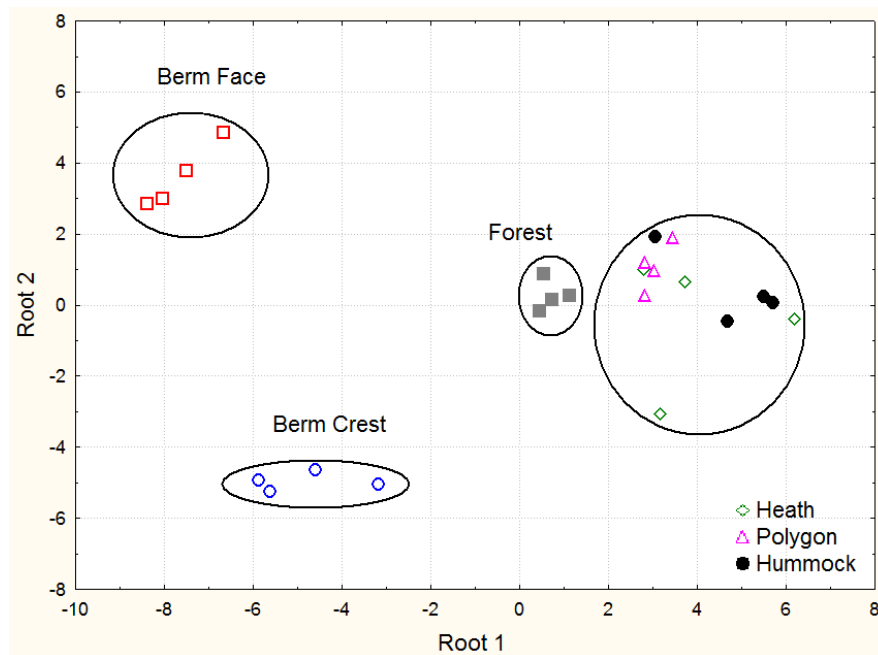
Fig.2.3. Multiple Discriminant analysis plots of the first 2 canonical variates, accounted for 69% and 22% of the variation in the dataset, respectively (P < 0.001, n=4). Four distinct sites are evident; Berm Face, Berm Crest, Forest, heaths based on three discriminatory variables: maturity index, obligate root-feeders, root-associated.

2.4.3. Taxonomic associations

Correlation analysis (P < 0.05) was used to examine associations between taxa from the heath and Forest sites since these sites had similar nematode taxa. Root-associated Tylenchidae were positively correlated with the taxa *Tylencholaimus* sp. and *Eudorylaimus* sp. The obligate root-feeder, *Criconemoides* sp., was negatively correlated with the cp-3 bacterial feeding nematodes, *Teratocephalus* sp. and *Metateratocephalus* sp. *Teratocephalus* was positively correlated to *Metateratocephalus* sp., both members of family Teratocephalidae. *Metateratocephalus* sp. was positively correlated with another cp-3 bacterial-feeder, *Prismatolaimus* sp. Fig.2.4 shows the relationship between *Criconemoides* sp. and *Metateratocephalus* sp., these were taxa with the highest correlation coefficient. This revealed that correlation coefficients although statistically

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significant were not robust and that the relationships were inconclusive, thus,

interpretation should be taken with caution.

Table 2.4. Spearman rank correlation coefficient (r) of taxa inland sites, Heath, Polygon, Hummock and Forest.

Nematode taxa	Tyl	Cri	Pris	Met
Tylenchidae (Tyl)	-	-	-	-
Criconemoides sp. (Cri)		-	-	-
Prismatolaimus sp. (Pris)			-	-
Metateratocephalus sp. (Met)		-0.58 (0.02)	0.55 (0.03)	-
Teratocephalus sp. (Tera)		-0.50 (0.05)		0.50 (0.05)
Tylencholaimus sp. (Tyls)	0.57 (0.02)			
Eudorylaimus sp. (Eud)	0.55 (0.03)			

Only significant correlations at P < 0.05 are shown, P value given in parenthesis
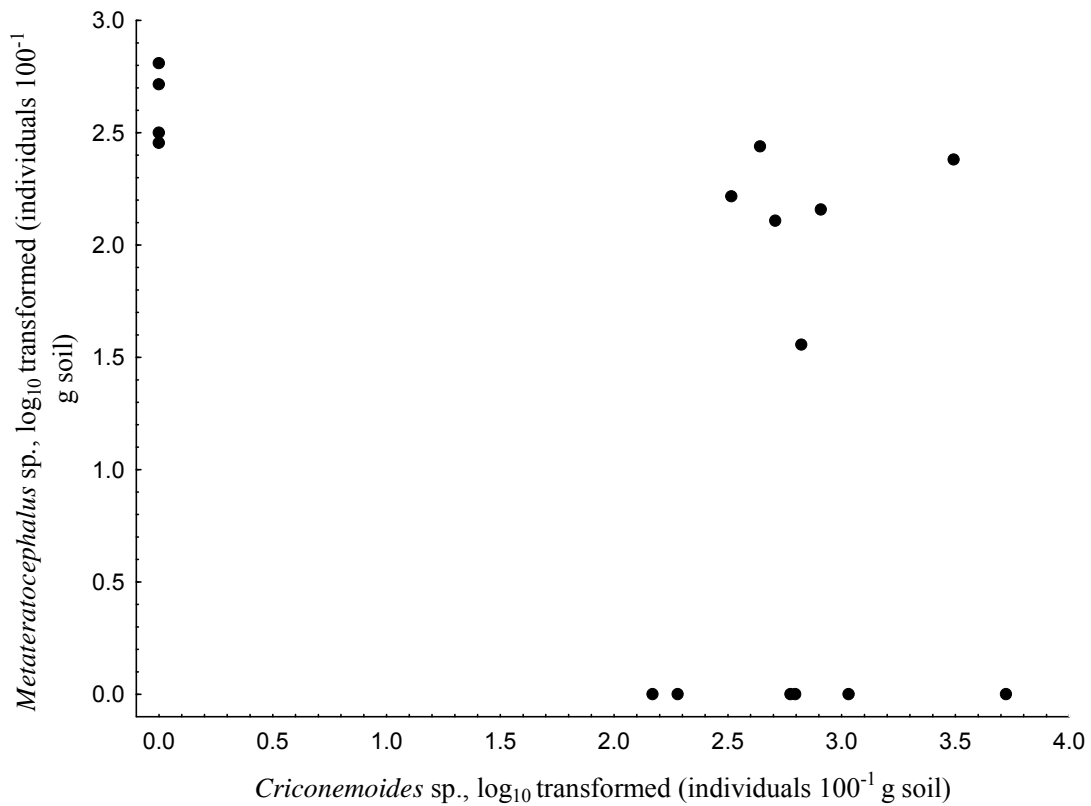
Fig.2.4. Relationship between *Criconemoides* sp. and *Metateratocephalus* sp. in inland sites. Spearman (r) = -0.58, P < 0.05, n=16

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2.5. Discussion

2.5.1. Nematofauna

Hitherto, there are very limited published reports regarding arctic and sub-arctic nematode taxa distribution. This study provided information on the nematofauna of six sub-arctic sites.

A worldwide survey on nematode biodiversity in the terrestrial ecosystem was done by Boag and Yeates (1998) where they pointed out that species richness is influenced by sampling intensities. An intensive sampling (sampling of an area from various vegetation on a frequent basis) from five arctic tundra habitats averaged 81 species (Procter, 1979; Procter, 1984). Another intensive sampling that was done at 14 tundra habitats in Siberia gave 162 species (Kuzmin, 1976). Intensive sampling from various habitats of Ellesmere Is., Canada (see Spaull, 1973) and Spitzbergen, Svalbard archipelago, Norway (Loof, 1971) gave 75 and 89 species, respectively (Boag and Yeates, 1998). The mean species richness for a single sampling occasion was 29.2. Similarly, this study which is a single sampling had an average of ~27 morphospecies.

With regard to taxa composition, the family Tylenchidae is ubiquitous and is oftentimes found in high abundance in terrestrial ecosystems (Bongers et al., 1989). The ubiquity of *Plectus* spp. and *Teratocephalus* sp. is noteworthy in this study. *Plectus* is a cp-2 while *Teratocephalus* sp. *is* a cp-3 nematode. In subarctic heathland and sub-antarctic moss sites, Plectidae were the dominant group of bacterial-feeding nematodes (Spaull, 1973; Yeates, 2003). *Plectus* spp. dominate many high latitude terrestrial nematode fauna (Procter, 1984). *Plectus* spp. and *Teratocephalus* sp. were the most abundant genera in the fauna of Swedish tundra soil (Sohlenius and Bostrom, 1999a).

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Plectids accounted for 70% of the specimens collected by Cobb in1921 from the Canadian Arctic and Alaska and contributed five of the 11 species recorded from the Antarctic continent (Timm, 1971; Procter, 1984). This implies their high adaptability or ability to evolve rapidly in response to their environment. The similarity of ubiquitous nematodes in a cold environment may be due to similar characteristics that enable them to survive in this extreme environment, such as cold-stress genes. Plectidae is a cosmopolitan taxon according to Yeates (2003) and some species are better adapted to extreme conditions. A species of *Plectus* from the Antarctic region has been studied for its genetic-based responses to desiccation and freezing (Adhikari et al., 2009).

2.5.2. Vegetation effects

Nematode assemblages showed strong indication of vegetation differences. This association was revealed by the PCA and Discriminant analysis results. Vegetation was found to have important influence on nematode assemblages.

2.5.2.1. Berm sites

The berm sites had the highest nematode abundance which was due to a single dominant taxon, *Panagrolaimus* sp. for berm face, while *Pratylenchus* sp. for berm crest. Coupled with a lower number of taxa, this led to a lower diversity (H'). The berm sites were also characterized by a low Maturity Index which was due to dominance and abundance of cp1 and cp2 taxa and absence of K-selected predators which have high cp values. The berm being the foremost beach dune of a retreating shoreline of Hudson Bay (Ritchie,

1956), is a young, exposed and disturbed ecosystem. These characteristics explain why taxa adapted to this environment dominate and flourish, like cp1 and cp2 taxa. However, the absence of predators in this study is in contrast with the results of Wall et al. (2002) wherein two predatory species, *Clarkus papillatus* (Bastian) Jairajpuri and *Mylonchulus* sp., represented 27% of the fore-dune nematode community of a beach site in Scotland. A high percentage of predators were also reported from coastal sand dunes in Poland (Goralczyk, 1998). The Scottish and Polish sites however differ from the berm sites studied here in not being subject to isostatic rebound and gradual retreat of the shoreline.

It was also interesting to note that in this study, marine nematodes were not detected in the coastal sand dune site, which recently emerged from the Hudson Bay. A reconnaissance that was done in Aug 2007 at another coastal sites showed abundance of taxa from the family Monhysteridae, However, the taxa in this family could either be marine, limnic or terrestrial nematodes (Fonseca and Decraemer, 2008).

Berm sites, being dominated by a single plant species, were separated from the multi-plant species sites: Heath, Polygon, Hummock and Forest. Berm Face (BF) and Berm Crest (BC) had contiguous mats of *H. peploides* and *L. mollis*, respectively. Despite being adjacent, their nematode taxa were different.

The Berm Face had a dominance of the r-strategist, cp-1 bacterivore (an ephemeral r-strategist), *Panagrolaimus* sp. The Berm Face sites, located on the seaward side of the berm is subject to influence by high tides and storms, depositing organic materials, especially the brown seaweed of the Phaeophyceae, *Fucus disticus* L. from Hudson Bay. The algae are visibly intermingled with *H. peploides* which may be a source of decomposable material to support microbial growth. Thus, this organic enrichment may

have caused the high dominance of *Panagrolaimus* sp. On Signy Island, Antarctica,

Panagrolaimus dominated the areas frequented by birds and seals (Spaull, 1973).

Similarly, a particular species, *Panagrolaimus davidi* Timm, was restricted to coastal

sites associated with penguin colonies and ornithogenic soil (Porazinska et al., 2002).

This taxon belonging to the lowest category (cp-1) of the colonizer-persister (cp)

continuum has a short generation time and high metabolic activity where population

grows explosively upon enrichment or microbial blooms (Bongers, 1990). During such

periods of increased food availability, *Panagrolaimus* belonging to family

Panagrolaimidae along with families Rhabditidae and Diplogasteridae can make up >50%

of the total nematode fauna of soil (Yeates, 2003). They form dauer larvae when the

environment is no longer favourable. Dauer larvae were not found in the samples

examined. These cp-1 nematodes were also found to be tolerant to pollution and

chemical-induced stress (Korthals et al., 1996; Bongers and Ferris, 1999; Neher, 2001;

Tenuta and Ferris, 2004).

The Berm Crest site, which was vegetated with *Leymus mollis*, was dominated by

the endoparasitic obligate root-feeder, *Pratylenchus* sp. This site had the highest

nematode abundance among all sites, but low diversity due to dominance of this taxon.

