Response of soil invertebrates to pastoral management, and their links to soil services

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Abstract

Sustained pasture production requires soils which are fertile, porous, and can support invertebrate populations. Soil invertebrates influence soil processes, supporting soil services (e.g., nutrient and water supply) required in pastoral soils. The hypothesis, that invertebrates would show some consistent responses to pastoral management was tested and used in the development of a biological indicator. Specifically, this thesis explored the response of soil invertebrates (macrofauna, mesofauna and nematodes) to a diversity of pasture managements (livestock type, stocking rate, fertiliser application, irrigation), collecting soil samples from nine sheep grazed, 17 dairy grazed and 15 ungrazed long term research and commercial pastures. Focus was on the influence of management practices on soil physical condition and potential food resources for the soil food web.

Food resources influenced invertebrates, particularly in soils with lower stock live weight loading. Nematodes tended to respond positively to increased pasture production with increases in plant feeding nematodes. The physical disturbance associated with dairy cow treading was pronounced (compared with that of sheep treading) and this had consequences for the invertebrate community. Oribatida were low in abundance in dairy grazed pastures and slow to recover when treading pressures were removed. Some larger, predatory nematodes were sensitive to treading, but recovered when treading pressures were removed. Earthworms are capable of creating their own burrows and were more resistant to stock treading, especially anecic species. The calculated effect of earthworms on nitrogen mineralisation was greater under organic than conventional dairy pasture management. The importance of soil invertebrates in regulating nitrogen supply to plants in a compacted and high nitrogen fertility soil was demonstrated in a constructed mesocosm.

The influences of management on food resources and soil physical condition, and their relationships with invertebrates form critical components of a proposed invertebrate threshold indicator. Habitable pore space appeared to be a reliable indicator of invertebrate populations, as food may not always limit populations in pastures. The indicator, based on invertebrates (i.e., Nematode Channel Ratio, Plant Parasitic Index, abundances of earthworm functional groups, Oribatida, nematodes and herbivorous macrofauna) was linked to soil services by establishing thresholds at which soil services might be 'limited' or 'sustained'. Suggestions on how to manipulate invertebrate abundance are made. The proposed indicator may provide land managers with a tool linking invertebrates to soil services required for sustained pasture production.

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Preface

Each chapter of this thesis has been written in the form of a standalone paper. As a result there is some repetition between the chapters. Some chapters have already been submitted for publication. I am the first author with the largest input into methodology, data collection, analysis and write up in all chapters. My supervisors made significant contributions to the thesis, and these are acknowledged below and in the authorship and acknowledgements of the published papers. Other contributions are shown in the acknowledgements.

Role of supervisors

Chapters 1 to 7 explore the affect of different factors on soil fauna at various sites. Maria Minor, Alec Mackay and Gregor Yeates gave guidance on experimental design and methodology. Maria Minor gave input into the statistical analysis. Alec Mackay contributed valuable ideas to site selection and the manuscripts. Maria Minor and Gregor Yeates provided training in microarthropod and nematode identification, respectively, and improved the write up of the manuscripts. Mike Hedley provided valuable comments, particularly in relation to nutrient cycling.

Chapter 8 is a laboratory study examining the interaction between bulk density, nitrogen fertility and soil invertebrates on nitrogen cycling. All supervisors helped finalise the methodology and experimental design. Mike Hedley gave guidance throughout the mesocosm and helped to calculate the fate of ^{15}N labelled litter. Maria Minor helped with the statistical analysis. All supervisors provided valuable comments on the manuscript.

Discussions with Alec Mackay and Gregor Yeates were valuable during the development of the indicator (Chapter 9 and 10). Comments from Maria Minor and Mike Hedley were also much appreciated.

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Introduction

Pastoral management and soil

Pastoral agriculture in New Zealand is characterised by legume based pastures grazed *in situ* by animals year round. In order to sustain feed for the grazing animals, pastures are fertilised. Both stock treading and fertilisation alter the soil environment, with its physical and chemical properties being changed. Land managers, in order to maintain profits, have been slowly increasing both fertiliser inputs and stocking rates. This puts increasing stresses on the soil environment, with both physical and nutrient loading having consequences on soil structure degradation and nutrient leaching. New Zealand pastures are particularly vulnerable to these stresses on the environment, because stock graze pastures even during winter when wet soils are most susceptible to compaction and nutrient losses (Greenwood and McKenzie, 2001).

Soils are important in providing ecosystem services such as food production, water quality and carbon sequestration. These ecosystem services are dependent on a range of soil services in which invertebrate activities are intimately involved, including decomposition, nutrient cycling and the maintenance of soil structure (Brussaard, 1998; Coleman et al., 2004; Wall, 2004; Lavelle et al., 2006). In order for these services to continue into the future, soils need to be managed to sustain appropriate biological communities. Sustained pastoral growth requires good quality soils, where soils are fertile, have a good physical condition for air and water movement and good biological activity (Wall, 2004). Organisms conducive to these conditions, such as earthworms with their ability to improve soil porosity and nutrient cycling (van Eekeren et al., 2007), need to be stimulated.

New Zealand pastures are highly modified aboveground, with manipulations from the exotic pasture species right through to introduced livestock. There is capability to stimulate soil invertebrates and the services they regulate (Guimares et al., 2010). Previously there has been little thought put into the manipulation of invertebrates but, as with the successful inoculation of selected *Rhizobium* strains for legumes (Brock et al., 1989), and the introduction of earthworms (Stockdill, 1982), benefits may be seen.

Soil macro-, meso- and microfauna

Soils are a challenging medium in which to study organisms (Coleman, 2008). Despite this, good progress has been made in studying multicellular soil invertebrates, an important component of the soil decomposer food web. For studying their activities in soils they are best separated into different size classes (Swift et al., 1979), based on body width, the macrofauna, mesofauna and microfauna (see Fig. 1).

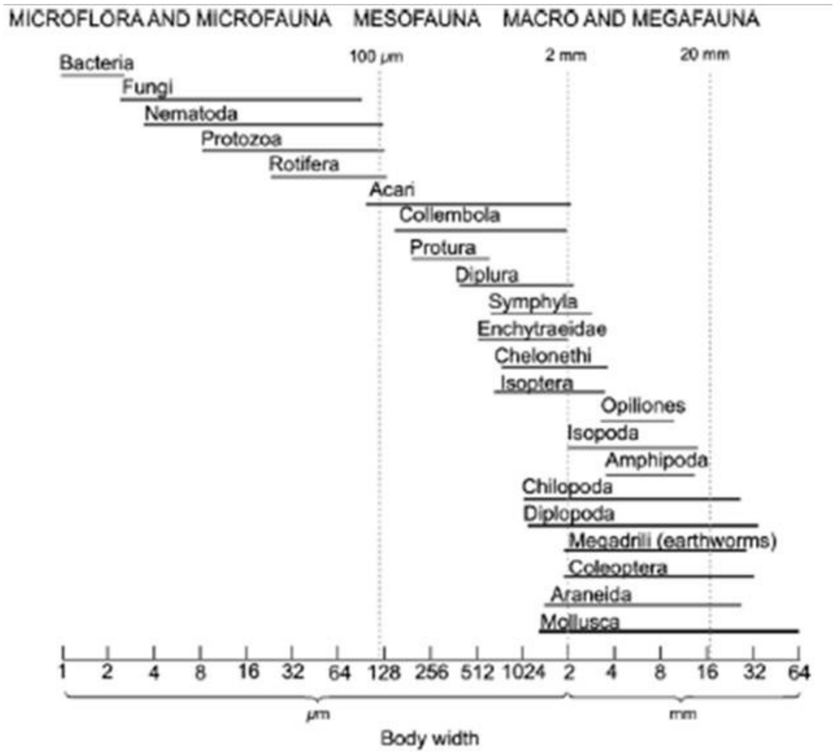

Fig. 1. Body widths of the soil fauna, microflora, microfauna, mesofauna, macrofauna and megafauna. From Swift et al. (1979)

In temperate grasslands the soil macrofauna, with body diameters (ø) >2 mm, is typically dominated by earthworms but also includes other invertebrates such as insect larvae. Earthworms have a low numerical abundance in the soil (<1200 ind./m^2) but a high biomass (<300 g wet weight/m^2) (Curry, 1994). By burrowing, earthworms can have large influences on soil porosity (Lee and Foster, 1991; Francis and Fraser, 1998), and hence are among the organisms termed ‘ecosystem engineers’ (Jones et al., 1994). They also play an important role in incorporating surface litter into the soil (Edwards, 2004). Three functionally different types of earthworms can be distinguished: epigeic, endogeic and anecic (Lee, 1959; Bouche, 1977; Springett, 1983) (Fig. 2). Epigeic and anecic earthworms are particularly useful in organic matter incorporation as they feed on the organic matter on the soil surface and carry it down into the soil profile. Endogeic and anecic earthworms are important for soil structure and porosity as they burrow through the soil profile.

The soil mesofauna (body diameter 0.1–2 mm), is dominated by Acari and Collembola (Fig. 3). These invertebrates can reach densities in the hundreds of thousands per square metre, but have a low biomass (~2 g wet weight/m^2) (Curry, 1994). Through their feeding activities Acari and Collembola have important roles in litter incorporation and nutrient cycling. Their nutrient rich faecal pellets are also important for soil structure (Barratt, 1971; Lee and Foster, 1991). A high proportion of soil Acari are represented by longer lived general detritivores Oribatida and shorter lived predatory Mesostigmata. Collembola are shorter lived general detritivores.

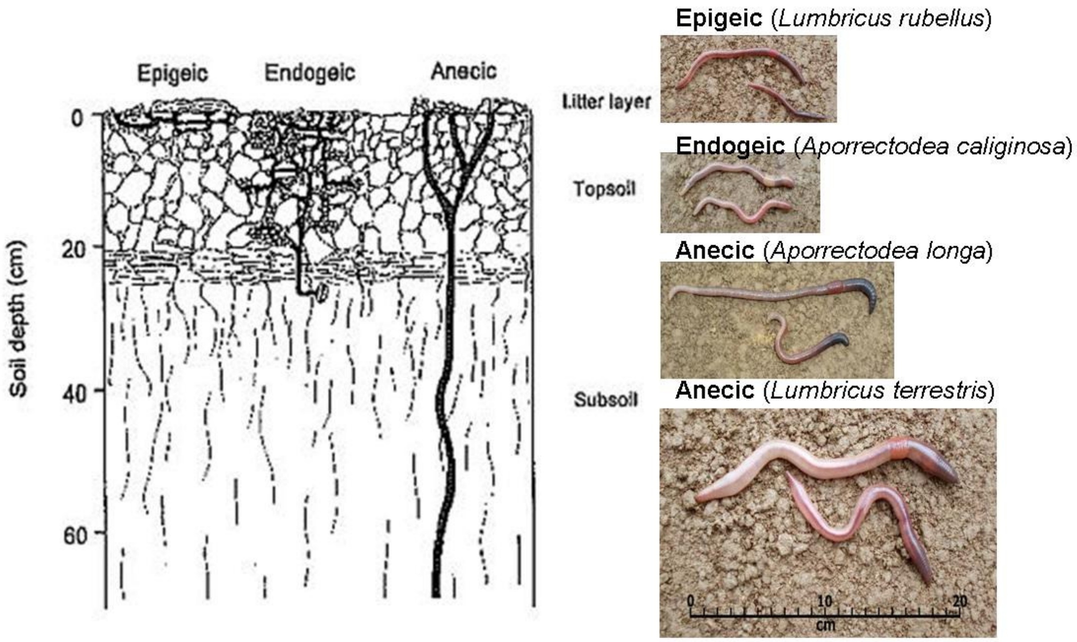

Fig. 2. Earthworm functional groups. Epigeic earthworms feed on litter on the soil surface and do not form permanent burrows. Endogeic earthworms ingest the soil, feeding on organic material within, through this process they form semi permanent burrows in the topsoil. Their burrows have few openings to the soil surface. Anecic earthworms draw litter from the soil surface into their burrows and feed on it underground, their burrows are deep and permanent. Figure from Fraser and Boag (1998), photos of common earthworms courtesy of R. Gray.

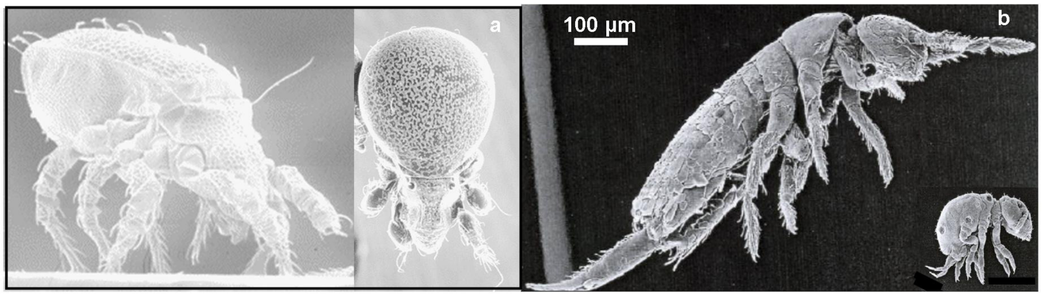

Fig. 3. Examples of a) Oribatida and b) Collembola. Images modified from Smith et al. (1996) and Greenslade and van Klinken (2006).

The soil microfauna (body diameter <100 µm) are dominated by nematodes. In grasslands nematodes can reach densities in the order of millions per square metre, but due to their small size they also have a low biomass (Curry, 1994). Nematodes are represented in all trophic groups within the decomposer food web, and have important roles in soil services (Yeates and Pattison, 2006) (Fig. 4). Bacterial feeding and fungal feeding nematodes are important for nutrient cycling, while predatory and omnivorous nematodes, in turn, regulate the populations of other microfauna. Plant feeding nematodes, or plant parasitic nematodes, while having pathogenic effects at high densities, may also stimulate plant growth at low densities.

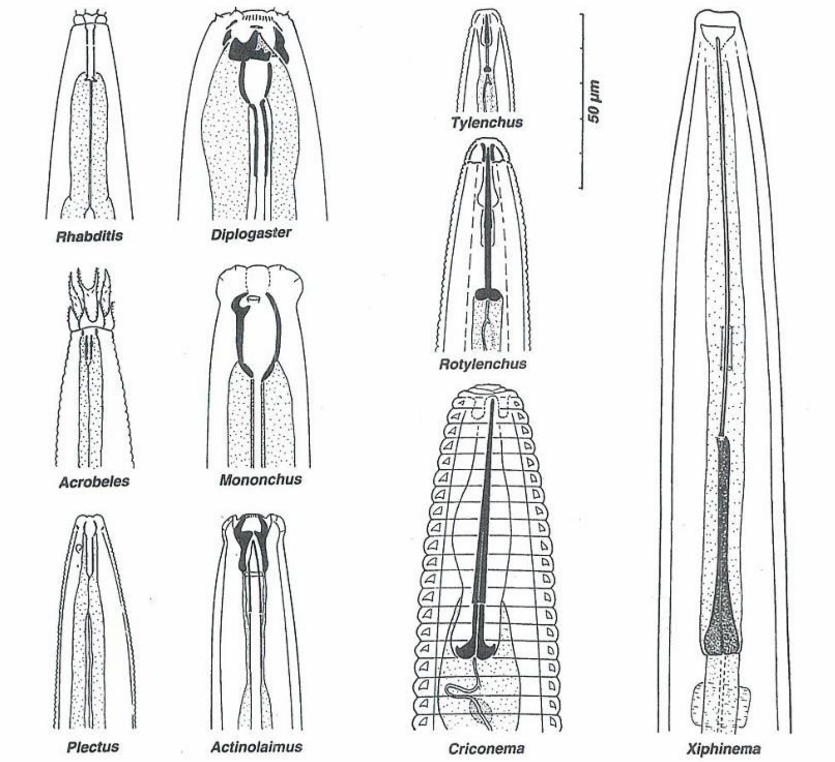

Fig. 4. Example of the trophic diversity in soil nematodes. Bacterial-feeding nematodes include *Rhabditis, Acrobeles*, and *Plectus*. Plant associated nematodes include *Tylenchus* and plant feeding include *Rotylenchus, Criconema* and *Xiphinema. Actinolaimus*is a predator/omnivore. *Diplogaster* and *Mononchus* are either predators or bacterial feeders. Diagram from Yeates (1999).

Soil functional biodiversity

The functional role of the micro-, meso- and macrofauna can be considered in the context of a soil food web. There are three important functional roles which can be represented in the soil food web: herbivores, decomposers (including the primary decomposers, grazers and predators) and ecosystem engineers (Brussaard, 1998). For a soil system to be stable it is not the diversity of the soil fauna which is important, but the functional diversity (Wardle et al., 2000). In other words, all functional groups within the soil food web need to be represented (Wardle, 1999). It is expected that pastoral systems which have diverse food webs may require fewer management inputs to sustain production under the pressures of grazing than more highly modified systems (Wardle et al., 1995; Yeates and King, 1997; Setälä et al., 1998).

Many studies have explored the influence of altering the decomposer food web structure on ecosystem services and have shown the importance of functional diversity. For example, in a simple food web the introduction of microbial grazers to mesocosms containing microbes increased nitrogen availability (Huhta et al., 1988). Similar observations were reported in a more complex food web, with the presence of a diverse soil community (all trophic groups represented) increasing primary production in comparison to a microbe only mesocosm (Setälä and Huhta, 1991). While these studies would suggest that the decomposing soil fauna always have a positive response on primary production, the addition of predatory microarthropods to mesocosms containing microbial grazers has been observed to inhibit mineralisation rates by controlling the microbial grazer populations (Mikola and Setälä, 1998).

Soil invertebrates in pastoral systems and their utility as indicators of soil services

Invertebrates are influenced by pasture management, responding to changes in the soil environment as fertiliser regimes and stocking rates vary. Management practices, such as fertiliser application, can stimulate invertebrate abundance and activity through increased pasture production, which leads to more food resources to the soil food web (Yeates, 1976; Zyromska-Rudzka, 1977; Cole et al., 2005; Oliver et al., 2005; Sjursen et al., 2005; Cole et al., 2006; Yeates and Pattison, 2006; Curry et al., 2008). Increased stocking rates, as a management practice to utilise additional forage, may inhibit invertebrate abundance and activity as stock treading can cause soil compaction, resulting in a reduction in habitable pore space (King and Hutchinson, 1976; Elliott et al., 1980; King and Hutchinson, 1980; Lambert, 1986; Clapperton et al., 2002; Drewry, 2006; Nielsen et al., 2008).

As well as stock treading, grazing by livestock can also impact on the invertebrate community through a number of different mechanisms including defoliation, changes in pasture composition and faecal return. By selectively grazing on different plant species aboveground herbivores alter the plant community and in turn the quality of litter to the soil food web (Bardgett et al., 1998). Further, defoliation by livestock alters root growth, morphology and exudation, important food sources to the soil food web (Ruess and Seagle, 1994; Bardgett et al., 1998). By consuming pasture and returning this to the soil surface as dung and urine, grazing by livestock speeds up the rate of nutrient cycling and concentrates nutrients in patches (Ruess and Seagle, 1994).

Invertebrate response to management is, however, complex. Increased fertiliser application is typically associated with increased stocking rates, and whether invertebrate abundance is stimulated or inhibited depends on the type of invertebrate but also other local factors such as soil type and climate and their influence on pasture production and compaction (Yeates, 1984). Further, pastoral management regimes are very diverse. The response of soil invertebrates to pastoral management will in turn influence the soil services which they provide and regulate (Lavelle et al., 2006) (Fig. 5).

Soil invertebrates have the potential to be useful indicators of soil services as they influence, and are influenced by, both the physical and chemical properties of the soil (Bardgett, 2005; Lavelle et al., 2006). Measurements of organism density and biomass reflect changes in land management, but they fluctuate spatially and temporally (McMillan, 1969; Luxton, 1982, 1983; Yeates, 1984; Fraser and Piercy, 1996). While particular taxa vary, characteristics of the invertebrate assemblage, such as trophic groups, life history strategies and body size may fluctuate less and yield information more suitable for assessing their contribution to soil services (Bongers, 1990; Yeates, 1994; Paoletti, 1999; Yeates, 2003).

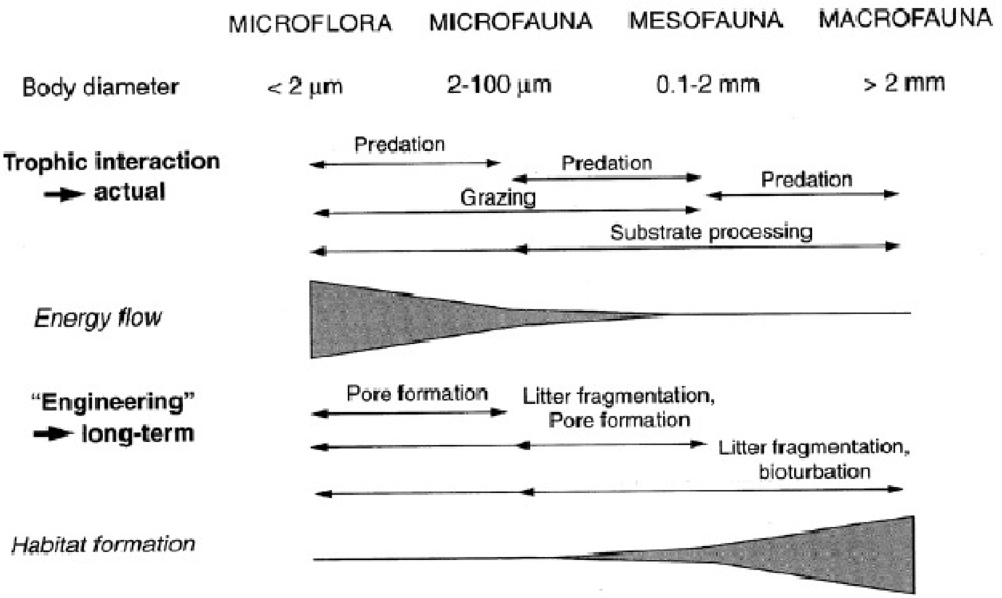

Fig. 5. Interactions between soil biota of different body widths and their effects on energy flow and habitat formation. These two services are size dependent, but biota of all body widths complement both the current trophic interactions in energy flow and the longer term engineering on habitat formation. These services are at different scales. Figure from Scheu and Setälä (2001).

The trophic structure of the invertebrate community may change as the quantity and quality of food resources entering the soil food web are altered by pastoral management (Bardgett, 2005). Improved quality of food resources increases the relative dominance of bacterial mediated decomposition over fungal mediated decomposition in the soil food web, and this is described in the indices such as the Nematode Channel Ratio (NCR) (Yeates, 2003). The bacterial decomposition pathway is associated with faster nutrient cycling in the short term, but may also be associated with greater nutrient leaching from the soil (Bardgett et al., 2005).

Organism life histories and body size are often related (Bongers, 1990; Grishina, 1991; Ritz and Trudgill, 1999). Large invertebrates such as earthworms have greater mobility to move away from disturbances. However, within a given invertebrate group, large and (typically) longer lived species are particularly vulnerable to change (Siepel, 1996). Agricultural practices which cause disturbance or disruption to soil invertebrates can influence population structure by favouring particular life history and size characters. For example, physical disturbances, such as stock treading, which alter soil pore size distribution, may result in the reduction of larger species (Ritz and Trudgill, 1999). As the frequency of disturbance is increased it is expected that the species dominating the system will have shorter generation times and have greater colonization abilities, particularly in the case of mites (Ruf, 1998; Cianciolo and Norton, 2006). Bongers (1990) proposed the use of life histories in the Maturity Index (MI), separating the plant feeding and plant associated nematodes in the Plant Parasitic Index (PPI), as an alternative in using nematodes to assess soil quality. There is ongoing debate about weighting life history and trophic habits using nematodes to indicate soil disturbance (Yeates, 1994; Bongers and Korthals, 1995; Ferris et al., 2001).

Indicators such as the NCR and MI can provide useful information on the soil invertebrate community and some soil services. To be useful to land managers, biological indicators of soil processes need to be understood and linked to management practices (Stockdale and Watson, 2009). A practical system for land managers in New Zealand is the visual soil assessment (VSA), but in this the only biological component is an earthworm count (Shepherd, 2000). From the VSA and extensive work on nematodes (Yeates, 1984) it is well established that soil type is important in regulating the soil fauna. It has been suggested that an indicator of soil quality should include information about the soil microflora, earthworms and one mesofauna group (Breure et al., 2005). There have been no attempts that I am aware of in New Zealand to construct an indicator, using all size classes of multicellular soil invertebrates, to assess the soils capacity to provide and maintain the soil services required for sustained pasture production.