The high abundance of this site agrees with the finding in the arctic tundra of Siberia,

where highest nematode abundance occurred in grass stands among 14 sites (Kuzmin,

1976). *Pratylenchus* spp. are specialist feeders of plants. Further, they can be a parasite of

coastal sand dune grasses e.g. *Ammophila arenaria* L. Link and *Leymus arenarius* (Van

der Putten and Van der Stoel, 1998; Brinkman et al. 2004; Rodriguez-Echeverria et al,

2009).

There was an absence of fungivores in the Berm Crest even though *Leymus mollis* at the site is known to form association with arbuscular mycorrizhal fungi (AMF) (Dr. Terence McGonigle, pers. comm.). *Leymus arenarius,* a European dunegrass and old name of *Leymus mollis* was observed to be in association of AMF in Iceland (Greipsson and El-Mayas, 2000). The migratory endoparasite, *Pratylenchus,* overwhelmingly dominated the berm crest sites of Hudson bay. Root herbivory by *Pratylenchus* might have affected the AMF association because some AMF species are known to decline in response to herbivory more than others (Klironomos et al., 2004). Species of *Pratylenchus* are known to have different effects on AMF communities (Rodriguez-Echeverria et al., 2009). Hence, fungal grazing by nematodes might have been affected. A more plausible explanation for the lack of fungal-feeders, is that *Eudorylaimus,* known to be omnivore and predator (Yeates et al., 1993), may be the fungal-feeder in this habitat. This taxon was suspected to be a fungal-feeder in dune sites of Machair, Outer Hebrides, Scotland (Dr. Roy Neilson, pers. comm.). The taxon, *Eudorylaimus*, was also speculated to be feeding on a wide variety of microorganisms in high latitude habitats (Lagerloff et al., 1975; Freckman and Virginia, 1998).

2.5.2.2 Heath sites

The heaths (Heath, Polygon and Hummock) although geographically separated and likely having different origins of soil formation, had a similar soil characteristic, which is peat overlying ice or water. This similar soil contributes to the formation of similar vegetation, which is ericaceous plants underlain by mosses and lichens with patches of *Carex* spp. The heaths have similar nematode taxa and are distinct from Forest sites. There was one

heath plot though that was grouped within Forest sites as shown in the principal

component analysis graph (Fig. 2.2). This was due to the plot's absence of

Criconemoides, a taxon with high weighting and abundant in the other heath plots. The

particular plant species where *Criconemoides* is associated with, may have been scarce or

absent in that particular plot.

The high similarity between geographically isolated sites but with similar

vegetation and edaphic factors was also found by Norton and Hoffmann (1974) for plant-

parasitic nematodes in the three major vegetations from four northeastern and three

midwestern states in the USA. Thus, the dictum of Beijerink is still as true as at the time

it was presented. Even though sites are geographically separated, because vegetation is

similar, the nematode communities were also similar.

The heaths were found to have high proportion of the obligate root-feeder,

Criconemoides sp. This taxon may either feed on roots of ericaceous plants or on *Carex*

sp. Generally, obligate plant-feeders show higher abundance on graminoids than forbs

(De Deyn et al., 2004; Viketoft et al., 2005).

In terms of ecological indices (Table 2.2), the heaths were similar except that the

polygon had significantly lower MI than that of the heath. The Low MI value for the

polygon was due to more than twice higher mean abundance of the cp-2 fungivore,

Aphelenchoides sp., compared with heath. The Heath had twice higher mean abundance

of root-associated Tylenchidae compared with the polygon (Table 2.1). Members of the

Tylenchidae may be fungivores (Okada, 2005). Thus, *Aphelenchoides* sp. was likely the

main fungivores in the polygon, while nematodes in the Tylenchidae were likely the

fungivores in heaths.

2.5.2.3 Forest

The Forest site, although with an understory that was vegetated with ericaceous plants just like the heaths, is possibly functionally different due to the presence of *Picea glauca* trees, giving it distinct nematode taxa from the heaths. The forest sites, being furthest inland and likely the oldest of the sites, and also being a more complex and functionally diverse ecosystem than the rest of the sites had greater resource quantity and quality inputs. These features of the forest sites support taxa with wide trophic levels, resulting in a more complex assemblage of nematode taxa, and consequently, a complex soil food web structure. Thus, forest had the highest nematode diversity among the sites and the highest MI.

Conifer litter has high lignin and polyphenol content (Northup et al., 1995). Wasilewska et al. (1981) noted that higher lignin content is associated with higher densities of fungivore nematodes in soil.

Obligate root-feeders were absent in the Forest site. This site however had a high proportion of plant-associated feeders, the Tylenchidae. The feeding habit of Tylenchidae is still uncertain. Nematodes in this family are reported to be moss, algal and root ecto-parasites (Hooper, 1974; Andrassy, 1976; Siddiqi, 1986; Yeates et al., 1993) and recently, several species of the genus *Filenchus* were observed to be capable of reproduction on fungal mycelium (Okada et al., 2005). The absence of obligate plant-feeders could be ascribed to the absence of *Picea* roots in the soil sample or it could be because there were not many plant species in the site which are associated with plant feeders.

There was a trend of increasing proportion of omnivores in the Forest compared with the other sites. There was also a trend of hyphal-feeder increase which may indicate

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that fungi have a proportionally greater role in the Forest than the rest of the sites. Decomposition processes in soil are grouped either as bacterial-based energy channel or as the slower fungal-based channel (Moore and Hunt, 1988). Since nematodes graze on bacteria and fungi, they can be used as an indicator of decomposition pathways or channels in different natural ecosystems or agro-ecosystems with differing management practices (Ruess, 2003; Yeates, 2003). Several authors (Wasilewska, 1979; Sohlenius and Sandor, 1987; Freckman and Ettema, 1993; Neher and Campbell, 1994) proposed the ratio of fungal- to bacterial-feeding nematodes (f:b) as an indicator of decomposition pathways. The Forest had the highest f:b in this study which implied an increase in the importance of the fungal-feeders in this site (Wasilewska, 1979). The Trophic grouping found here supported this trend by showing a proportional increase of fungivores in the forest ecosystem.

2.5.3. Associations among taxa

Although association of taxa in this study was equivocal which was shown in Fig. 2.4, I still consider the results valuable information for nematode ecology. For instance, with the positive associations of Tylenchidae with *Tylencholaimus* sp. and *Eudorylaimus* sp., it can be extrapolated that these three taxa might be preying on the same food resource or that they may have similar ecological requirements. *Tylencholaimus* sp. is a known fungivore, while Tylenchidae and *Eudorylaimus* sp. were speculated to be also feeding on fungi (Okada, 2005; Freckman and Virginia, 1997). Positive association of *Teratocephalus* sp. and *Metateratocephalus* sp., genera belonging to family Teratocephalidae, showed that they were ecologically similar. These two bacterial-

feeding genera were shown to be in negative associations with the obligate root-feeder, *Criconemoides* sp. This negative association might be due to different ecological preferences of family Teratocephalidae and *Criconemoides* sp. Other known reasons of negative and positive associations between taxa may be specialized niche selection, competition, plant species' effects through differences in litter quality, and influence of soil environmental characteristics. Some of the reasons of increased observations of positive associations may be that a system has more microhabitats or that species may have highly overlapping resource requirements, and these characteristics facilitate coexistence of species even at an indefinite time without competitive exclusion to occur (Huston, 1994). Increased positive associations of nematodes in similar guilds may mean high functional redundancy in the system, which is important in this environment vulnerable to climate change by serving as an ecological buffer. Functional redundancy in soils may explain why decomposition processes are maintained even in highly disturbed soils (Lawton et al., 1996; Ettema, 1998).

2.5.4. Implications for climate change

This study showed a strong influence of vegetation on nematode community and consequently, to the soil food web. This change in nematode taxa had been observed not only in association with plant communities, but also in reaction to different microclimatic conditions (Ruess et al., 1999; Sohlenius & Bostrom, 1999b; Sinclair, 2001; Hoschitz and Kaufmann, 2004).

    With global warming, the increase in temperature may result in changes in soil microbial activity. Hence, a change in the nematode community and soil food web as a

whole. Changes in structure of vegetation and soil food webs are expected. Plant communities having intimate relationships with nematode taxa will be most affected. It is projected and inevitable that climate change will lead to vegetation change (Thomas et al., 2004). With vegetation change, there comes a change in the below-ground food web.

For instance, there was a dominance of *Pratylenchus* in BC, and its effect may be exacerbated by climate change. Climate change may result in imbalance in the ecological dynamics of the sand dune causing it to have weak resistance and resilience against plant pathogens, such as *Pratylenchus*. *Pratylenchus penetrans* Cobb was found to cause malfunctioning of roots, lowered vigour of plants and the eventual die-out of coastal sand dune grasses resulting to destabilization of dune sites (Van de Putten & Troelstra, 1990; Seliskar and Huettel, 1993).

Warming may facilitate increased growth and production of *Leymus mollis,* since it was reported to increase plant growth associated with the lengthening of the active growing season in the northern environments (Myneni et al., 1997). Such case may increase fecundity of *Pratylenchus* sp. resulting in their population growth. *Pratylenchus* sp. is a migratory endoparasitic nematode and follows the common nematode life cycle of four juvenile stages before it transforms to the adult stage (Moens and Perry, 2009). All life stages of *Pratylenchus* feed on their host' cortical tissue without establishing a permanent feeding site and move out to infect a new host. Parasitism by these nematodes result in cell death and necrotic lesions in host tissue, hence the common name, root lesion nematodes (Moens and Perry, 2009). These necrotic lesions are making the roots more susceptible to infection by other pathogens in the soil (LaMondia, 2003).

The typical duration of *Pratylenchus* life cycle is about 35-42 days but this varies with species, such that, *Pratylenchus penetrans*, a cosmopolitan nematode in temperate regions, can range from 30-86 days (Corbett, 1973). Temperature affects the life cycle, e.g. *P. penetrans* on *Cryptomeria* seedlings was completed in 86 days at 15ºC but in only 31 days at 30ºC (Mamiya, 1971). Another temperate nematodes, *Pratylenchus scribneri* and *Pratylenchus alleni* were found to have optimum reproduction at 35ºC in tomatoes and soybeans (Dickerson, 1979). *Pratylenchus neglectus*, also a temperate nematode, was reported to reproduce at a maximum temperature of 38ºC in just 28 days on tobacco (Mountain, 1954), and was shown to have rapid reproduction rate on soybeans at 30ºC (Acosta and Malik, 1979).

Therefore in this study, I hypothesized that higher temperature may possibly cause *Pratylenchus* to complete more generations in a growing season and flourish greater than *L. mollis* can grow roots to evade damage. Thus, with the expected dominance and activity of *Pratylenchus*, *L. mollis* may be in danger of being wiped out and causing destabilization of the foredune.

2.6. Conclusions

This study revealed differences among the nematode taxa of the six sites examined. Four distinct groups were shown; namely, BF, BC, heaths (Heath, Polygon and Hummock) and Forest. There was distinct separation of plant mono-species and multispecies sites. Mono-species systems (such as Berm Face and Berm Crest) had lower Maturity Index, lower diversity and nematode taxa indicative of disturbed and young soil. Inland, older and plant multispecies sites (heaths and Forest) had higher Maturity Index, more diverse nematofauna, and nematode taxa indicative of stable, competitive and older soil. All the sites, except BC, were dominated by bacterivores but a trend for higher abundance of fungivores was found in the Forest, an ecosystem which has a higher functional type (due to the presence of trees) and thus is more complex. The Forest ecosystem has *Picea* needle litter, which seems to undergo fungal decomposition. This study has shown evidence that, even in ecosystems lacking great primary production, there seems to be interdependency of above- and below- ground biota.

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3. SPATIAL DISTRIBUTION OF NEMATODE COMMUNITIES IN A VISUALLY HOMOGENEOUS SUB-ARCTIC TUNDRA FIELD AT CHURCHILL, MANITOBA

3.1. Abstract

A tundra heath site, by visual inspection to be homogenous in plant community composition and topography, was examined for the spatial distribution of nematode taxa and association to plant cover in the sub-arctic coastal environment of Churchill, Manitoba. Soil samples were taken using a 10-cm diameter core to a 10 cm depth along three, 300-m long and parallel transects, for a total of 93 sampling positions. Percent cover of plant species was recorded for each sample position. A total of 45 genera from 27 families were observed from the 93 sample positions. *Filenchus* spp. accounted for 22% of total nematodes observed. Other taxa which were abundant and present with a frequency of 90% or more were *Prodesmodora* sp. *Tylencholaimus* sp., *Malenchus* sp., *Rhabdolaimus* sp.*, Teratocephalus* sp. and *Plectus* spp. The within-field taxonomic variability was very high with more than 80% of the taxa having coefficient of variations greater than 100%. The most abundant taxa in this study were similar to those observed for other subarctic and arctic heath ecosystems. Common features to these ecosystems are a thin, surface, organic horizon and ericaceous/*Carex* vegetation. Within field site associations between plant and nematode communities were also revealed through RDA results, although the associations only accounted for 10% of the variation. This outcome shows the heterogeneous nature of the soil and a suite of edaphic factors are influencing the nematode communities. Considering the within site variability of the field and the nematode guild's spatial distribution, new challenges in the estimation of nematofaunal indices were found.