Aims and hypotheses

The aim of this thesis was to:

1. Explore the response of three size classes of soil invertebrates to pastoral management under a variety of agricultural systems on the basis that there would be some consistent responses by soil fauna to pastoral management.
2. Determine the contribution of invertebrates to the availability of nitrogen in pastures.
3. Utilise the functional characteristics of invertebrate groups sensitive to changing food availability and habitable pore space in the development of a biological indicator linked directly to soil services such as nitrogen supply.

It was hypothesised that invertebrates would respond to pastoral management as food availability and habitable pore space changed. More productive pastures have more food entering the soil food web, and this should be reflected in increased faunal abundances. The negative effects of stock treading on habitable pore space were expected to be more pronounced in soils with limited physical structure, and should be reflected in decreased abundances of more sensitive invertebrate groups, such as those with limited mobility. The response of invertebrates to changes in pastoral management would depend on both their functional characteristics, as well as soil characteristics (soil characteristics influence the impact of management practices on the invertebrate environment).

Further, it was hypothesised that the presence of increased functional diversity (with more invertebrate groups present) would have a positive influence on plant nitrogen supply. However, it was expected that under pastures where nutrients were not limiting that invertebrates would not stimulate plant nutrient supply.

Lastly it was hypothesised that there would be some consistent responses by the soil fauna to pastoral management. Functional characteristics of invertebrate groups sensitive to changing food availability and habitable pore space with pastoral management could be used in the development of a biological indicator related to soil services such as nitrogen supply.

Research approach

To develop a biological indicator linked to soil services for New Zealand pastoral soils, I required a better understanding of how soil invertebrates responded to management practices across soil types in New Zealand. Invertebrate populations are not static, showing marked temporal behaviours. Several New Zealand studies have observed and reported on the temporal dynamics of a diversity of soil invertebrates (McMillan, 1969; Yeates, 1978a,b; Fraser et al., 1996). Because the aim of the thesis was to develop a biological indicator, focus was given to establishing the response of three size classes of soil invertebrates to a diversity of pasture managements (livestock type, stocking rate, fertiliser application, irrigation), rather than exploring temporal changes at just one study site. Our understanding of annual cycles in invertebrate populations was used in the design of sampling regime and in the interpretation of the findings. To ensure the major pastoral ecosystems in New Zealand were represented a number of sites with varying soil types and in different climatic zones were specifically selected in determining the relationship between invertebrates and pastoral management.

A previous study by Schon et al. (2008) reported changes in the soil invertebrate community as sheep grazed hill country was subjected to higher rates of phosphorus fertiliser application and higher sheep stocking rates. These observations by Schon et al. (2008) were believed to reflect changes in food availability within the soil food web, and in habitable pore space as affected by stock treading pressures. In order to better understand these two factors across the sampled sites, the potential amount of dry matter entering the soil was calculated, food webs of standing faunal biomass established, and habitable pores determined using resin embedding techniques (for more details see Chapter 1, Appendix 1). Chapters 1 to 7 describe the trials studied. The rationale behind the studies in the chapters was:

a) Soils in dairy cow grazed pastures are often subjected to higher nutrient inputs and stock live weight loadings (with higher treading pressures) than sheep grazed pastures. To examine how the invertebrate community responded to increases in fertiliser application and stocking rates under dairy grazed pastures two research farms were sampled. One farm was situated on a well structured Allophanic soil, with pastures grazed at different stocking rates, a cut and carry system, and a fallow, allowing the influence of changes in food availability within the soil food web and in stock treading pressures to be examined (Chapter 1). Soil type is known to be an important factor affecting both soil properties and soil invertebrates. Pastoral management often differs on different soils, making it difficult to compare the effects of management among different soil types. A mosaic of different soil types on a single farm in the Waikato allowed the assessment of management (increasing stocking rates, fertiliser and supplements) on soil invertebrates on two different soil types (Chapter 2).

b) Organic systems are often seen as less intensive, with strict limits on nutrient inputs, and are often managed to promote biological activity. Whether organic systems indeed encouraged biological activity was examined in two studies. One study examined the influence of commercial dairy grazed organic systems paired with conventional systems, on four different soils (Chapter 3). Another study examined organic and conventional sheep grazed farmlets in which two important management factors which influence the soil fauna, stocking rates and fertiliser application, remained the same (Chapter 4).

c) Stocking rate, fertiliser inputs and soil type are not the only important factors affecting soil invertebrates. Water balance is also important, with the land area under irrigation increasing in New Zealand. To determine the effects of irrigation (in a drought prone region) on soil invertebrates, and to examine how invertebrates responded to fertiliser application and stocking rates where summer irrigation reduced moisture stress, a sheep grazed irrigation trial in Canterbury was sampled (Chapter 5).

d) The absence of stock treading is included among treatments in Chapters 1 and 4, but is examined in more detail in Chapter 6. Here, the vulnerability of soil invertebrates to stock treading was examined on three different soils. Their sensitivity to treading was examined in grazed pastures with respect to an adjacent permanent fence line. The resilience of these same invertebrate communities was examined in the same paddock, where grazing pressure had been removed three years previously and different combinations of nitrogen and phosphorus fertiliser applied, with subsequent mowing and irrigation.

e) A case study examining the predictability of the response of soil invertebrates to increases in phosphorus fertiliser and sheep stocking rates in two contrasting soils was carried out. A previous study by Schon et al. (2008) of sheep grazed pastures on a Luvisol was compared with a study of sheep grazed pastures on Andosol (Chapter 7).

In order for a biological indicator to be useful to land managers, it must be linked to soil services of interest to the land manager. A mesocosm study was conducted to determine the influence of two soil bulk densities and two rates of nitrogen inputs on four different combinations of soil fauna and their effects on nitrogen turnover, uptake and leaching (Chapter 8). The study sites were used to explore the relationships between potential food resources, soil physical condition and soil invertebrates (Chapter 9). The study sites described in the above Chapters (with the exclusion of Chapter Four and ungrazed pastures) were used to develop a soil invertebrate threshold indicator linked to soil services in grazed New Zealand pastures (Chapter 10).

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Chapter One:

The influence of intensification on the abundance and diversity of soil invertebrates in dairy pastures

Schon et al. (2008) found that the invertebrate community was influenced by increasing fertiliser inputs, pasture production and sheep stocking rates. This chapter explores the influence of a change in defoliation regimes (pastoral fallow, cut and carry, cow grazing), feed availability to ruminants (pasture and pasture supplemented with maize) and dairy cow stocking rates (3, 4 and 5 cows/ha) on the abundance and diversity of soil invertebrates (macrofauna, mesofauna and microfauna) in an Andosol.

N.L. Schon, A.D. Mackay, G.W. Yeates, M.A. Minor. 2010. Separating the effects of defoliation and dairy cow treading pressure on the abundance and diversity of soil invertebrates in pastures. *Applied Soil Ecology* 46, 209-221.

Abstract

The impact on soil invertebrates of changes in the physical environment and feed availability in intensive pastoral systems is difficult to predict given the number of interacting factors. This study explores the influence of a change in defoliation regimes (pastoral fallow, cut and carry, cow grazing), feed availability to ruminants (pasture and pasture supplemented with maize) and dairy cow stocking rates (3, 4 and 5 cows/ha) on the abundance and diversity of soil invertebrates (macrofauna, mesofauna and microfauna). Samples were collected from two depths (0–7.5 and 7.5–15 cm) on a well structured loamy Andosol soil in two seasons (autumn and winter sampling). Treatments allowed an independent assessment of the influence of changes in food sources to the soil food web from that of stock treading.

In this well structured soil, increasing stocking rates from 3 to 5 cows/ha did not produce any change in soil porosity. Anecic *A. longa* showed little susceptibility to treading, becoming progressively more abundant at higher stocking rates as food availability increased (18 vs. 128 ind./m^2, under 3 and 5 cows/ha, respectively). Even though there was little change in soil structure as stocking rates increased, oribatid abundance decreased (8100 vs. 2000 ind./m^2, under 3 and 5 cows/ha, respectively). Oribatid abundance (and size) was greatest under the less disturbed fallow where porosity was highest (28% under fallow vs. 11–13% under other treatments). Under fallow, the nematode community was more mature (i.e., higher MI) and had a higher dominance of bacterial feeding nematodes (NCR 0.97) reflecting the still high quality litter from previous management. Grazed pastures had higher abundances of plant feeding and plant associated nematodes as they were stimulated by increased root growth (abundances up to 1.2 $x10^6$ ind./m^2). Functional diversity, as observed through a food web of standing faunal biomass, was reduced under grazed pastures with the absence of macrofauna predators. However, not all diversity was negatively influenced by intensification with earthworm diversity increasing, as litter incorporating anecic earthworms increased. We propose that anecic earthworms can substitute for epigeic earthworms in intensively managed pastoral systems by incorporating litter, as well as being important ecosystem engineers.

Chapter One

Introduction

Pastoral agriculture continues to intensify pasture production, animal performance and stocking rates in order to sustain economic profitability. To sustain these higher production levels, production of legume based dairy pastures in New Zealand has increasingly been augmented by the addition of fertilisers and through the importation of supplementary feed. Supplementary feeding means ruminants deposit more dung on the soil surface, leading to the faster return of nutrients to the soil plant system (Ruess and Seagle, 1994). Faster growing pastures, as a consequence of high nutrient inputs, increase the quantity of plant detritus to the soil and decrease the soil C:N ratio, with an overall increase in nutrient input into the soil food web. As a result, fertilised pastures (without other disturbances) often support a greater abundance of soil invertebrates (Yeates, 1976; Zyromska-Rudzka, 1977; Cole et al., 2005; Oliver et al., 2005; Sjursen et al., 2005; Curry et al., 2008). The increase in pasture growth stimulates populations of plant and bacterial feeding fauna (Yeates and Bongers, 1999), with the bacterial based decomposition pathway becoming relatively more dominant than the fungal based pathway (Yeates and Pattison, 2006).

The effects of increased nutrient availability in fertilised pastures are frequently compounded by other factors such as the negative effect of increased stocking rate on soil porosity. Macroporosity, a measure of pores >30 µm diameter (ø) (Greenwood and McKenzie, 2001), of less than 10% has been shown to have negative impacts on pasture growth. Nearly half of the New Zealand dairy farms sampled by Sparling and Schipper (2004) have macroporosity values in this range. Compaction as a consequence of stock treading can reduce available habitable pore space for soil invertebrates (Elliott et al., 1980; Nielsen et al., 2008). While 'ecosystem engineers' such as earthworms may be less affected by compaction and typically increase in abundance in intensively grazed pastures (Lambert et al., 1996; Curry et al., 2008), the soil mesofauna relies on soil structural integrity and frequently declines in abundance in compacted soils (King and Hutchinson, 1976; Clapperton et al., 2002). Nematodes, and their activities, are influenced by available habitable pore space (Yeates et al., 2002).

Increased fertility and stock treading tends to cause a decline in Oribatida as physical disturbance increases, while other Acari and Collembola show less consistent trends due to local complexities in factors such as fertiliser regimes, stocking rates and soil type (King and Hutchinson, 1976; Cole et al., 2008; Schon et al., 2008). Nematodes have also shown varying responses to management practices depending on soil type

(Yeates, 1984), however, several studies have shown that soil and plant nematodes respond in tandem and predictable ways to the same environmental factors (Yeates et al., 2009). Overall, more intensively managed and more disturbed systems are less diverse and favour species, in a given invertebrate group, with smaller body sizes, shorter generation times and lower ‘maturity’ scores (Bongers, 1990; Swift and Anderson, 1993; Siepel, 1994; Ruf, 1998; Coja and Bruckner, 2006).

Many intensively managed pastures in the North Island of New Zealand are situated on Andosol soils. Andosols are well structured volcanic soils with a high macroporosity and low bulk density, allowing for rapid drainage and root penetration (Hewitt, 1993). Even though Andosols have a low structural vulnerability (Hewitt and Shepherd, 1997), they can suffer from compaction (Singleton and Addison, 1999). This study explores the influence of a change in defoliation regimes (fallow, mown and grazed), feed availability to ruminants (grass only and grass supplemented with lucerne) and increases in dairy cow treading (3, 4 and 5 cows/ha), on soil fauna in an Andosol. Treatments allowed an independent assessment of the influence of changes in food sources to the soil food web, and that caused by stock treading. Any increase in available substrate and nutrients to the soil should benefit a range of soil invertebrates, including earthworms and nematodes. However, a decline in available habitable pore space through compaction may adversely affect some soil invertebrate populations (Elliott et al., 1980; Nielsen et al., 2008). This would impact on those species such as Oribatida, which are not ‘ecosystem engineers’ as well as larger species within a given invertebrate group. Intensively managed systems, with their faster nutrient turnover, should be dominated by short lived organisms (i.e., lower maturity index). As food quality and quantity changes, we expected changes in trophic groupings, with an increase in plant and bacterial feeding nematodes in the most intensive systems (i.e., higher NCR).

Methods

Study paddocks

The study was carried out at the DairyNZ, Westpac Taranaki Agricultural Research Station, Taranaki, New Zealand (39°36'S 174°18'E). The average air temperature was 12.9ºC and rainfall was 1124 mm in the year preceding the study. The soil is classified as an FAO (1988) Andosol (NZSC: Allophanic, Egmont black loam)

(Hewitt, 1993), a well drained volcanic loam (55% sand, 23% silt, 22% clay) with high porosity (New Zealand Soil Bureau, 1968; Barratt, 1971).

Five treatments (four paddocks of 0.1 ha for each treatment) were imposed in 2002 until April 2007. Treatments included a fallow, cut and carry, and dairy cows grazing at 3, 4 and 5 cows/ha (Table 1). The fallow treatments received no fertiliser and were not defoliated. The cut and carry treatments were mown to coincide with grazing events and received dairy shed effluent to replace removed nutrients. Among the grazed treatments, 4 and 5 cows/ha included supplements (lucerne pellets and some pasture silage) to maintain similar intakes of metabolizable energy by dairy cows. Grazed treatments received 47 kg P/ha/yr as superphosphate. All treatments, except for the fallow, were grazed at 3 cows/ha after April 2007.

Table 1. Treatment properties and management inputs for pastures under different defoliation regimes and stocking rates, Taranaki, New Zealand (2007).

Management	Fallow	Cut & carry	Grazed	Grazed	Grazed
Stocking rate (cows/ha)	0	0	3	4	5
Live weight (kg/ha)[1]	0	0	1 350	1 800	2 250
Management inputs					
P (as superphosphate) (kg P/ha/yr)	0	24*	47	47	47
N (kg N/ha/yr)	0	210*	0	0	0
Supplement (kg DM/ha/yr)	0	0	0	3850	8250
PASTURE PARAMETERS (1000's kg DM/ha/yr)					
Pasture production (from actual data)	n.d.	11.9	14.0	14.6	15.4
Pasture intake[2]	n.d.	10.1	11.9	12.4	13.1
DM from litter[3]	32.0	16.9	21.9	23.7	25.2
DM from dung [4]	0	0.5	4.2	5.7	7.5
DM from roots[3]	6.0	7.0	8.0	9.0	9.0
Total DM	38.0	24.4	34.1	38.4	41.7

[1] Standard cow: 450 kg live weight. Treading pressure of a cow 138 kPa and a tractor 58 kPa(Greenwood and McKenzie, 2001).

[2] 0.85x pasture production. Pasture production was not determined under fallow.

[3] Calculated from Parsons et al. (1983), for details see Appendix 1. DM: Dry matter.

[4] 0.35x of animal intake. Dung applied through the application of effluent calculated using 0.9% dry matter (Longhurst et al., 2000).

*Estimated nutrients applied through dairy shed effluent application.

In the month before the autumn (March) 2007 sampling, the modelled water deficit (Scotter et al., 1979) had predominantly been at approximately 0 mm available water (difference between 10 and 1500 kPa for 0–7.5 cm soil depth), while prior to the winter (August) 2007 sampling it had been at approximately 20 mm available water. Soil temperature (Checktemp, Hanna Instruments, UK) and moisture (TDR 300 Soil Moisture Probe, Spectrum Technologies Inc., USA) at 0–10 cm depth were recorded in the field at the time of sampling.

Soil biological sampling

Three cores for macrofauna (15.5 cm ø, 0–15.5 cm depth) were collected from each paddock in winter 2007 (total of 60 samples). Macrofauna cores were hand sorted in the laboratory, fauna identified and wet weights determined (Wimbledon et al., 1996).

Five soil cores for mesofauna (5 cm ø, 0–7.5 and 7.5–15 depths) were collected from each paddock in both autumn and winter 2007. Mesofauna were extracted using a modified Berlese-Tullgren apparatus (mesh size ~2 mm). Organisms were collected in 70% ethanol for counting and identification. The mesofauna was then classified into trophic groups according to Petersen and Luxton (1982) and Symstad et al. (2000). Adult oribatid mites were cleared with 70% lactic acid and identified to species level using keys by Balogh and Balogh (1992a, b), Luxton (1985), Norton (unpublished), and Hammer (1966, 1967, 1968). Morphospecies were designated if species identification was not possible. The body width (soma only) of oribatid species was measured on selected adults.

One composite soil sample for microfauna (nematodes) (5 cores, each 2.5 cm ø pooled) was collected from each paddock, from 0–10 cm soil depth in autumn 2007, and from 0–7.5 cm and 7.5–15 cm soil depth in winter 2007. Nematodes were extracted by the modified tray method described by Yeates (1978a). Nematodes were counted, fixed by adding boiling 8% formaldehyde and mounted onto temporary slides for identification. Nematodes were identified to nominal genera and allocated to feeding groups following Yeates et al. (1993a; 1993b). The Nematode Channel Ratio (NCR), Maturity Index (MI), Plant Parasitic Index (PPI) and ΣMaturity Index (ΣMI) were calculated (Bongers, 1990; Yeates, 1994, 2003).

The Shannon-Wiener diversity index (H'), Margalef's richness (SR) and Pielou's evenness (J') were calculated to describe the diversity of soil fauna (Yeates, 1984; Ludwig and Reynolds, 1988).

Soil microbial biomass activity was estimated using substrate induced respiration. Three composite samples (20 cores, each 2.5 cm ø, 0–7.5 cm depth) were collected from each paddock in winter 2007. Moisture content and water holding capacity were determined. Samples were sieved (<2 mm) and stored at 4ºC. Duplicate soil samples (50–60% water holding capacity) were weighed (10 g ±0.1) and incubated at 25ºC for seven days; 60 mg glucose dissolved in 0.1 ml distilled water was added to the first sample, 0.1 ml distilled water was added to the second sample. Samples were sealed in 560 ml jars, and incubated at 25ºC. The amount of CO_2 respired was estimated by collecting 25 ml of headspace gas in a preevacuated (-80 kPa for two minutes) 12 ml Exetainer® and analysing the gas samples in a Gilson 222XL autosampler (Gilson, Inc., Middleton, USA) and Shimadzu-20190 gas chromatograph (Shimadzu Scientific Instruments, Columbia, USA).

Soil and pasture sampling

After extraction the mesofauna cores were sieved and analysed for soil pH (1:2.5 soil:water), Olsen P (Olsen et al., 1954), total nitrogen (N) and total carbon (C) (dry combustion using LECO-2000, LECO Equipment Corp., St. Joseph, USA). Bulk density was determined by collecting two intact soil cores (10 cm ø, 0–7.5 cm depth), and macroporosity from one intact soil core per paddock in winter 2007.

Percent cover for each species of vegetation was estimated in 0.5 m^2 quadrats. Eight quadrats in each paddock were measured. Quadrats were located systematically at 5 m intervals along a 40 m transect. Root biomass was determined by collecting three composite soil samples (20 cores, each 2.5 cm ø, 0–7.5 cm depth) from each paddock in winter 2007. Samples were crumbled into a hydropneumatic root washer, soil washed from the roots, roots and tillers towel dried, separated, dried at 60ºC, and weighed.

Pore size distribution for water filled pores <60 µm ø was determined using tension plates (Danielson and Sutherland, 1986). Pores >50 µm were characterised using a fluorescent resin technique. For details see Appendix 1.

Statistical analysis

To investigate the effect of pasture management on the abundance of macrofauna, mesofauna, and microfauna the data were log (x+1) transformed and analysed using PROC MIXED in SAS v.9.1 (SAS Institute Inc., USA), using Satterthwaite degrees of freedom. The effect of management was determined for both sampling dates and both soil depths (where appropriate). Depth was treated as a repeated measure. The graphs and tables show untransformed arithmetic means. Least square means were used to show treatment differences in a given season in the tables. Error bars in figures represent the standard errors of the means. To determine the trends resulting from increased stocking rates, samples were analysed using PROC REG in

SAS v.9.1. for a significant (α=0.1) and consistent $\geq$10% increase or decrease from 3 cows/ha to 5 cows/ha

Results

Soil and pasture properties

Soil moisture was lowest in the undefoliated pastoral fallow in both seasons (Table 2). Soil under the fallow also had lower bulk density and higher macroporosity (28%, with an average of 16% for the other treatments), than the cut and carry and grazed treatments. Similarly, the fallow had a larger average pore area estimated by the fluorescent resin technique, with more pores <3 mm ø (Table 2, Fig. 1). Soil under the cut and carry had similar bulk densities and pore size distributions to the soil under the grazed pasture treatments. In the sieved soil there were more pores 6–30 µm ø under cut and carry and 3 cows/ha than the other treatments.

Olsen P, soil C%, and C:N ratio were similar across all treatments (Table 2). Total C was lower under fallow (43 200 kg C/ha under fallow vs. 56 300 kg C/ha for 0–7.5 cm depths under other treatments). Legumes were not observed in fallow treatments, pasture in this treatment being dominated by low fertility pasture species including, *Agrostis* sp. (bentgrass), *Dactylis glomerata* (cocksfoot), *Bromus willdenowii* (prairie grass) and *Prunella vulgaris* (self heal). Grazed and mown pastures were dominated by *Lolium perenne* (ryegrass), with *Trifolium repens* (white clover) the dominant legume and *D. glomerata*. The proportion of legumes in the pasture sward was highest under cut and carry.

Soil fauna

Earthworm abundance was highest under fallow, 4 and 5 cows/ha (Table 3). Highest earthworm biomass was found at 5 cows/ha (261 g/m^2), where the large anecic *Aporrectodea longa* was abundant. In grazed treatments, there was a significant (*P*=0.007) trend of increasing earthworm biomass and diversity (H') with increased stocking rate, reflecting the increasing abundance of this anecic species. In this Andosol, earthworm abundance was lower than that reported from a range of New Zealand grazed pastures by Springett (1992) and Schon et al. (2008).

Other macrofauna were most diverse in the fallow treatment and H' showing a consistent decline with increasing stocking rate (Table 3). Caterpillars of the native pasture pest *Wiseana cervinata* (porina) (P=0.011) and large Chilopoda (P=0.001) were only found in the fallow treatment.

Table 2. Soil and herbage properties in pastures under different defoliation regimes and stocking rates, Taranaki, N.Z. (winter 2007).

Management	Fallow	Cut & carry	3 cows/ha	4 cows/ha	5 cows/ha
Soil moisture (%)[1]	**47^{a}**	**51^{b}**	**57^{c}**	**56^{c}**	**58^{c}**
Soil temperature (°C)[1]	10	11	11	10	11
Bulk density (Mg/m^{3})[2]	**0.56^{a}**	**0.70^{b}**	**0.73^{b}**	**0.72^{b}**	**0.70^{b}**
Macroporosity (%)	**28^{a}**	**19^{b}**	**15^{b}**	**15^{b}**	**14^{b}**
Porosity (% v/v sieved soil)					
0.2–6 µm*	19	19	19	23	23
6–30 µm*	**8^{a}**	**9^{b}**	**13^{b}**	**6^{c}**	**5^{c}**
Porosity (intact cores from 2.5 cm depth)					
Porosity (%)	**28^{a}**	**13^{b}**	**11^{b}**	**13^{b}**	**11^{b}**
Mean pore area (mm^{2})	2.2	1.1	1.7	1.3	1.6
Pores that fit <175 µm16-sided polygon (%)	**18^{a}**	**36^{b}**	**29^{c}**	**35^{bc}**	**33^{c}**
Pores that fit >350 µm16-sided polygon (%)	**59^{a}**	**37^{b}**	**44^{b}**	**41^{b}**	**42^{b}**
Microbial biomass (µg C/g soil)[2]	1660	2644	1945	1769	832
pH[2]	5.8	5.8	5.6	5.8	5.9
Olsen P (mg/L)[2]	46	38	39	45	46
Total N (%)[2]	0.98	1.02	1.01	1.05	1.10
Total C (%)[2]	10.2	10.3	10.2	10.6	11.1
C:N ratio[2]	10.5	10.1	10.1	10.1	10.1
HERBAGE COMPOSITION (%)					
Grass	78	59	89	89	89
Legume	0	28	6	8	5
Other (including weeds)	22	13	5	3	6
Root biomass (g dry wt/m^{2})[2]	330	567	315	348	471

[1] 0–10 cm depth.