3.2. Introduction

Soil supports the functioning of terrestrial ecosystems; it contains complex interactions of both above- and below- ground biotic and abiotic components. A major process in soil is the linkage of plants and soil biological communities to regulate ecosystem functioning (Lavelle, 2002). Plants affect soil organisms through the quality of energy resources, such as litter and root exudates, while soil organisms play a major role in nutrient cycling and decomposition, which are very important to provide nutrients for plant growth. Accordingly, spatial patterning of plants is likely influenced by the spatial distribution of soil organisms, and vice versa.

Arctic and sub-arctic tundra are characterized by a frost-molded landscape, and large carbon stocks of peats that are vulnerable to climate change. Climate change will affect plant productivity in these regions (Chapin et al., 1992; Chapin and Korner, 1995). In addition, global warming may cause higher rates of decomposition of soil organic matter. Consequently, dramatic changes on soil biota and plant communities are therefore expected (Phoenix and Lee, 2004). Increased knowledge of the linkage of plant communities and soil fauna in these soils is therefore necessary.

Nematodes, being highly adaptable to environmental conditions, are known to be the dominant invertebrate fauna in the arctic and subarctic regions, and have important roles in soil food webs (Procter, 1990). Nematodes are ubiquitous, abundant and diverse. Nematodes occupy most of the trophic levels in the soil food web. The feeding habits of a nematode are easily inferred from observing anterior feeding structures (Bongers and Ferris, 1999). The previously mentioned attributes are just one of the numerous characteristics that have made nematodes useful organisms in soil community studies.

Examining the associations between nematode taxa and plant communities can be used to assess the linkage of above ground and below ground systems. It is known from several ecosystems that the spatial distribution of soil biota are structured by plant growth, size and spacing, ranging in pattern from centimeters to meters, and is often very patchy (Ettema and Wardle, 2002). Results of the previous chapter of this thesis indicated nematode taxa vary greatly depending on the plant community sampled. However, spatial variation in nematode taxa within a plant community was not examined in the previous chapter of this thesis. This study attempted to continue to unravel the nematodes in the region which are understudied and evaluate the extent of influence of plants on nematodes within a visually homogeneous field.

Typically, soil samples for nematofaunal analysis within a plant community are taken at multiple positions and the samples are bulked. In this way, spatial distribution of nematodes within a sample site is unknown. In this study, I sampled 93 sample positions. This number of sample positions allowed evaluation of the required sample size to reliably estimate the mean value of nematode number accounting for the spatial heterogeneity of the site. Larger sample sizes generally permit more accurate calculation of sample statistics, but sampling is oftentimes limited by time and economic constraints.

The development of MI by Bongers (1990) has made nematodes a widely used bioindicator in terrestrial ecosystems (http://www.nem.wur.nl/UK/Research/Maturity+index/). MI is an arbitrary grouping based on life history strategies of nematode families on a colonizer-persister (cp) scale ranging from cp-1 (r-strategist) to cp-5 (K-strategist). MI was enhanced by Bongers and Bongers (1998) by incorporating feeding habit (Yeates et al., 1993) to obtain a better

understanding of nematode biodiversity and soil functioning. The resolution was further enhanced by Ferris et al. (2001) by assigning weightings to each functional guild in relation to enrichment and structure of the food web (Pls. refer to Fig.1.1). However, these weightings for EI (Ba_1) and SI (OV_4, OV_5, $PRED_4$, $PRED_5$) may greatly magnify variation effects of these guilds on inferences from nematode faunal analysis. Knowing the impact of variation and error in estimating mean abundance for functionally important nematodes impacting EI and SI will provide a recommendation as to the optimal number of samples to improve the utility of nematodes as bioindicators.

To improve the use of nematode communities as indicators of soil condition, more observations are needed to know their ecology; however, arctic and subarctic nematodes are understudied and underrepresented particularly in their relationship to plants. Assessing the spatial distribution of nematode taxa is useful in understanding the ecology of nematodes, their population dynamics in relation to their environment and food resources as well as other soil ecological processes. Considering the ecological services that this group of organisms provides to the soil ecosystem, prediction of possible consequences due to global change phenomena (e.g. climate change) can be made (De Deyn and Van der Putten, 2005).

This study used a visually homogeneous tundra field site to: (1) provide information on nematode taxa and their within site distribution; (2) test if uncertainty in determining abundance of low abundant taxa, which are functionally important, introduces error in assessment of soil food web structure; (3) examine the extent of influence of plant species cover on distribution of nematode taxa; and (4) determine

associations among nematode taxa to provide an understanding of their ecology, niche and resource partitioning.

3.3. Materials and methods

3.3.1 Site description and sampling

The study was conducted in a visually homogeneous field in the sub-arctic coastal region of Churchill, Manitoba in August 2008. The site was located along Launch Road, 18 km east of the town of Churchill. The site was situated 300 m SW of the former Churchill Rocket Range twin radar system (locally known as the "Golf Balls") on the south side of Launch Road at coordinates 58.75°N and 93.94°W. The site was chosen for its apparent homogeneity in plant composition and flat terrain. It was ensured that within the three 300 m long transect, there was not any presence of other plant covers, such as taller shrubs and dwarf trees near the sample points that may strongly influence the soil being sampled. The presence of a sand layer below 10 cm of peat indicates the site is of relatively young lichen-heath vegetation because of the proximity of Hudson Bay being just 1 km north of the site. Lichen and moss was common as ground cover. Ericaceous plants dominated the vascular flora of the site including *Andromeda polifolia* L*., Rhododendron lapponicum* L*., Vaccinium uligonosum* L*., Arctostaphylos rubra* (Rehd. & Wils.) Fern. with *Dryas integrifolia* (M.) Vahl., *Saxifraga aizoides* L., *Saxifraga oppositifolia* L*., Tofieldia pusilla* (Michx.) Pers. and *Carex* sp. occasionally present.

Sampling was done in August 2008. Three 300-m parallel transects, 2 m apart from each other, were established using a measuring tape and hand-held GPS unit (Garmin GPS 60). One person held an end of the measuring tape, a second person held the other

end, a third person held the center making sure that the tape was kept straight against the strong wind coming from the bay and the fourth person marked the sample positions with wooden stakes inserted into the soil. Each transect had 31 sample positions, with spacing varying from 10cm to 50m distance from each other (Fig.1).The layout of the transect was recommended by Dr. Steven Siciliano (Soil Science, University of Saskatchewan), leader of the Soils Group in the CICAT, IPY project to match transects sampled at two arctic sites studied by the group. This layout is done for geostatistical analysis which will be done later.
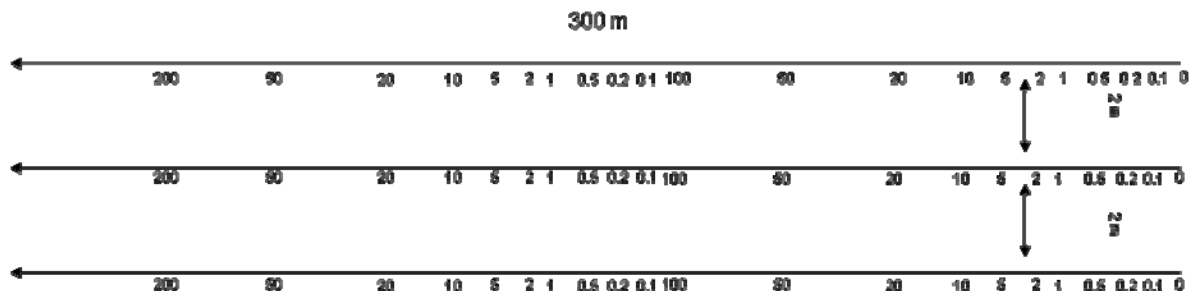
Fig. 3.1. Transect design. Distribution of sample positions repeated three times in each of the three transects.

Walking on or near transect sample positions was avoided to prevent trampling damage. Soil sampling positions were situated to the right of each marker. Two teams of two people were involved in the sampling. One team was charged with vegetation cover examination while the other team was charged with soil sampling. Percent cover of plants within the area of the core was estimated by visual inspection. A 10 cm diameter cutout in cardboard was placed to the right of the position marker. Identification of vascular plant taxa in the cutout was done using Johnson (1987). A polyvinyl chloride (PVC) core (10 cm diameter x 10 cm height) was then inserted to the right of the position marker

where vegetation cover had been recorded. A 5 cm thick piece of lumber was placed on top of core and the lumber pounded to ground level. With the core flush to the ground, another core was placed on top and the pounding was continued so the first core was driven 0.5 to 1cm below the soil surface. The core was gently extracted using a trowel. After which, the trowel was placed under the core while it was gently lifted out to prevent loss of soil. The faces of the core were then trimmed with a knife and the soil was placed inside a labeled polyethylene bag. The core was immediately placed inside an ice chest. Soil sampling was aseptically done by cleaning each core after every sampling position with water and ethanol. In the laboratory, the soil for a sample position was mixed by hand and partitioned into equal subsample weights for nematode analysis, soil property determinations, and microbial molecular community analysis. The present study presents the nematode examination. Soil for nematode examination was stored at $4^{o}C$. Nematodes were extracted from soil within one week of sampling.

3.3.2. Extraction and identification of nematodes

A subsample of 50 g soil (wet weight) was used for extraction of nematodes. Nematodes were extracted from soil using Cobb's sieving and decanting method. Screens used in the procedure were USA Standard Test Sieve 45 and 400 mesh. Nematodes collected on the 400 mesh screen were separated from soil debris by density separation in sugar at a concentration of 454 g sugar L^{-1} (Ingham, 1994). The total number of nematodes was immediately counted using a stereo microscope at 40x magnification, and then the nematodes were preserved in hot 4% formaldehyde. A temporary microscope slide mount of the nematode suspension was made and the first 100 individuals identified using a

compound microscope at 400 x magnification and genus determination done following

Bongers (1994). Nematode taxa were then assigned a functional guild following Ferris et

al. (2001). A functional guild was a combination of feeding habit (Yeates et al., 1993)

and colonizer-persistor (cp) scaling (1-5) according to Bongers (1990). This resulted in

the following guilds: bacterivores-cp1 (Ba_1), bacterivores-cp2 (Ba_2), bacterivores-cp3

(Ba_3), bacterivores-cp4 (Ba_4); fungivores-cp2 (Fu_2), fungivores-cp4 (F_4); predators-cp4

(PRD_4), omnivores-cp4 (OV_4), omnivores-cp5 (OV_5) , obligate root-feeders-cp3 (ORF_3)

and Root-associated-cp2 (RA_2). All nematode counts were adjusted for soil moisture to

give number of nematodes 100 g^{-1} dry soil. Taxa that were not detected in a sample were

recorded as having a number of zero. The Maturity Index (Bongers, 1990) and Shannon

diversity index (H') (Magurran, 2004) were used to characterize the nematode taxa for

the site.

3.3.3. Data analysis

All descriptive statistics (Mean, Frequency, coefficient of variation (CV), standard

deviation, standard error and Spearman rank correlation analysis) were done using

STATISTICA v.8 software package (Statsoft Inc., Tulsa, OK.). CANOCO v.4.5

(Microcomputer Power, Ithaca, NY) was used for Redundancy Analysis (RDA).

Redundancy analysis was used to examine the relationship of plant species cover and

nematode abundance. Nematode abundance and plant species cover were the response

and predictor variables, respectively. Total abundance values were log(x+1) transformed

prior to analysis to meet assumptions of normality. To estimate the number of sample

positions required for each nematode guild (Ferris et al., 2001) to obtain a mean

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abundance that is representative of the population within a specified confidence interval, equation described by Petersen and Calvin (1986) was used:

$$n = t_\alpha^2 s^2 / D^2$$

where n is the required sample size, t_α is the Student's t statistic, 1.66 and 1.96 for 90% and 95% confidence levels, respectively; s is the standard deviation of each nematode guild, and D is the specified error limit which is the allowable margin of error of the sample mean. The required number of sample positions at an α of 90% and 95% and with specified error limit of 20% from the sample mean was estimated.

3.4. Results

3.4.1. Taxonomic composition and within-field variability

A total of 45 genera from 27 families were observed from the 93 sample positions (Table 3.1). *Filenchus* spp. of the family Tylenchidae accounted for 22% of the total population of nematodes. Other taxa which were abundant and present with a frequency greater than 90% were, in decreasing order of abundance, *Prodesmodora* sp., *Tylencholaimus* sp., *Malenchus* sp., *Rhabdolaimus* sp., *Teratocephalus* sp. and *Plectus* spp. Only *Filenchus* spp. and *Teratocephalus* sp. were present in all sample positions. The within-field taxonomic variability was very high with more than 80% of the taxa having CVs greater than 100%. Taxa with CVs less than 100% were more abundant and frequent. Taxa in this category were *Acrobeles* sp., *Rhabdolaimus* sp., *Teratocephalus* sp., *Tylencholaimus* sp., *Filenchus* spp. and *Malenchus* sp. The Maturity Index was 2.98 and the Shannon diversity (H') was 2.4.