[2] 0–7.5 cm depth.

^{a,b,c,d,e}indicate significant difference at α=0.05 (least squares means) in a given row.

*Pores 0.2–6 µm ø retain mostly plant unavailable water and excludes most microorganisms, with no predation on bacteria. Pores 6–30 µm ø retain mostly plant available water and accommodate most bacteria and their predators (Brewer, 1964).

Mesofauna abundance, particularly total Collembola (P=0.0001), tended to increase with stocking rate in autumn (Table 4). In contrast, mesofauna abundance decreased with stocking rate in winter as Collembola abundance decreased (P=0.025). Neelipleona were more abundant under fallow. Collembola abundance in this study were higher than those reported by Schon et al. (2008) but similar to those reported by McMillan (1969) and Adams (1971) in New Zealand grazed pastures. Of the 23 groups listed in Table 4, ten showed significant management effects in autumn and six in winter. Eleven and six mesofauna groups showed consistent trends with stocking rate in the two seasons, but only Coleoptera showed the same consistent trend in both seasons. In autumn, H' diversity declined with stocking rate.

Oribatida abundance was significantly influenced by treatment – it was highest in the fallow treatment in both seasons (*P*=0.028 in autumn, *P*=0.001 in winter), and progressively declined in grazed treatments as stocking rate increased. Two adult Oribatida species showed significant management effects in autumn, and four in winter (Table 5). Most Oribatida species were of medium size (body width 175–350 µm, Fig. 2) and herbifungivores; the most abundant species overall was the cosmopolitan *Liebstadia similis*. *Lanceoppia* sp., *Achipteria* sp., and *Oribatella* sp.2 were restricted to the fallow treatment. Mesostigmata populations were not significantly influenced by treatment and were dominated by Parasitidae, *Hypoaspis* and *Rhodacarellus silesiacus.* In this study Acari abundances were lower than those reported by Schon et al. (2008) but similar to those reported by McMillan (1969) and Adams (1971) in New Zealand grazed pastures.

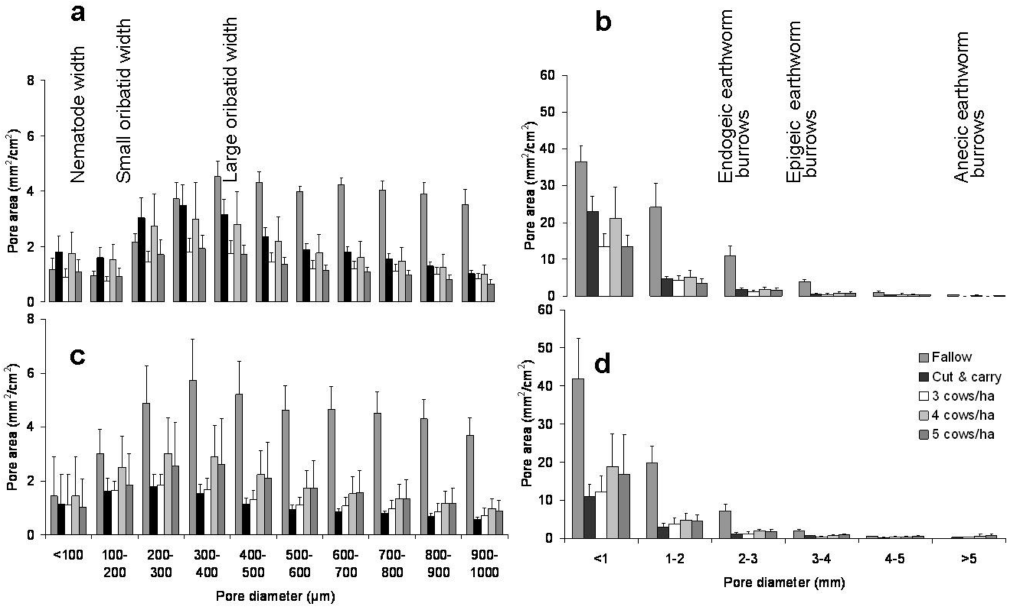

Fig. 1. Pore areas (mm^2/cm^2) over ranges of pore sizes as estimated from resin embedded cores from pastures under different defoliation regimes, Taranaki, New Zealand. (a) Pores <1 mm ø at 2.5 cm depth. (b) All pores (<1 to >5 mm ø) at 2.5 cm depth; the <1 mm bar is the sum of pores shown in (a). (c) Pores <1 mm ø at 5 cm depth. (d) All pores (<1 to >5 mm ø) at 5 cm depth; the <1 mm bar is the sum of pores shown in (c).

Chilopoda extracted in Berlese-Tullgren funnels were more abundant in the fallow treatment in autumn and Diplopoda were more abundant in winter (Table 4). Thysanoptera were more abundant in the cut and carry treatment in autumn (*P*=0.01). Formicidae, Psocoptera, Amphipoda and Symphyla were found in low abundance and are not reported in tables.

Total nematode abundance was not significantly influenced by treatments (Table 6). Forty nematode taxa were discriminated, nine of which showed significant effects of management intensity in one or both (Hoplolaimidae only) seasons. Fourteen taxa showed consistent trends in abundance with stocking rate, but only *Tripyla* showed the same consistent trend in both seasons. *Longidorus* was highest in 5 cows/ha, while *Prismatolaimus* was most abundant in fallow, in both seasons. The plant feeding *Heterodera, Meloidogyne* and Hoplolaimidae were least abundant in fallow. Nematode abundances in this study were similar to those reported by Yeates (1976, 1984) in New Zealand grazed pastures.

The food web of standing faunal biomass in winter showed macrofauna predators absent from all treatments except fallow (Fig. 3). The biomass of mesofauna was highest under fallow where the biomass of nematodes was lowest. The biomass of fungal feeding nematodes was low in all treatments and is not included. Total faunal biomass was lowest under 3 cows/ha and highest under 5 cows/ha.

Influence of season

Season significantly influenced soil moisture (P=0.001) and temperature (P=0.001) (data for winter sampling shown only, Table 2). Soil temperatures were higher in the autumn than winter (16ºC vs. 10ºC, respectively), when soil moisture was lower (25% vs. 54%, respectively). Many mesofaunal groups, as well as total mesofauna abundance, tended to be higher in autumn (Table 4). The abundance of mesofauna was higher in autumn than winter, due to a large abundance of Collembola (P=0.10), consistent with other New Zealand studies (McMillan, 1969; Adams, 1971). The overall abundance of Acari was higher at the autumn than winter sampling, due to higher abundance of Prostigmata and Scutacaridae (P=0.006). Several mesofaunal groups appear to be less influenced by season in the fallow treatment than the other treatments. Oribatida species detected in winter, but not autumn were *Lanceoppia* sp., *Oppiella nova, Achipteria* sp., *Minunthozetes semirufus, Galumna rugosa, Oribatella* sp.2, *Maculobates minor* and *Setobates scheloribatoides* (Table 5). Total nematode abundance was higher in autumn (P=0.0001), following an atypically dry summer, in comparison to winter. Yeates (1978b) found highest nematode abundance in autumn in irrigated pastures (soil moisture approximately 20% in autumn compared with 25% in this study). Exceptions were larger CP4 *Eudorylaimus* and *Doryllium* which were more abundant in winter. Many nematode genera and some trophic groups were significantly influenced by season. There was an increase in bacterial feeding and CP1 nematodes (P=0.0001), and a decrease in plant feeding and plant associated and CP5 nematodes (P=0.001) from autumn to winter (Table 6). Large *Aporcelaimus* (♀ L >2 mm) decreased with stocking rate in autumn, while large *Longidorus* (♀ L ~5 mm) increased with stocking rate in autumn. *Pungentus* (♀ L ~1.8 mm) increased with stocking rate in winter.

Table 3. Earthworms and other macrofauna at 0–15 cm soil depth in pastures under different defoliation regimes and stocking rates, Taranaki, N.Z. (winter 2007).

Management	Fallow	Cut & carry	3 cows/ha	4 cows/ha	5 cows/ha	T
EARTHWORMS (ind./m^2)						
Lumbricus rubellus (Hoffmeister, 1843)	93	22	9	26	22	
Eisenia andrei (Bouche, 1972)	**31^{a}**	**0^{b}**	**0^{b}**	**0^{b}**	**4^{b}**	
Aporrectodea caliginosa (Savigny, 1826)	433^{α}	$230^{\alpha\beta}$	269^{α}	$411^{\alpha\beta}$	340^{α}	
Octolasion cyaneum (Savigny, 1826)	**13^{α}**	**4^{α}**	**9^{α}**	**26^{β}**	**13^{α}**	
Aporrectodea rosea (Savigny, 1826)	0	4	0	4	4	↑
Aporrectodea longa (Ude, 1885)	13	53	18	53	128	↑↑
Total earthworms	**583^{a}**	**314^{b}**	**305^{b}**	**521^{a}**	**512^{a}**	
Earthworm biomass (g wet wt/m^2)	**187^{a}**	**138^{b}**	**101^{c}**	**186^{a}**	**261^{d}**	↑↑
Anecic: total earthworm abundance	**0.07^{a}**	**0.38^{b}**	**0.17^{ab}**	**0.28^{b}**	**0.49^{c}**	↑↑
Anecic: total earthworm biomass	**0.15^{a}**	**0.44^{b}**	**0.14^{a}**	**0.31^{b}**	**0.60^{c}**	↑↑
SR	**2.04^{α}**	**$3.16^{\beta\chi}$**	**3.45^{β}**	**$2.30^{\alpha\chi,}$**	**$2.32^{\alpha\chi,}$**	
J'	**0.28^{ab}**	**0.26^{ab}**	**0.16^{a}**	**0.33^{bc}**	**0.39^{c}**	
H'	**0.50^{a}**	**0.47^{a}**	**0.28^{a}**	**0.60^{b}**	**0.69^{b}**	↑↑
OTHER MACROFAUNA (ind./m^2)						
Wiseana cervinata (Walker, 1865) larvae (Hepialidae, Lepidoptera)	**18^{a}**	**0^{b}**	**0^{b}**	**0^{b}**	**0^{b}**	
Costelytra zealandica (White, 1846) larvae (Scarabaeidae, Coleoptera)	0	9	9	9	13	↑
Click beetle larvae (Elateridae, Coleoptera)	18	40	13	18	13	
Weevils (Curculionidae, Coleoptera)	22	31	93	115	44	
Coleoptera (adult)	4	0	0	0	0	
Gastropoda	**31^{a}**	**4^{b}**	**0^{b}**	**4^{b}**	**0^{b}**	
Chilopoda (Myriapoda)	**75^{a}**	**0^{b}**	**0^{b}**	**0^{b}**	**0^{b}**	
Total other macrofauna	168	84	115	146	71	
Other macrofauna biomass (g wet wt/m^2)	17	5	4	3	2	↓
SR	4.08	1.64	2.05	1.53	1.50	
J'	0.15	0.08	0.08	0.06	0.05	
H'	0.34	0.18	0.17	0.13	0.11	↓

^{a,b,c,d,e}indicate significant difference at α=0.05, $^{\alpha,\beta,\chi,\delta}$indicate significant difference at α=0.1 (least squares means) in a given row at a given date.
T: consistent 10% change across stocking rates (↓ or ↑), ↑↑significant regression at α=0.1.

Table 4. Mesofauna at 0–7.5 cm depth in pastures under different defoliation regimes and stocking rates, Taranaki, N.Z. (autumn and winter 2007).