3.4.2. Trophic groups, functional guild and within-field variability

With the presence of 19 genera, bacterivores were the most abundant trophic group followed by the root-associated nematodes belonging to family Tylenchidae. The number of taxa contained in each trophic group was proportional to the group's abundance. For example, obligate root-feeders had the lowest abundance although containing five taxa. Conversely, root-associated nematodes had four taxa but were the second-most abundant feeding group. Among trophic groups, only predators and obligate root-feeders had CVs greater than 100%.

The guild Ba_1 had only one taxon, *Bunonema*. The guilds Ba_2 and Ba_3 had eight taxa while Ba_4 had two taxa. Two taxa comprised the Fu_2 guild with one for Fu_4. There were three taxa under PRD_4, and eight and three for OV_4 and OV_5, respectively.

Table 3.1 Soil nematode taxa observed in the 93 sample positions. Numbers in bold are total abundance values for a trophic group.

Trophic group	cp	Taxon	Total[1] abundance	Mean[2] abundance	Frequency (%)	Coefficient of variation (%)
			$100 \ g^{-1}$ dry soil			
Ba			**28862**	**310**	**100**	**44**
Ba	1	*Bunonema* sp.	90	1	15	264
Ba	2	*Acrobeles* sp.	2512	27	84	88
Ba	2	*Acrobeloides* sp.	1745	19	81	106
Ba	2	*Anaplectus* spp.	427	5	35	187
Ba	2	*Cervidellus* sp.	126	1	13	361
Ba	2	*Eucephalobus* sp.	63	1	8	384
Ba	2	*Eumonhystera* spp.	812	9	70	107
Ba	2	*Plectus* spp.	2902	32	91	104
Ba	2	*Wilsonema* sp.	1256	14	84	101
Ba	3	*Achromadora* sp.	876	9	67	114
Ba	3	*Bastiania* sp.	686	7	60	139
Ba	3	*Metateratocephalus* sp.	495	5	49	144
Ba	3	*Odontolaimus* sp.	282	3	37	151
Ba	3	*Prismatolaimus* sp.	1349	15	76	110
Ba	3	*Prodesmodora* sp.	6851	74	98	94
Ba	3	*Rhabdolaimus* sp.	4386	47	96	63
Ba	3	*Teratocephalus* sp.	3812	41	100	58
Ba	4	*Alaimus* sp.	29	0.3	3	563
Ba	4	*Amphidelus* sp.	162	2	24	200
Fu			**5555**	**60**	**99**	**70**
Fu	2	*Aphelenchoides* sp.	295	3	44	131
Fu	2	*Aphelenchus* sp.	31	0.3	4	508
Fu	4	*Tylencholaimus* sp.	5229	56	97	75
PRD			**847**	**9**	**71**	**104**
PRD	4	*Coomansus* sp.	427	5	44	149
PRD	4	*Eurystomina* sp.	70	1	11	330
PRD	4	*Mylonchulus* sp.	351	4	43	146
OV			**3224**	**35**	**99**	**79**
OV	4	*Ecumenicus* sp.	129	1	17	287
OV	4	*Enchodorus* sp.	227	2	15	275

Trophic group	cp	Taxon	Total[1] abundance	Mean[2] abundance	Frequency (%)	Coefficient of variation (%)
			100 g^{-1} dry soil			
OV	4	*Eudorylaimus* sp.	413	4	39	196
OV	4	*Epidorylaimus* sp.	298	3	35	169
OV	4	*Labronema* sp.	955	10	66	118
OV	4	*Mesodorylaimus* sp.	293	3	23	292
OV	4	*Prodorylaimus* sp.	584	6	45	170
OV	4	*Thornia* sp.	27	0.3	3	691
OV	5	*Aporcelaimellus* sp.	242	3	29	182
OV	5	*Aporcelaimus* sp.	44	0.5	5	446
OV	5	*Thornenema* sp.	13	0.1	1	964
ORF			**546**	**6**	**31**	**199**
ORF	3	*Ditylenchus* sp.	18	0.2	3	556
ORF	3	*Hemicycliophora* sp.	425	5	23	226
ORF	3	*Merlinius* sp.	37	0.4	3	615
ORF	3	*Trophonema* sp.	41	0.4	6	444
ORF	3	*Tylenchorynchus* sp.	24	0.3	4	491
RA			**18206**	**196**	**100**	**47**
RA	2	*Basiria* sp.	463	5	52	129
RA	2	*Filenchus* sp.	12743	137	100	53
RA	2	*Malenchus* sp.	4488	48	91	92
RA	2	*Tylenchus* sp.	511	6	54	139

[1]Total number of individuals detected in all the 93 sample positions.
[2]Average number of individuals detected in all the 93 sample positions.

The sample size to estimate mean abundance of nematode guilds ranged from 15-479 and 21-667 for 90% and 95% confidence levels, respectively (Table 3.2). Ba_1, a guild that grows rapidly during microbial blooms, had only one taxon, the lowest mean abundance, the highest CV, and thus required the greatest number of sample positions (N). A high cp scaled bacterivore (Ba_4) and omnivore (OV_5) that usually occur infrequently also had low mean abundance and high CV thereby requiring many samples to estimate with confidence mean abundance. Fu_2 and ORF were present very infrequently, consequently they had a low mean abundance, high CV, and thus required

many samples to estimate with confidence mean abundance. The calculations show that

frequently guilds need fewer samples while rare guilds require more samples.

Table 3.2. Required number of sample positions per guild to estimate the guild
population mean[2] at the 90% and 95% probability levels.

Guild	Impacted Index[3]	Faunal Analysis Weighting[4]	Mean Abundance 100 g^{-1} dry soil	Standard deviation	Coefficient of variation (%)	Required n	
						90%[1]	95%[1]
Ba$_1$	EI	3.2	1	3	264	479	667
Ba$_2$	EI, SI	0.8	106	51	48	16	22
Ba$_3$	SI	1.8	202	108	54	20	28
Ba$_4$	SI	3.2	2	4	183	230	321
Fu$_2$	EI, SI	0.8	4	5	129	115	161
Fu$_4$	SI	3.2	56	42	75	38	53
PRD$_4$	SI	3.2	8	9	104	74	104
OV$_4$	SI	3.2	32	26	83	48	66
OV$_5$	SI	5.0	3	5	162	181	252
ORF	NA	NA	6	12	199	272	379
RA	NA	NA	196	93	47	15	21

[1] confidence level
[2] within 20% of the sample mean
[3] refer to the indices in faunal analysis where these guilds are being used (Fig.1.1; Ferris et al., 2001)
[4] weightings used in faunal analysis according to Ferris et al. (2001)
Guild designation is the combination of feeding habit according to Yeates et al. (1993) and cp value according to Bongers (1990). Ba- Bacterivore; Fu- Fungivore; PRD- Predator; OV- Omnivore; ORF- Obligate root-feeder; RA- Root-associated; EI- Enrichment Index; SI-Structure Index; NA- not applicable

3.4.3. Associations between taxa

Spearman rank correlation was done to examine the associations between nematode taxa

(Table 3.3). In this analysis, only correlation coefficients with significance at P < 0.001,

since this p level gave coefficients of (r) > 0.4, were considered to potentially indicate an

association of taxa. All the associations observed were positive. The root associated

nematode, *Malenchus* sp. was positively associated with the cp2 bacterivore,

Acrobeloides sp. and three cp3 bacterivores *Achromadora* sp., *Rhabdolaimus* sp. and

Teratocephalus sp. The cp2 bacterivores and both members of family Cephalobidae,

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Acrobeles sp. and *Acrobeloides* sp., were positively associated. These two were positively associated with a cp3 bacterivores, *Prodesmodora* sp. *Acrobeloides* sp. was positively associated with an omnivore, *Labronema* sp. The cp3 bacterivore, *Prodesmodora* sp. was also positively associated with the omnivore, *Labronema* sp. and another cp3 bacterivores, *Teratocephalus* sp. and *Rhabdolaimus* sp. *Teratocephalus* sp. and *Rhabdolaimus* sp. were positively correlated. *Teratocephalus* sp., was positively associated *Rhabdolaimus* sp. and *Achromadora* sp. *Prismatolaimus* sp., also a cp3 bacterivores, was associated with *Achromadora* sp. The association with the highest correlation coefficient, *Teratocephalus* sp. with *Achromadora* sp. (r=0.55) was shown in Fig. 3.2. A clear relationship was revealed.

Table 3.3. Spearman correlation coefficients between select nematode taxa across all sample positions. Only correlation coefficients > 0.4 are shown. All are significant at P < 0.001.

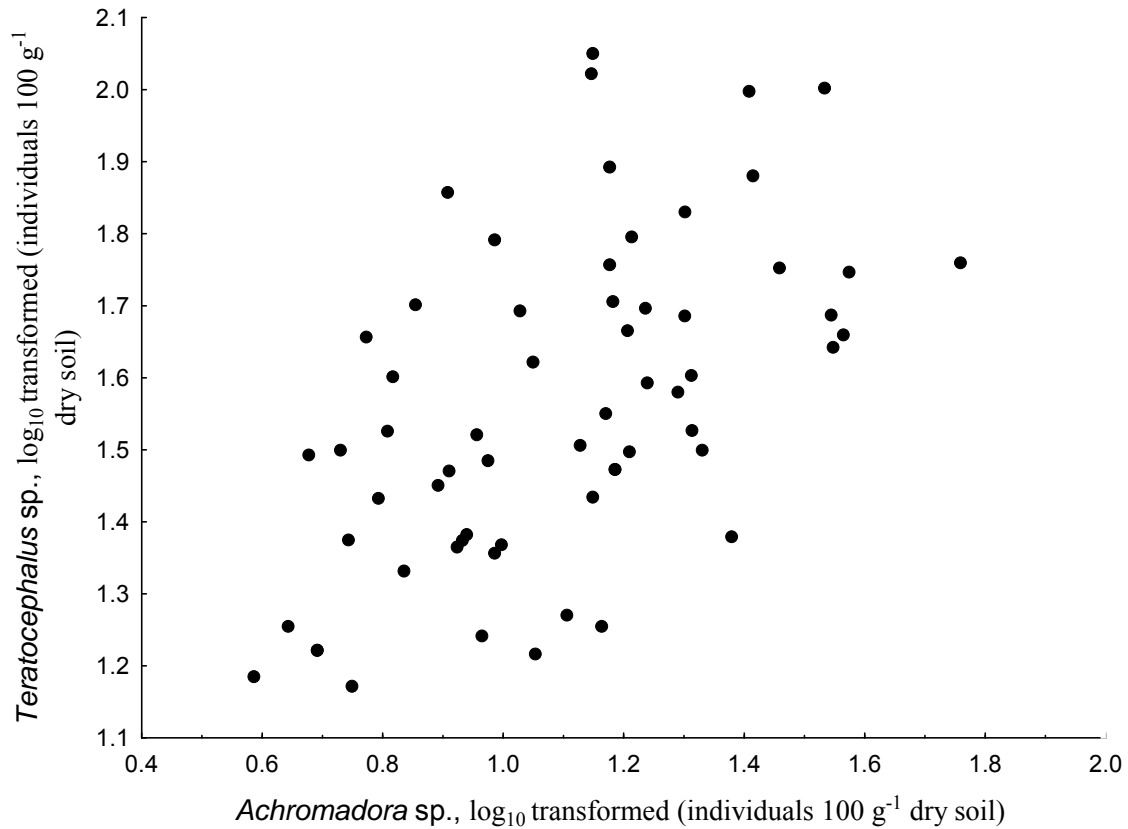| Trophic	cp	Taxa	Mal	Acr	Acs	Ach	Pro	Rha
RA	NA	*Malenchus* (Mal)	-	-	-	-	-	-
Ba	2	*Acrobeles* (Acr)		-	-	-	-	-
Ba	2	*Acrobeloides* (Acs)	0.49	0.41	-	-	-	-
Ba	3	*Achromadora* (Ach)	0.50			-	-	-
Ba	3	*Prismatolaimus* (Pri)				0.54	-	-
Ba	3	*Prodesmodora* (Pro)		0.49	0.40		-	-
Ba	3	*Rhabdolaimus* (Rha)	0.40				0.47	-
Ba	3	*Teratocephalus* (Ter)	0.49			0.56	0.40	0.52
OV	4	*Labronema*			0.52		0.48	

Fig.3.2. Relationship between *Teratocephalus* sp. and *Achromadora* sp. Spearman (r) = 0.56, P < 0.001 n=62

Spearman rank correlation analysis was also done to determine associations between nematode taxa and cover of plants (Table 3.4). Associations of *Andromeda polifolia* and moss with nematode taxa were observed. The member of the plant family Ericaceae, *Andromeda polifolia,* was negatively correlated with root- associated nematodes of family Tylenchidae, *Filenchus* spp. and two bacterivores, *Acrobeloides* sp. (cp2) and *Prodesmodora* sp. (cp3). *A. polifolia* cover was positively associated with a fungivore, *Tylencholaimus* sp. Cover of moss was negatively associated with *Filenchus* spp. Scatterplot was made to examine the associations between plant cover and nematode taxa with the highest correlation coefficient, r = -0.51. Fig.3.3 reveals a very

weak relationship between *Andromeda polifolia* and *Acrobeloides* sp. This shows that

results were inconclusive and interpretation should be take with caution.