Season	Autumn						Winter					
Management	Fallow	Cut & carry	3 cows/ha	4 cows/ha	5 cows/ha	T	Fallow	Cut & carry	3 cows/ha	4 cows/ha	5 cows/ha	T
MESOFAUNA (1000's ind./m^{2})												
Oribatida	**13.3**^{a}	**7.5**^{b}	**4.9**^{c}	**4.6**^{c}	**2.6**^{c}	↓	**21.0**^{a}	**10.4**^{b}	**8.1**^{b}	**3.9**^{c}	**2.7**^{d}	
Mesostigmata	7.1	8.6	6.3	8.7	6.9		6.5	5.1	7.1	4.7	4.6	
Prostigmata	6.8	13.2	11.8	10.1	8.1		1.6	1.1	1.9	0.8	1.0	
Astigmata	0.7	0.8	2.1	0.5	0.3	↓↓	1.1	0.2	0.2	0.1	0.1	
Scutacaridae	1.1	2.9	2.0	0.7	4.3		0.2	0.4	0.8	0.8	0.3	
Total Acari	29.0	33.2	26.9	24.7	22.3	↓	**30.5**^{a}	**17.5**^{b}	**18.1**^{b}	**10.3**^{c}	**8.7**^{c}	
Entomobryomorpha	**9.7**^{a}	**9.9**^{a}	**13.3**^{b}	**30.1**^{c}	**41.8**^{d}	↑↑	**1.5**^{a}	**4.9**^{b}	**8.4**^{c}	**9.7**^{c}	**3.9**^{b}	
Poduromorpha	**0.6**^{a}	**1.4**^{b}	**2.0**^{c}	**2.3**^{c}	**1.5**^{b}		**0.03**^{a}	**0.9**^{b}	**1.6**^{c}	**0.3**^{d}	**1.1**^{e}	
Sminthuridae	**0.1**^{a}	**0.6**^{b}	**1.1**^{c}	**2.7**^{d}	**1.9**^{e}		0.3	0.7	1.3	0.6	0.6	↓
Neelipleona	**2.8**^{a}	**0.1**^{b}	**0.2**^{b}	**0.1**^{bc}	**0.1**^{c}	↓	1.2	0.2	0.2	0.1	0.1	
Total Collembola	**13.2**^{a}	**12.1**^{a}	**16.6**^{b}	**35.1**^{c}	**45.3**^{c}	↑↑	**3.0**^{a}	**6.8**^{b}	**11.4**^{c}	**10.7**^{c}	**5.8**^{b}	
Diplura	0.3	0.1	0.1	0.3	0.2		0.03	0	0	0	0	
Protura	0	0	0.03	0.03	0	↓	0.1	0.1	0.03	0	0.1	
Lepidoptera	0.3	0.4	0.3	0.3	0.2	↓	0	0	0	0	0	
Coleoptera	**0.3**$^{\alpha\beta}$	**0.1**$^{\alpha}$	**0.1**$^{\alpha}$	**0.1**$^{\alpha}$	**0.2**$^{\alpha\beta}$	↑	0.2	0.1	0.1	0.2	0.2	↑
Diptera	0	0	0	0.3	0		0.1	0.2	0.2	0.2	0.1	↓
Hemiptera	**0.5**^{a}	**0.1**^{b}	**0.1**^{c}	**0**^{d}	**0.1**^{b}		0.2	0.2	0.03	0.03	0.2	
Thysanoptera	**3.0**^{a}	**6.7**^{b}	**4.1**^{c}	**4.9**^{c}	**3.5**^{ac}		3.9	0.3	1.4	0.2	0.2	
Arachnida	0.4	0.3	0.1	0.3	0.3		0	0	0	0	0	
Chilopoda	**0.1**^{a}	**0**^{b}	**0**^{b}	**0**^{b}	**0**^{b}		0.1	0.03	0.1	0.03	0.1	
Diplopoda	0.8	0.3	0.03	0.2	0.2	↑	**0.2**^{a}	**0.03**^{b}	**0.1**^{c}	**0**^{d}	**0**^{d}	
Pauropoda	1.1	1.2	0.5	0.6	1.5	↑	0.6	0.3	0.1	0.1	0.2	
Total mesofauna	49.3	54.4	48.9	66.9	73.6		39.0	25.5	31.5	21.7	15.5	
SR	6.3	5.4	5.2	4.8	4.8		5.4	5.8	5.3	5.6	5.6	
J'	0.44	0.45	0.42	0.39	0.38		0.36	0.39	0.10	0.33	0.36	
H'	1.36	1.42	1.30	1.23	1.19	↓↓	1.09	1.18	1.20	1.01	1.09	

^{a,b,c,d,e}indicate significant difference at α=0.05, $^{\alpha,\beta,\chi,\delta}$indicate significant difference at α=0.1 (least squares means) in a given row at a given date.

T: consistent 10% change across stocking rates (↓ or ↑), ↑↑significant regression at α=0.1.

Table 5. Average abundance (ind./m^{2} at 0–7.5 cm depth) of Oribatida in pastures under different defoliation regimes and stocking rates, Taranaki, N.Z. (autumn and winter 2007).

Season	Autumn						Winter					
Management	Fallow	Cut & carry	3 cows/ha	4 cows/ha	5 cows/ha	T	Fallow	Cut & carry	3 cows/ha	4 cows/ha	5 cows/ha	T
Platynothrus peltifer (Koch, 1839)	0	100	0	30	0		260	50	0	0	0	
Tectocepheus sarekensis (Trägårdh, 1910)	0	150	0	30	0		**0**^{a}	**430**^{b}	**30**^{c}	**0**^{a}	**0**^{a}	
Lanceoppia sp.	0	0	0	0	0		30	0	50	0	0	
Microppia minus (Paoli, 1908)	320	0	180	100	50	↓	180	150	30	80	70	
Oppiella nova (Oudemans, 1902)	0	0	0	0	0		130	0	30	0	0	
Achipteria sp.	0	0	0	0	0		**2090**^{a}	**0**^{b}	**0**^{b}	**0**^{b}	**0**^{b}	
*Minunthozet*es *semirufus* (Koch, 1841)	0	0	0	0	0		50	50	0	0	0	
Punctoribates punctum (Koch, 1839)	0	0	0	0	0		30	180	50	0	0	
Oribatella sp.1	**1880**^{a}	**280**^{b}	**0**^{c}	**30**^{d}	**50**^{e}	↑	**640**^{a}	**0**^{b}	**0**^{b}	**0**^{b}	**0**^{b}	
Oribatella sp.2	0	0	0	0	0		76	0	0	0	0	
Liebstadia similis (Michael, 1888)	4910	5780	2650	3310	1150		**10750**^{a}	**7970**^{b}	**6700**^{b}	**3440**^{c}	**2520**^{c}	
Maculobates minor (Hammer, 1967)	0	0	0	0	30		**330**^{a}	**0**^{b}	**0**^{b}	**0**^{b}	**0**^{b}	
Setobates minor (Hammer, 1967)	0	0	0	0	0		130	0	0	0	0	
Setobates scheloribatoides (Ramsay, 1966)	0	0	0	0	0		0	0	100	0	0	
Eupelops sp.	**0**^{a}	**690**$_{b}$	**0**^{a}	**100**^{c}	**0**^{a}		50	260	380	180	0	
Total Oribatida (adult)	**7110**^{a}	**5660**^{a}	**2830**^{b}	**3590**^{b}	**1270**^{c}		**14740**^{a}	**9090**^{b}	**7360**^{b}	**3690**^{c}	**2590**^{c}	
Nymphs	6180	2160	2040	1020	1380		**6290**^{a}	**1300**^{b}	**710**^{c}	**230**^{d}	**90**^{d}	

^{a,b,c,d,e}indicate significant difference at α=0.05 (least squares means) in a given row at a given date.

T: consistent 10% change across stocking rates (↓ or ↑).

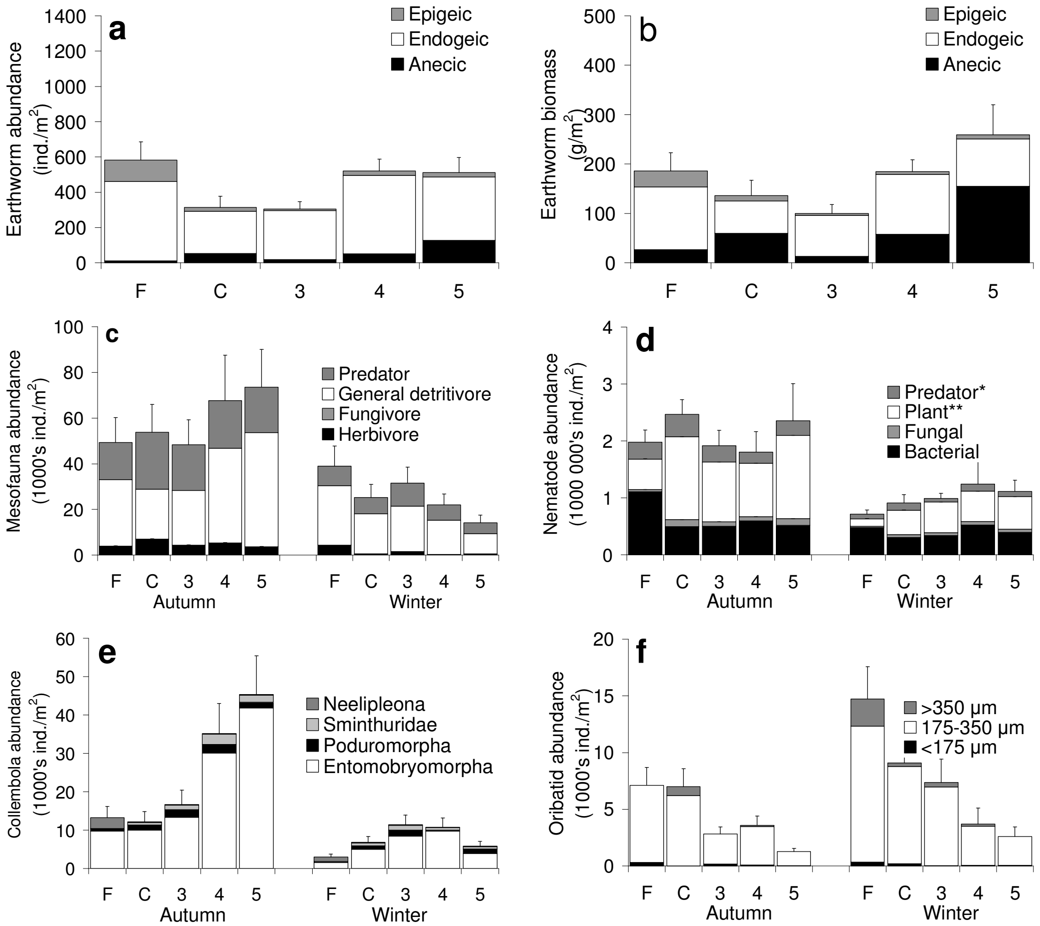

Fig. 2. Invertebrates under different defoliation regimes and stocking rates in Taranaki, New Zealand. (a) Abundance of earthworm functional groups, (b) biomass of earthworm functional groups, (c) abundance of mesofauna trophic groups, (d) abundance of nematode trophic groups, (e) abundance of Collembola groupings, and (e) abundance of body sizes of adult Oribatida. Treatments: fallow (F), cut and carry (C), 3 cows/ha (3), 4 cows/ha (4) and 5 cows/ha (5).
*Predacious and omnivorous nematodes.
**Plant feeding and plant associated nematodes.

Influence of depth

Soil depth influenced soil physical, chemical and biological properties. Bulk density increased with depth (*P*=0.004) and Olsen P (*P*=0.0001), soil total N (*P*=0.0001) and soil total C (*P*=0.0001) decreased with depth (data not shown).

The abundance of many mesofauna groups decreased from 0–7.5 and 7.5–15 cm depth in both autumn (58 600 to 17 900 ind./m^2) and winter (26 700 to 11 900 ind./m^2) (*P*=0.0001, Tables 4 and 7). Some nematodes showed depth differences, including total abundance which declined with depth in winter (*P*=0.0001, 0.99 x10^6 to 0.54 x10^6 ind./m^2) (Tables 6 and 7).