Table 3.4. Spearman correlation coefficients for associations for select nematode taxa and plant cover across the 93 sample positions. Shown are coefficients at P< 0.01.

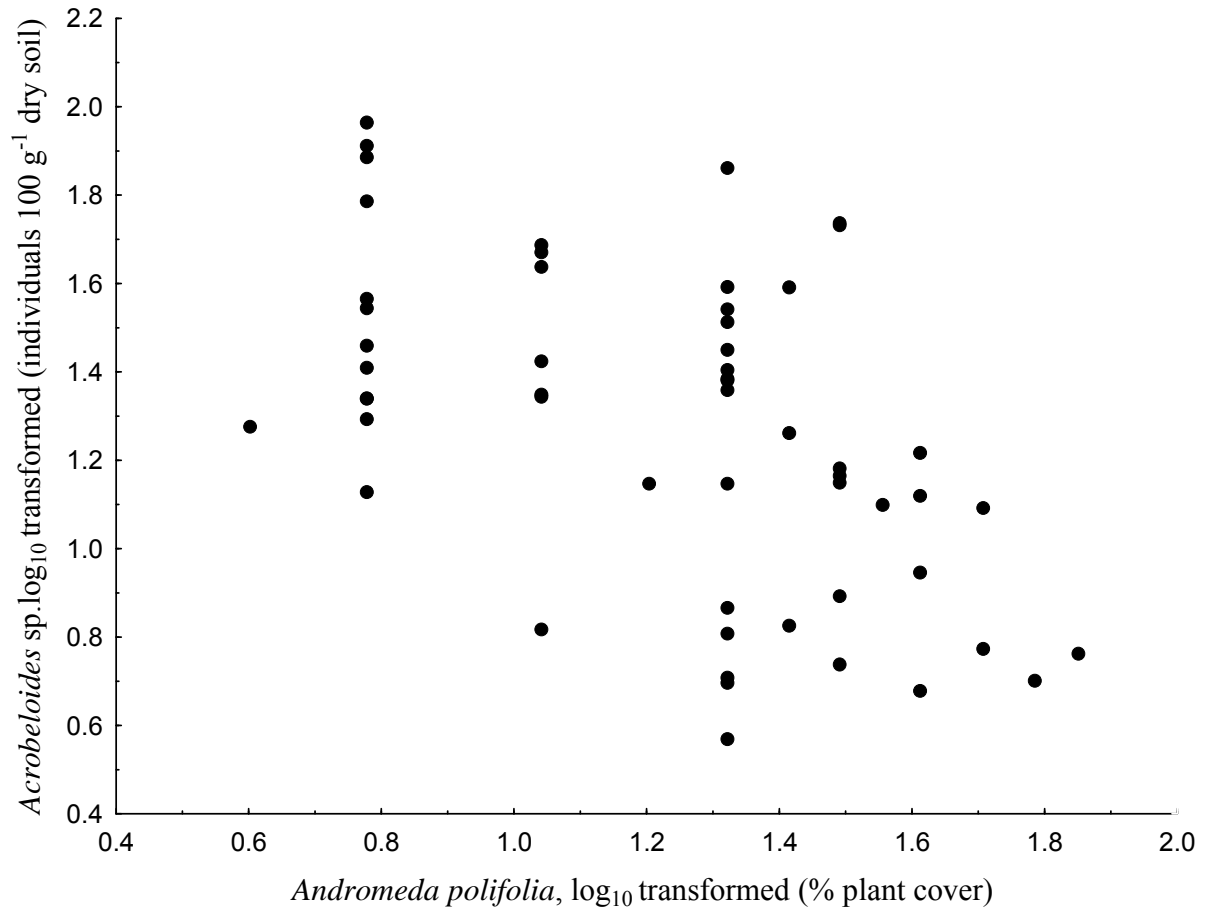| Trophic	cp	Nematode taxa	Plants	
			Andromeda polifolia	Moss
RA	NA	*Filenchus* spp.	-0.43	-0.48
Ba	2	*Acrobeloides* sp.	-0.51	-
Ba	3	*Prodesmodora* sp.	-0.32	-
Ba	3	*Tylencholaimus* sp.	0.35	-

Fig.3.3. Relationship between area of cover (%) of the heath plant, *Andromeda polifolia*, and soil number of the bacterivorous nematode, *Acrobeloides* sp. Spearman (r) = -0.51, $P < 0.01$

Redundancy Analysis (RDA) was carried out to examine associations between plant cover and nematode taxa (Fig.3.4). The first two axes explained 10% of the total variance of the dataset. Monte Carlo permutation revealed that the first two axes were significant at $P < 0.01$. This implies that although the percentage of the variation accounted for was low, plant cover was able to explain a portion of the distribution of nematode taxa. An RDA ordination diagram revealed that *Rhododendron lapponicum* was positively associated with the abundance of *Eumonhystera* sp. and *Odontolaimus* sp.,

that *Andromeda polifolia* was positively associated withthe dorylaimid taxa,

Epidorylaimus sp., *Mesodorylaimus* sp. and *Eudorylaimus* sp. and *Plectus* spp., and that

Saxifraga aizoides was positively associated with *Prodesmodora* sp. and *Malenchus* sp.

The sedge, *Carex* sp. was positively associated with *Prodorylaimus* sp. and

Hemicycliophora sp. Higher cover of lichen was positively associated with *Bastiania* sp.
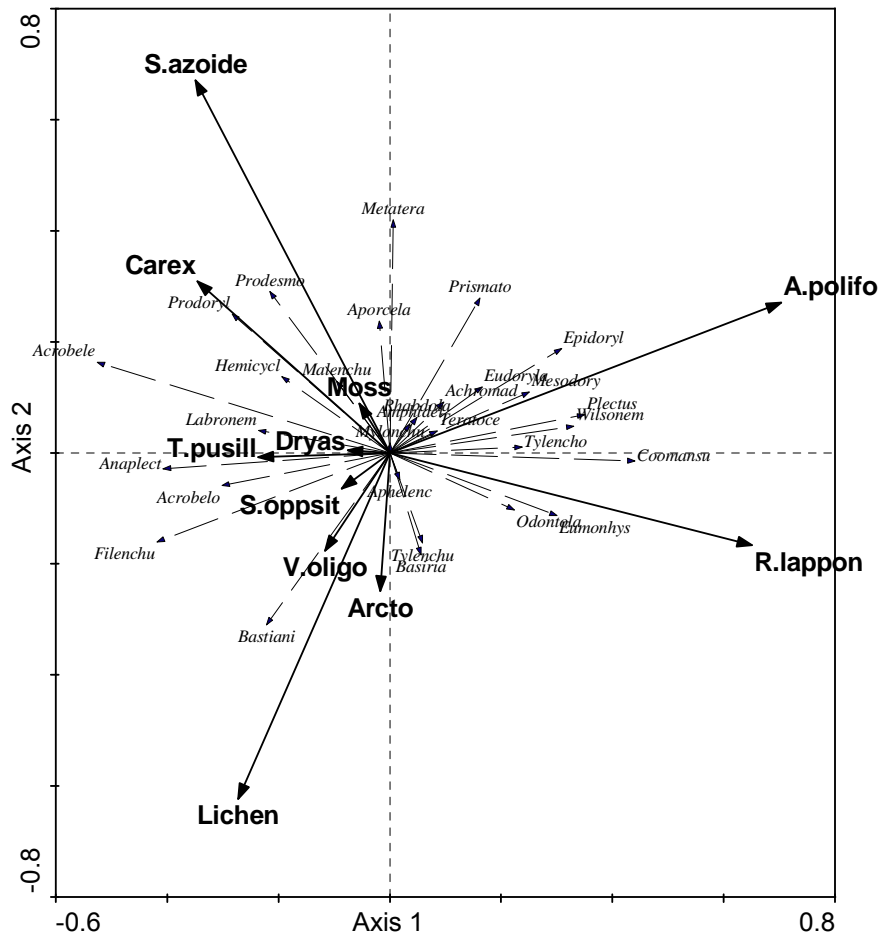

Fig.3.4. Redundancy Analysis (RDA) showing variation of nematode taxa (dashed line) associated with plant cover (solid line). Plant legend: A. Polifolia – *Andromeda polifolia*; R. Lapponicum - *Rhododendron lapponicum*; S. aizoides – *Saxifraga aizoides*; S. Oppsit – *Saxifraga oppositifolia* V. uligo – *Vaccinium uligonosum*; Arctosta – *Arctostaphylus rubra*; T. pusill- *Tofielda pusilla*; Dryas – *Dryas integrifolia*; Sedge – *Carex* sp. First two axes explained 10% of the variance in the species data.

3.5. Discussion

3.5.1. Comparison of taxa to other northern regions

This research provided more information on the understudied nematofauna in the subarctic region. It is inherent in both above- and below- groundecosystems that there are only few dominant species and most species being rare (Adl, 2003). *Filenchus* is abundant in almost every terrestrial soil that includes plants (Bongers et. al., 1989). The most abundant taxa found in this study were similar to that found in other cold climate heath ecosystems. Hoschitz and Kaufmann (2004) found Tylenchidae and *Plectus* to be most abundant lichen heath in Austrian Alps of Obergurl, Tyrol. *Teratocephalus* and *Malenchus* were most abundant in a dwarf shrub dominated tree-line heath in Swedish Lapland at Abisko (Ruess et al., 1999). *Plectus*, *Teratocephalus* and *Malenchus* were most abundant in a ombrotrophic bog also at Abisko (Sohlenius and Boström, 1999). The most dominant nematode in the tundra heath of Taimyr, Siberia, was *Prodesmodora* (Kuzmin, 1976). The common feature of these systems is their ericaceous vegetation which is most likely the influential factor on the taxonomic composition of nematode assemblages. Vegetation type and litter quality are influential factors in determining the structure of nematode fauna (Ruess et al., 1999).

3.5.2. Variability and implication to nematofaunal analysis

The distribution of each nematode taxon was highly variable. Among the trophic groups, ORF was the most variable. It also had the lowest abundance (Table 3.1). Obligate root-feeder was also less abundant in the heath sites of Abisko sub-arctic Sweden (Ruess et al., 1999). The finding of a high CV for ORF was similar to the result of Robertson and

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Freckman (1995) who found that ORF had about four times lower, mean abundance than other groups. Robertson and Freckman (1995) speculated that the low abundance, and thus high CV, was because they did not sample at the time of peak plant growth when these herbivore nematodes feed and reproduce the most. However, the present study was conducted in July, which is mid growing season for the Churchill area. Thus, time of sampling likely did not account for the high CV found with ORF nematodes. This result of Chapter 3 contrasts with that for the study presented in Chapter 2. There, the ORF nematode, *Criconemoides,* was abundant in the three heath sites sampled. This difference may be because the plant species to which ORF nematodes are attracted were not abundant in the transect field site. These ORF nematodes are very dependent on specific plant species' root exudates (Yeates, 1987).

Bacterivores were the most abundant trophic group of nematodes, which is a result similar to the finding of other studies done in cold climates (Kuzmin, 1976; Ruess et al., 1999; Sohlenius and Bostrom, 1999; Ruess et al., 2002; Hoschitz and Kaufmann, 2004). *Bunonema*, a Ba_1 nematode common in soil litter, was infrequently found at the site. Ba_1 are r-strategist ephemeral nematodes that reproduce rapidly during sudden bacterial blooms. The rarity of this nematode implies this heath system did not undergo periods of abundant litter deposition. Perhaps proximity to the strong winds of Hudson Bay effectively transported fall litter away from the site. A low abundance of *Bunonema* was also observed at Abisko in sub-arctic Sweden (Ruess et al., 1999).

Ba_1 is a functionally important guild in nematofaunal analysis, because it is used to calculate the Enrichment Index (Fig.1.1). The abundance of Ba_1 nematodes is ephemeral and responds to bacterial blooms at least four times more than the guild, Ba_2 (Ferris et al.,

2001; Mahran et al., 2009). As such, Ba_1 is given a scaling factor of 3.2 to calculate the Enrichment Index of a sample whereas Fu_2 is given a scaling factor of only 0.8 (Ferris et al., 2001). However, considering the great within field variability of Ba_1 and Fu_2 found in this study, the resulting estimated EI would magnify the variation more because of Ba_1 than variation in Fu_2. OV_5 with a scaling factor of 5 in estimating the SI, was another highly variable guild. However, due to the abundance of other guilds in this study used to estimate a SI value (Ba_3, Fu_4 and OV_4), the problem of magnification of variability to estimates of this index is not expected to be as great as for estimating EI values. Ba_3 has a scaling factor of 1.8, and Fu_4 and OV_4 a factor of 3.2, which with their greater abundance, contribute more so to estimates of SI than does low abundant OV_5 of scale factor 5. Thus, high within field variability can be a serious limitation in nematofaunal analysis, particularly when estimating an EI value. An effort to improve the indices should be made by taking into consideration the variability of the sample. Indices should be calibrated relative to ecosystem. Appropriate sampling techniques should be carried out. Calibration of indices per ecosystem might be necessary to obtain a higher resolution (Neher, 2001).