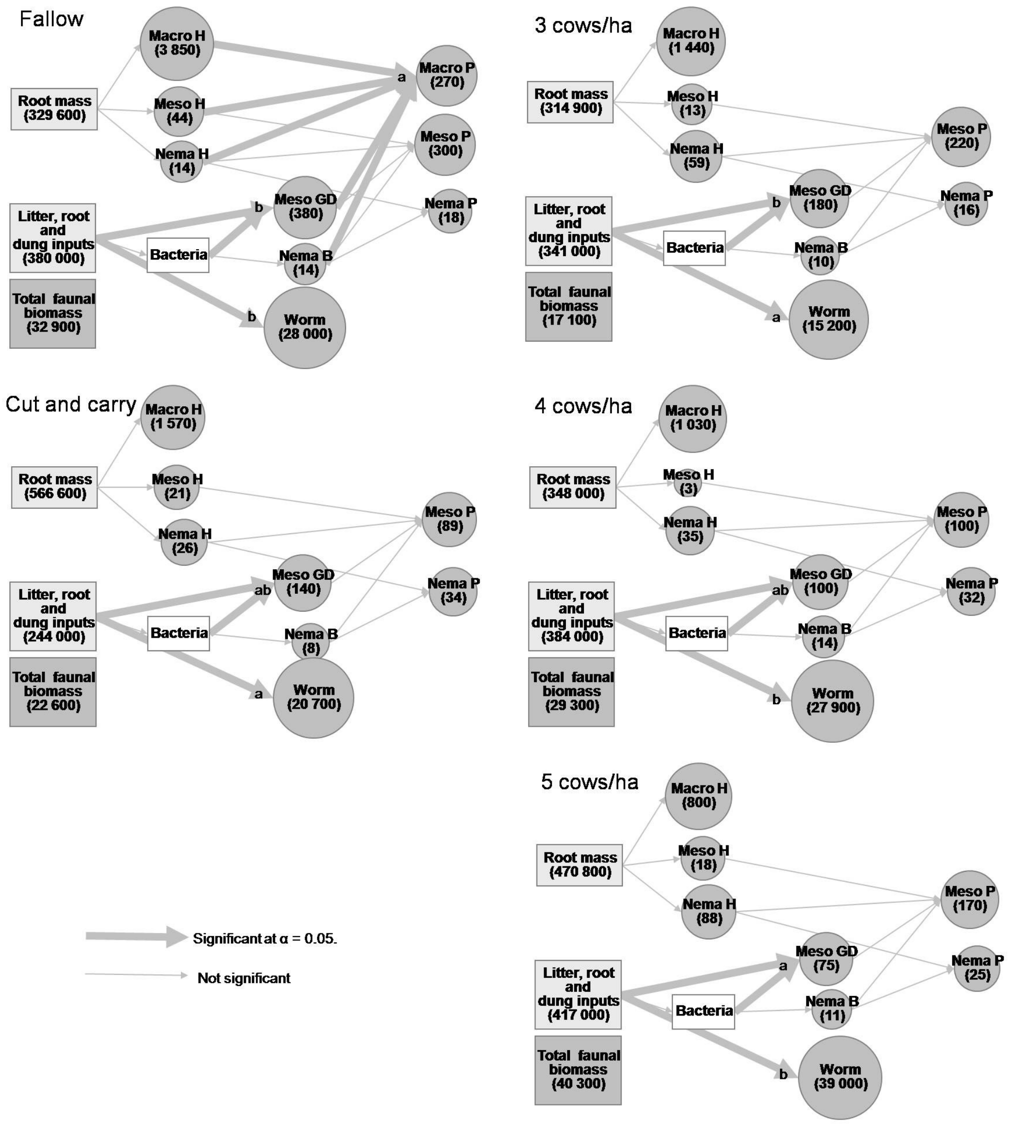

Fig. 3. Food-webs of selected soil faunal groups in pastures under five different defoliation regimes and stocking rates, Taranaki, New Zealand (winter 2007). Food web and calculations after Hunt (1987) and Mulder et al. (2005). Resource inputs are given in mg dry weight/m^2. Macrofauna (Macro), mesofauna (Meso) and nematode (Nema) herbivores (H) feed on plant material. Earthworms (Worm), mesofauna general detritivores (GD) and nematode bacterial feeders (B) feed on detrital inputs and associated microflora. The macrofauna, mesofauna and nematodes are in turn consumed by predators (P). Circle areas represent the log biomass of the fauna, with actual biomass (dry weight mg/m^2) given in parentheses. Biomass calculated as shown in Appendix 1. Trophic groups, including fungal feeders, with biomass <1.5 mg dry weight/m^2 were excluded. Wide arrow and $^{a, b}$ given in the arrow head indicate significant difference at $\alpha=0.05$ within the functional group to which the arrows lead.

Table 6. Nematode abundance in pastures under different defoliation regimes and stocking rates in autumn (0–10 cm depth) and winter (0–7.5 cm depth), Taranaki, N.Z. (autumn and winter 2007).

Season	Autumn						Winter					
Management	Fallow	Cut & carry	3 cows/ha	4 cows/ha	5 cows/ha	T	Fallow	Cut & carry	3 cows/ha	4 cows/ha	5 cows/ha	T
NEMATODA (1000's ind./m^{2})												
Tylenchus	122.8	162.9	140.8	131.2	119.1	↓	73.4	147.3	97.5	107.8	141.3	↑
Cephalenchus	26.5	21.1	17.4	23.2	32.3	↑	2.3	4.7	13.2	12.7	9.2	↓
Ditylenchus	9.6	27.1	7.7	11.6	5.0		0	2.3	5.3	9.5	0	
Heterodera juvenile	0	39.2	27.0	9.6	39.7		2.3	0	2.6	3.2	3.1	
Meloidogyne juvenile	**16.9**^{a}	**13.0**^{b}	**46.3**^{c}	**27.0**^{c}	**99.2**^{b}		0	4.7	0	12.7	9.2	
Hoplolaimidae	**105.9**$^{\alpha\beta}$	**386.1**$^{\chi}$	**360.7**$^{\chi}$	**237.3**$^{\beta\chi}$	**434.2**$^{\chi}$		**9.2**^{a}	**95.8**^{b}	**168.6**^{c}	**101.5**^{b}	**95.2**^{b}	↓
Pratylenchus	24.0	9.0	7.7	27.0	19.8		22.9	23.4	10.5	53.9	46.1	
Paratylenchus	21.7	90.5	15.4	59.8	220.8		11.5	21.0	50.1	38.1	33.8	
Aphelenchus	4.8	30.2	15.4	1.9	14.9		4.6	11.7	26.3	12.7	27.6	
Aphelenchoides	21.7	24.1	15.4	32.8	37.2	↑	4.6	2.3	5.3	22.2	3.1	
Diplogaster	2.4	0	0	0	0		0	2.3	0	0	3.1	
Rhabditidae	132.4	30.2	30.9	54.0	59.5		98.6	44.4	50.1	101.5	52.2	
Dauerlarvae	**14.4**$^{\alpha\beta}$	**0**$^{\chi}$	**0**$^{\chi}$	**17.4**$^{\alpha\beta}$	**2.5**$^{\beta\chi}$		94.1	21.0	52.7	3.2	9.2	
Panagrolaimus	26.5	12.1	15.4	11.6	19.8		75.7	67.8	55.3	139.6	95.2	
Cephalobus	21.7	75.4	42.4	21.2	29.8		80.3	77.1	63.2	145.9	98.3	
Heterocephalobus	108.3	57.3	63.7	69.5	57.1		2.3	2.3	18.4	3.2	30.7	
Acrobeles	96.3	57.3	92.6	96.5	72.0		22.9	9.4	13.2	38.1	21.5	
Cervidellus	91.5	42.2	32.8	32.8	42.2	↑	13.8	18.7	10.5	22.2	9.2	
Teratocephalus	31.3	30.2	50.1	30.9	17.4	↓	0	2.3	0	3.2	0	
Plectus	38.5	21.1	15.4	30.9	29.8		**32.1**$^{\alpha}$	**16.4**$^{\alpha\beta}$	**13.2**$^{\beta}$	**0**$^{\chi}$	**9.2**$^{\beta}$	
Anaplectus	105.9	6.0	9.6	15.4	12.4		4.6	9.4	23.7	15.9	18.4	
Prismatolaimus	**91.5**^{a}	**3.0**^{b}	**9.6**^{c}	**54.0**^{d}	**19.8**^{e}		36.7	7.0	23.7	15.9	18.4	
Wilsonema	9.6	9.0	1.9	0	0		2.3	4.7	2.6	3.2	0	
Monhystera	14.4	24.1	11.6	1.9	2.5		11.5	4.7	10.5	34.9	15.4	
Tripyla	0	0	0	1.9	2.5	↑↑	18.4	2.3	0	9.5	12.3	↑
Dorylaimus	19.3	6.0	0	0	0		4.6	7.0	7.9	6.3	0	↓
Mesodorylaimus	0	0	3.9	3.9	0		0	4.7	0	0	6.1	
Eudorylaimus	0	12.1	32.8	19.3	2.5	↓	20.7	74.8	21.1	50.7	36.9	

Season	Autumn						Winter					
Management	Fallow	Cut & carry	3 cows/ha	4 cows/ha	5 cows/ha	T	Fallow	Cut & carry	3 cows/ha	4 cows/ha	5 cows/ha	T
Labronema	86.7	81.4	108.0	52.1	49.6		**0**$^{\alpha}$	**0**$^{\alpha}$	**0**$^{\alpha}$	**3.2**$^{\beta}$	**18.4**$^{\chi}$	↑↑
Pungentus	28.9	135.7	113.8	71.4	111.6		**4.6**^{a}	**74.8**^{b}	**73.8**^{b}	**114.2**^{c}	**150.5**^{d}	↑↑
Aporcelaimus	108.3	205.1	86.8	81.0	76.9	↓	20.6	35.0	23.7	41.2	21.5	
Longidorus	**16.9**^{a}	**69.4**^{b}	**46.3**^{b}	**59.8**^{b}	**72.0**^{b}	↑	13.8	18.7	55.3	25.4	86.0	
Sectonema	0	0	0	0	2.5		0	0	0	0	0	
Dorylaimellus	28.9	63.3	63.7	77.2	84.4	↑↑	2.3	23.4	34.2	22.2	6.1	↓↓
Tylencholaimus	0	0	17.4	0	0		0	21.0	7.9	6.3	3.1	
Doryllium	2.4	36.2	21.2	17.4	39.7		4.6	23.4	13.2	25.4	18.4	
Clarkus	16.9	6.0	5.8	0	0		13.8	7.0	5.3	6.3	0	
Alaimidae	50.6	15.1	15.4	17.4	24.8		0	9.4	2.6	0	3.1	
Trichodoridae	**19.3**$^{\alpha\beta}$	**0**$^{\chi}$	**0**$^{\chi}$	**0**$^{\chi}$	**2.5**$^{\beta\chi}$		4.6	7.0	23.7	28.5	0	
Diphtherophora	2.4	0	0	1.9	0		0	0	0	0	0	
Total nematodes	1976.5	2467.3	1915.3	1802.0	2352.0		713.5	909.4	985.3	1240.2	1111.8	
SR	4.7	4.6	4.8	4.8	4.7		8.5	8.5	8.6	8.5	8.7	
J'	0.65	0.61	0.64	0.65	0.62		0.69	0.74	0.72	0.74	0.73	
H'	2.40	2.26	2.37	2.41	2.31		2.55	2.71	2.65	2.75	2.68	
NCR	0.96	0.81	0.85	0.90	0.82		0.97	0.84	0.87	0.89	0.88	
Maturity groups (%)												
CP1	13	6	6	7	6		38	15	16	20	14	
CP2	46	31	32	39	35		37	36	36	38	38	
CP3	16	30	30	26	34		13	15	21	16	17	
CP4	9	11	13	9	10		7	25	16	19	19	↑
CP5	**16**^{a}	**22**^{b}	**20**^{bc}	**19**^{c}	**15**^{a}		5	9	11	7	12	
MI	1.52	1.10	1.25	1.19	0.90	↓	1.56	1.56	1.25	1.40	1.07	
PPI	0.56	1.32	1.24	1.09	1.43		0.56	1.20	1.44	1.18	1.72	
ΣMI	**2.08**^{a}	**2.41**^{b}	**2.49**^{c}	**2.28**^{bd}	**2.33**^{d}		2.12	2.76	2.69	2.58	2.79	

^{a,b,c,d,e}indicate significant difference at α=0.05, $^{\alpha,\beta,\chi,\delta}$indicate significant difference at α=0.1 (least squares means) in a given row at a given date.

T: consistent 10% change across stocking rates (↓ or ↑), ↑↑significant regression at α=0.1.

Table 7. Average mesofauna and nematode abundance (1000's ind./m^2) at 7.5–15 cm depth in pastures under different defoliation regimes and stocking rates, Taranaki, N.Z. (autumn and winter 2007).