The spatial distribution of soil organisms is an important ecological characteristic. Knowledge of the spatial distribution of individuals, both horizontally and vertically, will help us in preparing sampling strategies and experimental designs (Taylor, 1984). More sample positions are required for rare taxa to obtain a mean representative of the population when considering the degree of spatial heterogeneity.

3.5.3. Associations between taxa

Maturity and other nematofaunal indices are subject to limitations, due in part to the designation of cp values to the family levels, assuming that genera in the family have similar life histories and feeding habits. Anterior feeding structures do indicate common feeding habit for taxa within a nematode family. In an effort to help improve utility of nematodes as an ecological indicators, more observations leading to information on nematode ecology is necessary particularly in an understudied region like the subarctic. Associations between taxa were included to look for relationships if taxa belonging to the same family could be positively associated, because they may be preying on the same prey or may have similar ecological requirements causing them to compete or coexist.

Positive associations on all the taxa observed showed that in this system, resources are not limiting. This is why bacterivores of the same family, such as, *Acrobeles* sp. and *Acrobeloides* sp. were positively correlated. Bacterivores with different families but similar life history strategies were also positively associated. For instance, cp3 bacterivores, *Prodesmodora* sp., *Teratocephalus* sp. and *Rhabdolaimus* sp. were positively associated. Another reason for the positive associations of taxa could also be that the soil supports more microhabitats or that the species may have highly overlapping ecological requirements. These characteristics facilitate coexistence of species (Huston, 1994). These may be among the reasons why several bacterivores coexisted even those with different life history strategies. For instance, cp2 bacterivores, *Acrobeles* sp. and *Acrobeloides* sp. were both positively correlated with a cp3 bacterivore, *Prodesmodora* sp. Positive associations of taxa with different guilds, such as, *Labronema* sp., an omnivore with bacterivores, *Acrobeloides* sp. and *Prodesmodora* sp. may be because they

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prey on different resources. The reason could also be because of predation; *Labronema* sp., a big-bodied nematode, may be feeding on these small bacterivores. This was why *Labronema* sp. was found in high number where there was high number of *Acrobeloides* sp. and *Prodesmodora* sp. Specialized niche may be the reasons why *Malenchus* sp. was positively associated with several bacterivores, *Acrobeloides* sp., *Achromadora* sp., *Rhabdolaimus* sp. and *Teratocephalus* sp. Although feeding habit is not definite, *Malenchus* sp. was reported to be a fungivore and a fine root-hair feeder.

Since nematodes are widely used as soil ecological indicators, more information regarding their ecology, association with other biotic and abiotic parameters and niche in different ecosystems and at all geographical locations is necessary (Neher, 2001). This information will help improve the nematode indices that are currently being used, thus, improve the utility of nematodes as an ecological indicator. This information enhances our understanding about the mechanistic basis of the interaction among nematodes, microorganisms and plants.

3.5.4. Plants effects on nematode assemblages

Spearman correlation coefficients (r) of nematodes and plant communities showed only few significant associations (r > 40, P < 0.01). Evaluation on the relationship with the highest correlation coefficient using the scatterplot (Fig. 3.3) revealed the associations to be weak, although a weak trend in the associations shown in Table 3.4, was revealed in the Redundancy analysis (RDA).

Redundancy analysis showed that plant cover was significantly affecting the abundance of nematode taxa, although, it only accounted for a very low percentage of the

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variation found in abundance of nematode taxa. This showed that there are many other factors that also influence the taxa composition of nematode assemblages, to name a few: vegetation, pH, salinity, redox potential and water-holding capacity. Some of the associations shown in RDA do agree with previous studies. RDA revealed a relationship between *Carex* sp. and *Prodorylaimus* sp. and *Hemicycliophora* sp. Earlier reports showed that certain species of *Prodorylaimus* sp. were abundant near *Carex* sp. roots located in the wet soil of a pond bank in Spitzbergen, Svalbard archipelago, Norway (Loof, 1985). I also observed an abundance of *Prodorylaimus* sp. in a drier part of the same fen sampled in Chapter 2 in an area vegetated by *Carex* sp. A species of *Hemicycliophora* sp. in New Zealand was described from peat soil with mosses, ferns and *Carex* sp. (Yeates, 1978).

Although, as shown in RDA results, the variation in abundance of nematode taxa explained by plant cover was low, it can't be ignored that, in this visibly homogeneous field, plant communities wield influence at a low degree to the distribution of nematode taxa. It should be noted that the sample core was only 10 cm in diameter and 10 cm in depth. A tight linkage of plant cover and nematode taxa may have been more evident with a larger core. Other plant species surrounding the core were likely influencing nematode taxa within the sampled core.

3.6. Conclusion

On a field scale, even though visually homogeneous, the tundra heath sampled still showed individual plant effects on nematode taxa distribution. Only 10% of the variation in abundance of nematode taxa was explained by plant cover. I hypothesize that a greater

percentage of the variation in abundance of nematode taxa can be explained by incorporating soil physical and chemical data. Further, the sample area for nematodes and cover area of plants may be adjusted to maximize variation for plant influence on soil conditions and maximize variation of soil physical and chemical properties. Presumably, maximized variation in plant and edaphic properties would provide a greater test of the specificity of nematode taxa to soil conditions. It should be noted that in this second study, examination of the linkage is complicated since it only allowed for the extent of the aboveground plant cover and not the root coverage. Future studies integrating additional environmental factors and quantifying the spatial distribution with the use of geostatistics analysis would further add understanding of the factors driving nematode assemblages. Using geostatistic analysis, cross-correlation of environmental variables (plant cover and soil parameters) and nematode assemblages will be examined. This will also allow the necessary scale resolution for sampling purposes, so that accurate prediction of nematode abundance response to stress, disturbance or even global change phenomena.

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4. OVERALL SYNTHESIS

Living organisms are dependent upon each other and their abiotic environment. This interdependence exists between the soil (its physical, chemical, and biological components) and primary producers. Plants are the primary producers introducing most of the organic energy to drive the soil food web (Wardle, 2002). The association of plants and soil food webs determines community- and ecosystem-level functioning for the maintenance of ecosystem properties (Wardle, 2002).

Among all terrestrial regions, the tundra ecosystem is the furthest north that supports life. Tundra is also the ecosystem most vulnerable to climate change (Grogan and Jonasson, 2005). The lower layer of the soil is permanently frozen and dead organic matter remains largely undecomposed as peat. The soil layer above the permanently frozen layer supports most life. Any increase in temperature due to global warming will increase belowground activities such as decomposition and precipitate rapid changes in the soil food web and soil community structure (Coulson et al., 1996). In turn, because of the linkage between belowground and aboveground systems, it is expected that changes belowground will result in changes in vegetation, which again will cause changes in the soil, and so on.

Nematodes, because of their attributes and varied key roles in the soil food web and soil nutrient recycling (Bongers and Ferris, 1999), are ideal organisms for studying the linkage of above- and belowground processes and biota in terrestrial systems. In particular, one of these linkages is the intimate association of distinctive soil nematode assemblages with specific plant communities and/or individual plant species.

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Not much had been done on arctic and subarctic nematodes. Moreover, there have been very limited studies that looked into above- and below- ground linkage. In the tundra ecosystem, there were only two studies (Hoschitz and Kaufmann, 2004; Kuzmin, 1976) that looked into such linkage, but they were more on habitats rather than vegetation. Hence, to my knowledge, no previous study has ever been done on the linkage of nematode communities and vegetation in the tundra ecosystem.

4.1. Plants as determinants of nematode spatial variation

Plants influence the nematode communities belowground through root exudation and litter formation (Wardle et al., 2004). Different plant species secrete different amounts and kinds of substances from their roots, and these directly affect the organisms feeding on them (e.g. obligate root-feeding nematodes). Nematodes that do not feed directly on plants are affected indirectly, because the quality and quantity of plant litter affect the abundance and diversity of decomposer organisms (Yeates, 1999).

In my two studies, bacterivores were the most abundant in all sites except the berm crest which was dominated by obligate root-feeders. The berm face plots had high abundance of r-selectionist bacterivores which was likely caused by bacterial blooms resulting from the deposition of marine organic debris such as seaweeds. Abundance of bacterivores in heaths (comprising heath, polygon and hummock), forest and transect sites is in accordance with other studies done in tundra ecosystems (Kuzmin, 1976; Ruess et al., 1999; Sohlenius and Bostrom, 1999; Ruess et al., 2002; Hoschitz and Kaufmann, 2004). Second in abundance were the root-associated nematodes. Obligate root-feeders

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were just about similar in proportion to root-associated nematodes in the heaths, patchily distributed in the transect sites and almost absent in the forest.

Obligate root-feeders, being host-specific, are directly affected by vegetation because they take their carbon from roots (Yeates 1999). In the first study, obligate root-feeding *Pratylenchus* sp. was highly dominating (64%) in the coastal sand dune berm crest sites dominated by a grass, *Leymus mollis*. The high abundance of obligate root-feeders in this site agrees with the finding in the arctic tundra of Siberia where highest nematode abundance occurred in grass stands among 14 sites (Kuzmin, 1976). *Pratylenchus* was found to be associated with *Leymus arenarius* and other sand dune grass species in other studies (Van der Putten and Van der Stoel, 1998; Brinkman et al. 2004; Rodriguez-Echeverria et al, 2009). High dominance of a certain taxon would affect the nematode assemblage. The obligate root-feeder *Criconemoides* sp. was found in abundance in heaths, which are vegetated by ericaceous plants. Because heaths are diverse plant communities, the ORF was not dominating compared to the ORF in berm crest. Multiplant-species systems provide a high diversity of litter, which creates heterogeneous substrates for biota, thus supporting more organisms. Some of these diverse organisms may ward off predominance of one taxon. The surprising absence of ORF in the forest may mean that there were not many plant species in the forest sites that are attractive to the plant-dependent nematodes.

Nematodes that do not feed directly on the plants are affected indirectly, because the quality and quantity of plant litter affect the population sizes and diversity of decomposer organisms (Yeates, 1999). Through this resource, plant species may select the communities of microbial organisms and thus affect their palatability to the

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decomposer biota. Spruce forests are known to have high lignin and polyphenols, which are recalcitrant compounds that facilitate a more fungal-based decomposition. Thus, the forest site had a high proportion of fungivores, omnivores and root-associated taxa, which are speculated to be fungivores.

Plant species effects on nematode communities were also revealed by a recent study by Viketoft et al. (2009) in an experimental field in northern Sweden. Viketoft et al. (2009) looked at the effects of grasses, legumes and forbs on the nematodes: grasses were positively related to bacterial- and obligate root-feeders; legumes increased bacterial-feeding nematodes, particularly the r-selected ones; and fungal-feeders were enhanced by forbs. Plant effects were usually stronger on plant-, bacterial-, and fungal-feeding nematodes than on the other trophic groups (Viketoft et al., 2009).

4.1.1. Plants as determinants at the ecosystem level

The distinct groupings of nematode taxonomic composition according to vegetation, namely, Berm Face, Berm Crest, heaths and Forest, provide evidence that there is a parallel relationship between nematode taxa and vegetation properties. The berm sites, although adjacent to each other, were dominated by a different single species of plant, and differed in their nematode taxa. The heaths, in turn, although geographically separated and having different origins of soil formation, had similar vegetation and had similar nematode taxa that were distinct from Forest sites. The similarity of nematode assemblages in sites that are geographically isolated but with similar vegetation show that nematodes in the sub-arctic environments have effective dispersal mechanisms, which may be largely due to strong winds. The Forest site, although with an understory that was

vegetated with Ericaceous plant communities just like the heaths, is possibly functionally different due to the presence of *Picea glauca* trees and different moss species; thus, its nematode taxa composition was different.

Other studies were also successful in characterizing other ecosystems using nematodes. Hoschitz and Kauffmann (2004) used nematodes in characterizing alpine zones in the Austrian Alps. In the Netherlands, nematode communities were successfully used to classify habitats (grasslands, shrubs and forests) with differing soil and vegetation characteristics in the nature reserves (De Goede and Bongers, 1994).

4.1.2. Plants as determinants at within-ecosystem level

At within-ecosystem level, vegetation was found to be a determinant on nematode spatial distribution. It is interesting to know the extent of the influence of plants on nematodes; particularly specific plant species effect. In Chapter 3, the influence of plant cover (species) to nematode taxa was examined using a visually homogeneous field. The results of RDA demonstrated that plant cover was associated with nematode taxa, although, plant species only accounted for a low percentage of the variation in nematode taxa. This low percentage showed that besides vegetation, other factors are involved in determining within-field variation of nematode taxa. Within-field variation of soil properties such as pH, salinity, C:N ratio, texture and moisture may have contributed to the spatial variation in nematode taxa. Possibly, other plants surrounding the core influenced the nematode taxa found inside the core. It should also be noted that the sample core was only 10 cm in diameter and 10 cm in depth. A tight linkage of plant communities and nematode assemblages may be probably more distinctly shown in a sample using a bigger core

covering a wider plant cover area. Perhaps the plant species patch was not big enough to be able to observe its influence on nematodes, thus, a wider patch of plant cover may show greater association of plants and nematode assemblages. The study could also be done with the incorporation of root biomass.

Plants have overriding influence on nematodes, that is, even plants belonging to the same genus affected the nematode communities differently (De Deyn et al., 2004; Viketoft et al., 2005). Kuzmin (1976) used nematodes to characterize the habitats in the Siberian tundra ecosystem and reported vegetation to be one of the main driving factors in nematode distribution. Kuzmin (1976) found that increase in plant cover is clearly correlated with an increase in nematode genera and species.

4.2. Important considerations on nematodes as ecological indicator

Whilst this thesis provided important information on the use of nematode communities in characterizing differing vegetation, thus showing another proof of the group's utility as model organisms for ecological studies, it also revealed various challenges for the improvement of this group as a bioindicator. Nematode trophic structure needs further field and laboratory studies. For instance, absence of fungal-feeders in the AMF-associated *L. mollis* encourages the thought that some nematode taxa not originally classified as fungal-feeders might be preying on fungi. One such taxon is thought to be the omnivore, *Eudorylaimus*, which was reported to be prey of a wide variety of organisms in different habitats. Another taxon that needs further clarification is family Tylenchidae. This diverse family occupied a great proportion in the heaths and forest

sites and must have a key role either as herbivore, bacterivore or fungivore, and thus, a more reliable designation of its trophic role is necessary.

The study in Chapter three brought up a new challenge to improve nematofaunal analysis. The weighting given to Ba_1, an important guild in assessing enrichment of an ecosystem, should be calibrated taking into consideration spatial variability of the area. In this sub-arctic heath site, an ephemeral nematode, Ba_1 was very patchy and needs a higher number of sample cores for sample to be representative of the population. Thus, the high weighting of 3.2 for this nematode may be magnifying the Enrichment Index (EI) and thus distorting the nematofaunal analysis.

With the limitations mentioned above, it is therefore necessary to calibrate trophic structure, indices and weightings in each ecosystem particularly in an understudied site like the sub-arctic (Neher, 2001).

4.3. Implications of climate change

This study showed a strong influence of vegetation on nematode community and consequently, on the soil food web. Intimate associations between soil organisms and plant communities will give insight into how these organisms are directly and indirectly associated with each other and could reveal how they are vulnerable to global changes (Hendlund et al., 2004). That is, an increase in temperature due to climate change will cause changes in the composition of the belowground biota, and consequently the aboveground biota, because they are intimately associated with vegetation. These thesis results gave baseline data towards the understanding of the ecological roles and

interactions among the component species in the community, which will help make predictions of changes in biodiversity and ecosystem functioning (Johnson et al., 1996), particularly when changes arise due to global change phenomena (Wardle, 2004). These predictions might enable us to counteract the changes caused by anthropogenic disturbances or natural phenomenon (e.g. climate change), which is mostly the case in the sub-arctic regions.

Predominance of *Pratylenchus* in the coastal sand dunes and its adverse effect to *Leymus mollis* may be exacerbated by climate change. A higher temperature may cause *Pratylenchus* to complete more generations than normal in a growing season. This increase may then result in an imbalance in the ecological dynamics of the sand dune, causing it to have weak resistance and resilience against plant pathogens, such as *Pratylenchus*. Thus, with the expected dominance and activity of *Pratylenchus*, the coastal sand dune may be in danger of being wiped out. Infection of *Pratylenchus* may be counteracted by the association of *L. mollis* and AMF. An increase in temperature may facilitate high turn-over of AMF. High AMF infection of *L. mollis* is a possible defense mechanism against the predominance of pathogenic *Pratylenchus*.

I have brought up the importance of the associations of AMF with *L. mollis*. In the absence of a known fungivore such as *Aphelenchoides,* the taxon *Eudorylaimus* was thought to be the fungivore in this site. *Eudorylaimus* was reported to be sensitive to temperature increase (Ruess et al., 1999). Since warming will be negatively affecting *Eudorylaimus*, fungal turn-over will also be affected, thus making the coastal sand dune an ecosystem vulnerable to climate change.

Warming would cause the sub-arctic ecosystem to be wetter. As such, there would be a high reproduction rate of bacteria, as wet soil favors bacterial growth, resulting in a higher number of bacterivores. Consequently, there will be a substantial decrease in fungivores, root-associated taxa, and omnivores resulting to an imbalanced ecosystem.

4.4. Future prospects

This present research showed that at both scales, whether that of a plant community or of individual plant species, vegetation is one factor that drives nematode diversity and taxonomic composition of nematode assemblages in the soil. This study acknowledges the fact though, that the soil is a mixed heterogeneous environment and that many other factors are influencing nematode diversity. A greater percentage of the variation in the nematode values may probably be explained by incorporating physical and chemical data. Moisture content, pH, Salinity, C:N ratio, % total C, % total N, % total P, % total $CaCO_3$, and extractable NH^{4+} and NO^{3-} are among the soil parameters to be included in future analysis. Future studies integrating additional environmental factors and quantifying the spatial distribution with the use of geostatistics analysis would add to our further understanding of the spatial distribution of nematodes. This additional data will also allow us to know the necessary scale of resolution for sampling purposes, so that we may accurately predict the population response of nematodes in times of stress, disturbance or in relation to global change phenomena, so as to facilitate their use as soil ecological indicators. Inclusion of temporal variation should also be considered, because associations between nematodes and plants, or among other biotic communities depend, on abiotic conditions, food resources and space, all of which vary through time.

Abundance of plant-feeders would be greatly affected with sampling time as a factor

since their reproduction is affected by growth of plants. In addition, freeze-thaw would

affect abundance of free-living nematodes particularly, the bacterivores. Moreover, more

studies should be done on ecology of nematodes and their interactions, particularly in this

understudied ecosystem of the sub-arctic, in order to better understand processes in the

soil and consequently, ecosystem functioning.

4.4. Literature Cited

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5. APPENDICES

5.1. Extraction Method

There are various methods in extracting nematodes and their efficiencies vary with the material being used, soil type, moisture content of the soil and nematode taxa, among others. In doing the community analyses of the nematodes, the first important thing to consider is choosing the best extraction method available. There are two cheaper and commonly used methods, Baermann pan and centrifugation using sugar.

Thus, I did an experiment comparing these two methods. Results showed a marked difference in the total abundance of the nematodes with centrifugation method being thrice as much as the Baermann pan (Fig.5.1). The wide difference in the total abundance gave a remarkable difference in the trophic structure as reflected by the dominating number of bacterial-feeding nematodes in the Centrifugation method. The morphological structure of the bacterial-feeding nematodes, such as the presence of somatic and labial setae, strong body annulation and tail glands may impede their passage from the filter paper. This was also the reason why there were more unicellular feeding nematodes in the centrifugation than in the Baermann method (Fig.5.2).

Verschoor and De Goede (2000) cited that microbial flush may occur in the soil debris thereby attracting the bacterial-feeders to stay in the debris causing the low recovery of bacterial-feeders in the Baermann technique.
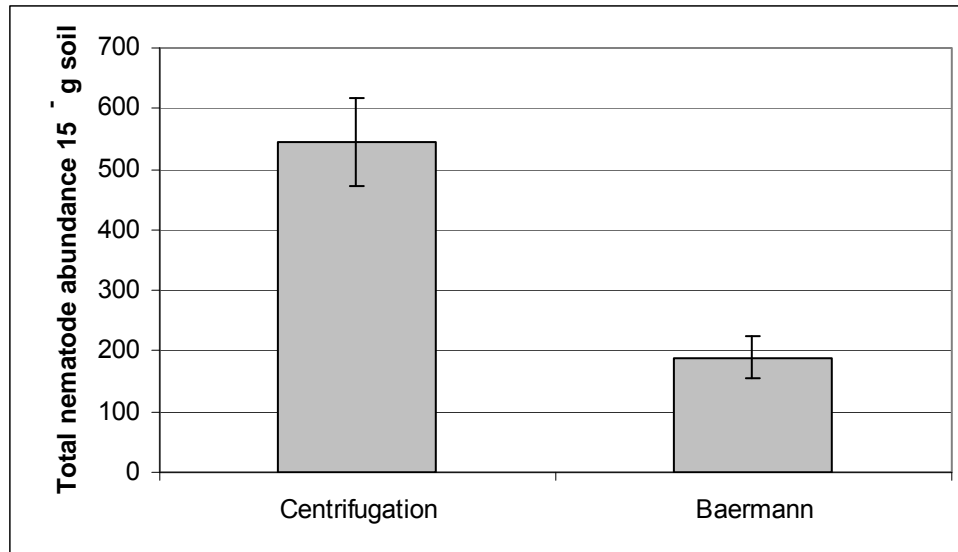
Fig.5.1. Comparison of total nematode abundance (15^- g soil) between two techniques-
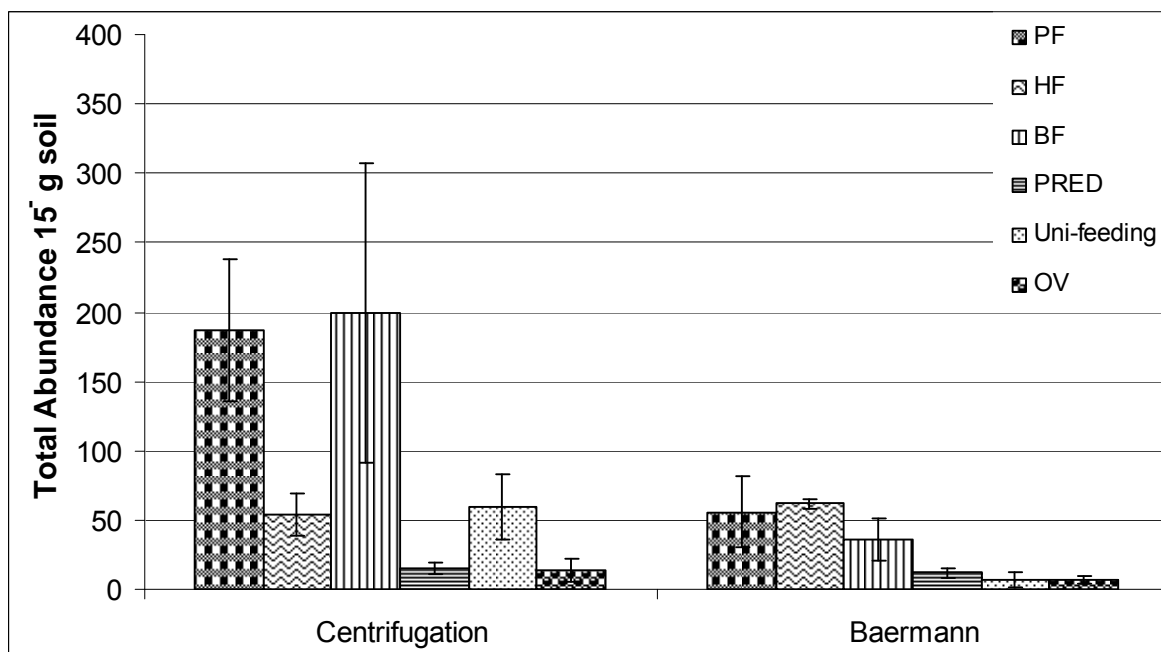Centrifugation and Baermann pan.

Fig.5.2. Comparison of the total abundance of each trophic group between two
extraction techniques. Legend: PF- plant-feeders (including Root-associated); HF-
hyphal-feeder; BF- bacterial-feeder; PRED- predator; Uni-feeding- unicellular-feeder
(*Achromadora* and *Odontolaimus*; included as bacterivores in the main text of the thesis);
OV- omnivore

Due to the difference in the extraction efficiencies, the Maturity Index values were affected. Because cp-1 was almost absent, the Baerman pan had a slightly higher maturity index compared with the centrifugation (Fig.5.3 and Fig.5.4). The experiment showed the disadvantage of using the Baermann as nematode extraction technique. Although commonly used, the Baermann technique is not a quantitative means for ecological studies of nematodes. As such, I decided to use the centrifugation method. To ensure maximum recovery, I used Baermann pan technique to extract nematodes that adhered in the soil debris that were left after the sieving and decanting step.
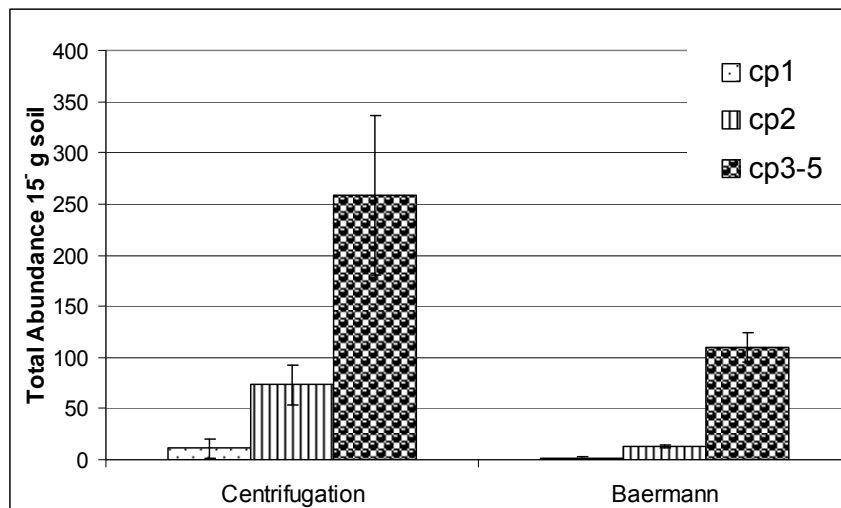
Fig.5.3. Comparison of the total abundance of cp classes between two extraction techniques.
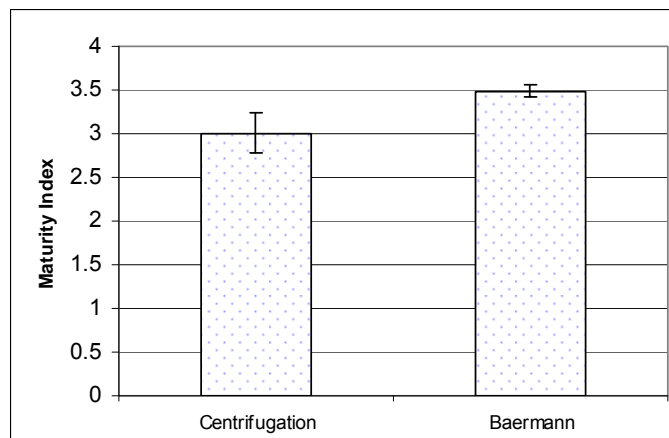

Fig.5.4. Comparison of MI values

5.2. Reconnaissance Results

A reconnaissance was done in Aug. 2007. A total of approximately 50 taxa with

Eumonhystera, a bacterivore, as the dominant taxon comprising 21% of the total

nematofauna followed by *Filenchus* (12%), *Rhabdolaimus* (8%), *Plectus* (5%) and

Prodesmodora (5%) on all the samples examined. The genus *Filenchus* is common in

most soils. What I find more interesting here is the dominance of the aquatic nematodes

Eumonhystera, Rhabdolaimus and *Prodesmodora* reflective of the area with tundra

biome characterized by having many forms of wetland bodies.

Bacterial-feeding nematodes had the highest proportion in all samples except those

in the *Picea glauca* shrub and Twinlake forest (Fig.5.5). There were a high proportion of

plant-feeders where you have higher plants and more vegetation. Family Tylenchidae was

placed under plant-feeders. This family was dominating in these samples.

The nematode activity in the soil was reflected through their life strategy

characteristics wherein there were abundant bacterial feeders in the wet sample sites (near

wetland bodies) as compared with the drier ones. Moist environments favoured bacterial

growth and is reflected by a high proportion of bacterial-feeding nematodes. Bacterial

feeders have lower score in the cp scale. As a consequence, the maturity index values

were lower in the samples that were near the coast or near wetland bodies (Fig.5.6).

Principal component analysis shown in Fig.5.7 revealed associations of

Pratylenchus with samples from *Elymus* plants and other coastal areas. It also revealed

that these areas had high taxa from family Monhysteridae, commonly comprising the

taxon, *Eumonhystera*. Soil sample from the fen also showed high abundance of

Monhysteridae. The fungivore *Aphelenchoides* was associated with samples from

Twinlake forest, lichen from Twinlake area and *Empetrum nigrum*.

Literature cited:

Verschoor, B. and de Goede, R. 2000. The nematode extraction efficiency of the Oostenbrink elutriator: cottonwool filter method with special reference to nematode body size and life strategy. *Nematology* **2**: 325–342.
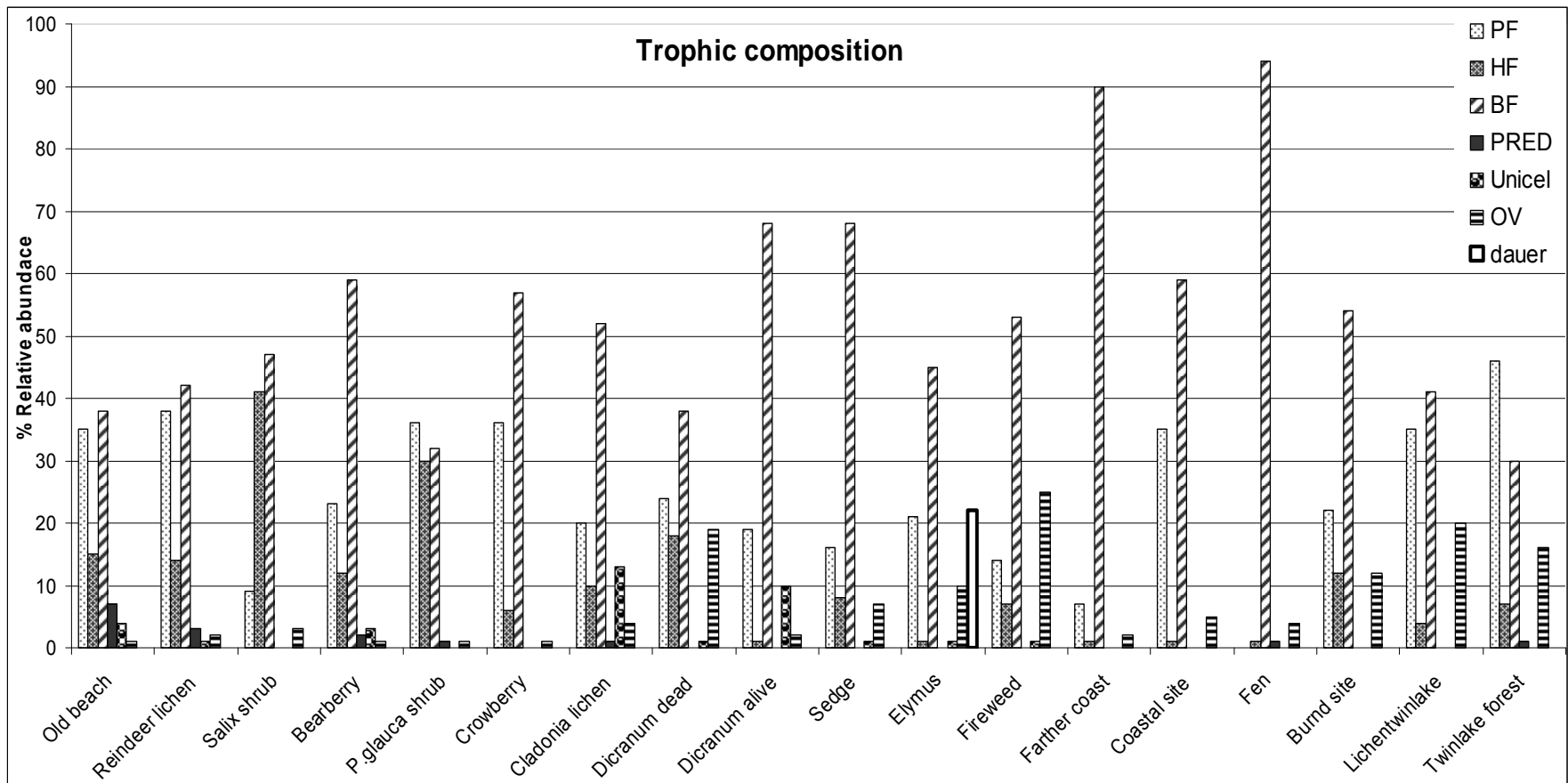
Fig.5.5. Relative abundance (%) of trophic composition in each sample. Legend: PF- plant-feeders; HF- hyphal-feeder; BF- bacterial-feeder; PRED- predator; Unicel- unicellular-feeder (*Achromadora* and *Odontolaimus*; included as bacterivores in the main text of the thesis); OV- omnivore; dauer- Dauerlarvae

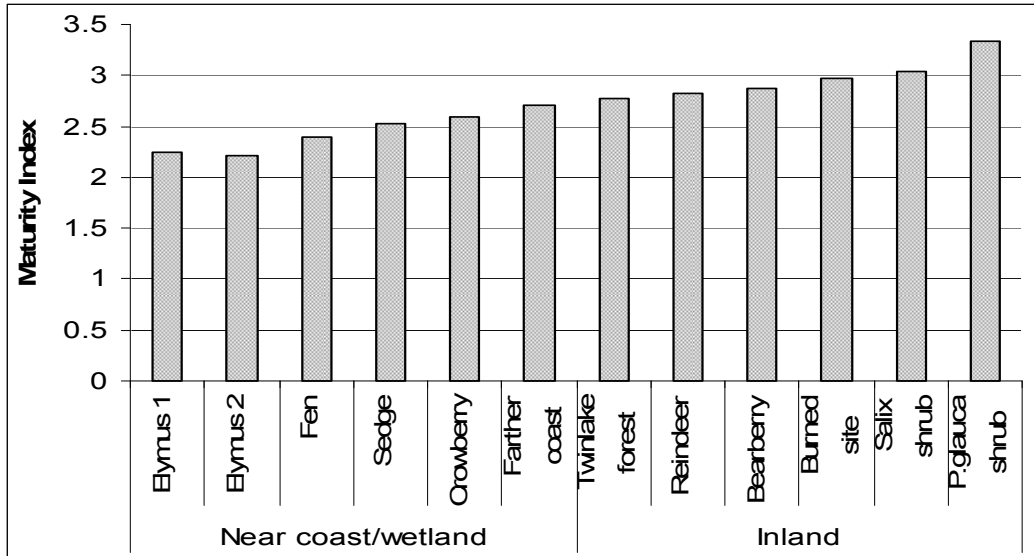Farther coast- sample taken from a coastal area but it was farther from the shoreline.

Fig.5.6. Maturity Index values comparing the samples' proximity to water bodies.
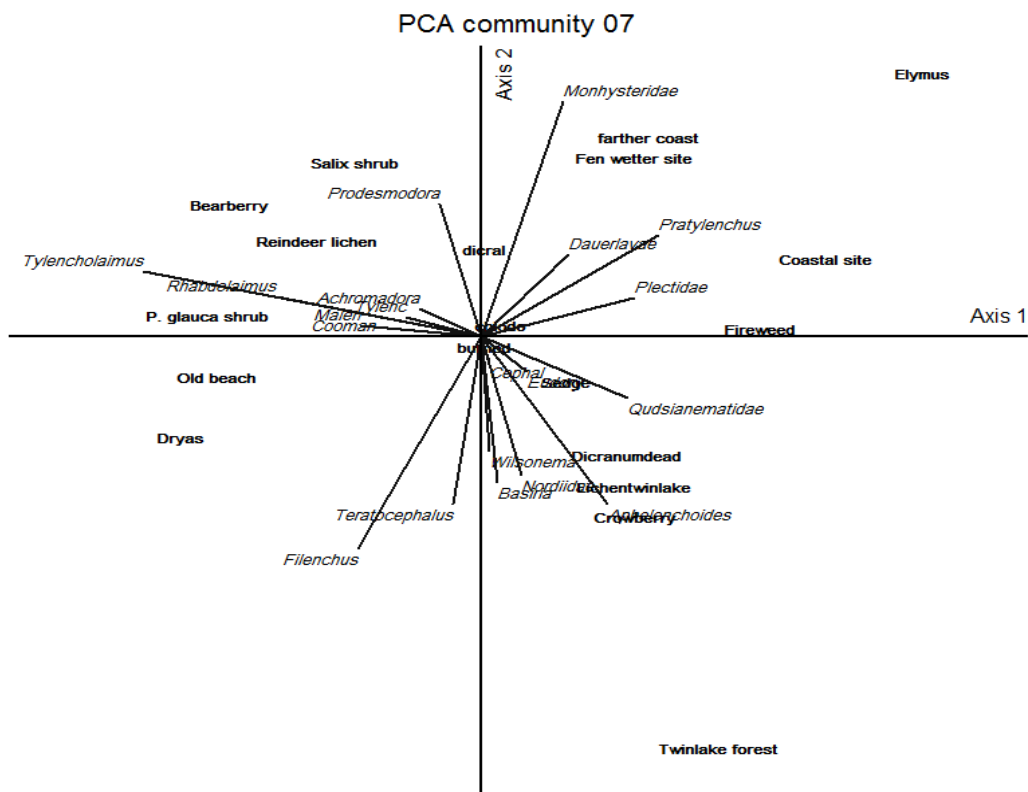

Fig.5.7. Principal Components Analysis of nematode taxa (shown as vectors that correspond to taxa weighting). PC axes 1 and 2 explained 25% and 16% of the variation, respectively.