Season	Autumn						Winter					
Management	Fallow	Cut & carry	3 cows/ha	4 cows/ha	5 cows/ha	T	Fallow	Cut & carry	3 cows/ha	4 cows/ha	5 cows/ha	T
Total mesofauna	18.9	15.3	15.7	20.1	19.4		15.9	12.9	10.6	9.1	10.8	
Oribatida	4.3	1.9	1.6	1.3	3.5		**5.7**^{a}	**0.7**^{b}	**0.4**^{c}	**0.7**^{b}	**0.5**^{c}	
Mesostigmata	2.5	4.7	4.5	6.0	4.9		3.0	4.0	4.2	3.6	3.4	↓
Acari	9.8	9.0	11.4	12.1	14.9	↑	10.0	5.9	5.8	5.7	5.6	
Collembola	4.7	1.8	1.8	1.8	1.1	↓	2.5	4.3	3.2	2.1	3.3	
Thysanoptera	0.1	0.9	0.6	3.8	0.3		0.5	0.5	0.4	0.1	0.2	
Total nematodes							1129.2	368.6	430.6	478.8	295.9	
Bacterial feeding							806.6	130.1	117.5	126.3	85.2	
Fungal feeding							11.5	21.7	14.4	18.6	12.2	
Plant and plant associated							265.0	163.2	278.3	281.9	164.8	
Predatory and omnivorous							46.1	53.6	20.4	51.9	33.7	

^{a,b,c,d,e}indicate significant difference at α=0.05 (least squares means) in a given row at a given date.

T: consistent 10% change across stocking rates (↓ or ↑).

Discussion

Andosol soils in New Zealand are tolerant to stock treading and are somewhat resistant to compaction (Singleton and Addison, 1999). The soil physical data collected as part of this study supports this assertion. Apart from the clear difference between fallow and all other treatments, the maximum stocking rate of 5 cows/ha was insufficient to produce any change in soil bulk density or porosity (Table 2 and Fig. 1), despite a live-weight loading increase from 1350 to 2250 kg/ha from 3 to 5 cows/ha. The continual burrowing activity of the earthworms, as ecosystem engineers, has the capacity to repair damage to pores caused by treading pressure. The lack of differences in pore size distribution, despite differences in earthworm functional groups (Fig. 2) may be due to a range in earthworm size and maturity within a species (Francis and Fraser, 1998), refilling of pores over time (Springett, 1983) and also earthworm type, with *A. longa* burrowing at depths below 5 cm (Felten and Emmerling, 2009).

Under grazing, earthworm abundance and biomass increased from the grass fed only system (3 cows/ha) to the supplemented grass fed system (4 and 5 cows/ha). On these well structured soils it appeared at a first glance that stock treading has no negative effect on earthworms. However, closer examination shows changes in the earthworm functional groups. Earthworm biomass was highest at 5 cows/ha (Table 3, Fig. 2), where the abundance of large anecic species, *A. longa* was highest and epigeic *L. rubellus* was low. That *A. longa* increased as stocking rate increased may be due to their behaviour and preferred habitat deep within the soil profile, whereas *L. rubellus* lives close to the soil surface. With burrows extending up to one metre below the soil surface, *A. longa* are protected from livestock treading (Cluzeau et al., 1992), which may give them a competitive advantage over epigeic earthworms. The increase in *A. longa* numbers also probably reflects increases in food availability. In the current study, calculated surface inputs of litter and dung increased with stocking rates (34 100 at 3 cows/ha to 41 700 kg DM/ha/yr at 5 cows/ha), with nearly a doubling of dung inputs between stocking rates of 3 to 5 cows/ha. While *A. longa* does not appear to have a preference for dung material (Doube et al., 1997), it consumes about twice the amount of material of *L. rubellus* (Edwards and Bohlen, 1996). In this study the estimated amount of litter consumed by *A. longa* was 4-fold that of *L. rubellus* at 3 cows/ha and 12-fold at 5 cows/ha. The increase in the proportion of anecic earthworms substitutes epigeic earthworms more sensitive to treading and their role in litter incorporation. An increase in anecic earthworms may also benefit soil structure (Lee and Foster, 1991).

Despite there being little change in habitable pore space with increased grazing pressure, there was a consistent decline in the proportion of Acari in the surface soil compared with 7.5–15 cm depth as stocking rate increased (73% in the surface 0–7.5 cm at 3 cows/ha but only 60% at 5 cows/ha). Similar trends were reported by King and Hutchinson (1976) and Schon et al. (2008). Among Acari, Oribatida abundance on this well structured soil was lower than that reported in sheep grazed pastures by Schon et al. (2008). Oribatida, which often appear sensitive to physical disturbance (Clapperton et al., 2002; Cole et al., 2008), decreased in abundance as stocking rates increased in the present study (Fig. 2). Oribatida and their physical habitat have been found to be disturbed by earthworm burrowing (Maraun et al., 2001), and it may the continual, restorative burrowing of endogeic and anecic earthworms that is having a detrimental impact on Oribatida as earthworm abundances increase. Under grazing there is no change in Oribatid size with stocking rate as, unlike in fallow, their assemblage is dominated by medium sized species.

Pasture management under fallow, where stock treading and pasture defoliation were absent, and where all litter returned to the soil surface, provide the most favourable habitat for some soil invertebrates as is highlighted by the portrayal of biomass in the soil food web (Fig. 3). Removal of stock treading alone (i.e., cut and carry with mechanical perturbations during harvesting) was not enough to improve the soil porosity and the habitable pore space for soil invertebrates such as Oribatida. Earthworm abundance was high under fallow pastures where *L. rubellus* was abundant (Fig. 2). That *L. rubellus* was more abundant under fallow, reflects their positive response to litter material (Doube et al., 1997), but may also reflect the greater susceptibility of these earthworms to stock treading (Cluzeau et al., 1992). Oribatid abundance was also highest under fallow where habitable pore space increased. More large pores and no disturbance under fallow resulted in more large Oribatida (>350 µm) than in the grazed treatments in winter (16% in fallow vs. <5% in grazed treatments) (Fig. 2). That both earthworm and Oribatida abundances were high under fallow indicates, as in the case of nematodes, improved food resources available to Oribatida more than offset any adverse impacts of earthworm activity. The surface activity of epigeic earthworms, which were more abundant under fallow, may not impact Oribatida as much as the burrowing actions of endogeic and anecic earthworms.

Although slower rates of nutrient cycling were expected under fallow, with no fast return of nutrients through dung, the soil food web was still found to be dominated by the faster bacterial decomposition pathway compared with the fungal feeding pathway. Even under fallow, fungal biomass was too low to be shown in the food web (Fig. 3). Substrate available within the fallow soil food web was predominantly from plant litter (32 000 kg DM/ha/yr under fallow vs. an average of 24 000 kg DM/ha/yr under grazed treatments, Table 1). Further, fallow pastures had a higher dominance of bacterial feeding nematodes than grazed pastures, with a higher NCR (Table 6, Fig. 3). A high NCR in this fallow soil is not inconsistent with the literature, because prior to these treatments being imposed the area supported high fertility pastures, consequently the quality of litter has remained high (soil C:N ratio 10.5 under fallow, 10.1 under grazed treatments). This stimulated the bacterial decomposition pathway, and resource competition between bacterial feeding nematodes and epigeic earthworms was avoided (Fig. 2) (Yeates, 1981). Faunal biomass was higher, including herbivorous, decomposer and predatory groups, under fallow (with the exception of earthworms at 5 cows/ha, Fig. 3).

Even though resource availability to bacterial populations was stimulated by litter inputs under fallow (Table 1), total nematode abundance was higher under grazed pastures. Grazed pastures stimulated populations of plant feeding and plant associated nematodes (Fig. 3), with higher root mass and a dominance of higher quality pasture species. For example, as root mass increased under grazed pastures, the large plant-feeding *Longidorus* increased from 46 000 ind./m^2 at 3 cows/ha to 72 000 ind./m^2 at 5 cows/ha (autumn), a response to increased plant growth also reported by Yeates et al. (2008). Further, plant feeding and plant associated nematodes may be responding to competition under fallow from herbivorous macrofauna, such as porina (Fig. 3). Even though plant feeding and plant associated nematodes were stimulated under grazed pastures, there was little change in either nematode trophic groupings or NCR. Substituting defoliation and dung deposition by livestock with mechanical harvesting and effluent application increased the proportion of legumes in the sward (6% in grazed vs. 28% in cut and carry) as well as increasing root mass (378 in grazed vs. 567 g dry weight/m^2 in cut and carry). While this resulted in a significant increase in the abundance of herbivorous Thysanoptera in autumn (Table 4), the proportion and abundance of plant feeding and plant associated nematodes, including clover feeding *Heterodera*, were not higher than in the grazed treatments.

This study also illustrates the importance of season. Of particular interest was the change in trends in collembolan abundance with grazing pressure. In autumn Collembola abundance increased with stocking rate. Prolonged soil moisture deficit had suppressed decomposition (Ross, 1989), causing an accumulation of litter and dung material, providing more potential food resources for detritus feeding Collembola, which play an important role in the incorporation of litter (and carbon) into the soil (Chamberlain et al., 2006). As soil moisture increased in winter Collembola abundance decreased with stocking rate and the bacterial pathway could quickly utilize this dung and litter, reducing food resources for Collembola and making them more susceptible to the effects of treading. Such changes in soil mesofauna with season were least pronounced in the fallow treatment. This may reflect the constancy of the management and resources under fallow, with the insulating and mulching effect of the accumulated litter (Nie et al., 1997). It may also reflect the change in pastoral management, as all other treatments were grazed at similar stocking rates for five months before the winter sampling.

Soil biological diversity may be expected to decline as pasture management is intensified, and while the implications of decreased diversity are poorly understood, it is suspected that it is important for all functional groups to be present (Wardle, 1999). In this study there was evidence for a decline in faunal diversity with increasing supplementation and dairy cow stocking rates, both elements of intensification. However, it was the absence of macrofauna predators in all treatments, except fallow (represented by Chilopoda and adult Coleoptera, Fig. 3), which was most obvious and may have important implications for soil functioning. The lack of macrofaunal predators in all defoliated treatments may be due to a lack of physical niches (including pores and litter) for these relatively large predators. All other faunal functional groups were represented in the soil food webs shown in Fig. 3, even though fungal feeding nematodes were present in low abundance (data not presented).

Not all faunal diversity declined with higher inputs and treading pressures in grazed pastures in this study. Earthworm diversity (H') increased significantly as the abundance and proportion of the anecic species increased, providing an example of the importance of initial diversity of functional groups to increasing external pressures. In New Zealand pastures, introduction of earthworms has been largely accidental, with anecic species being patchily distributed (Springett, 1992). Anecic earthworm establishment in New Zealand pastures may be essential in maintaining soil services, particularly as litter incorporating epigeic earthworms become increasingly vulnerable to treading, with positive effects on water infiltration and litter incorporation down the soil profile. In this study their increased abundance was associated with stable soil porosity or soil carbon contents. The extent to which anecic species can substitute for the epigeic species in intensively managed dairy grazed pastures requires further investigation. The introduction of anecic earthworms might offer a bioengineering option for sustaining these key soil services (Baker et al., 1994).

Conclusion

There were large differences in soil physical and faunal characteristics between fallow and grazed treatments. Under fallow, where there were larger pores and greater litter inputs, abundances of epigeic earthworms, bacterial feeding nematodes and large Oribatida were stimulated. Under grazed pastures plant feeding and plant associated nematodes increased in abundance. As stocking rates increased under grazing, large anecic earthworms increased in abundance while Oribatida declined. Possible lack of physical habitats resulted in an absence of macrofaunal predators from all grazed pastures. High inputs and cow stocking rates, elements of intensive pastoral systems, tended to influence soil invertebrates predictably with earthworms and nematodes responding to food availability and Oribatida to habitable pore space. However, among earthworms, functional groups responded differently, with anecic earthworms more competitive under intensive management.

This study highlights the importance of initial functional diversity in pastoral systems under intensive management and shows that soil faunal diversity does not necessarily decline as pastures intensify.

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Appendix One

Methods used in this thesis are described, along with references, in the appropriate chapters. Three areas that justify further description and explanation, are expanded on in this appendix. They include:

1. Construction of the food webs,
2. Calculation of the potential dry matter returned to the soil,
3. Quantification of soil pore size and shape (to describe in short communication).

1. Construction of the food webs

Food webs were constructed to simplify the large data sets that were collected. Food webs were derived after Hunt (1987) as shown in Fig. 1. Invertebrates were allocated to trophic groups according to Petersen and Luxton (1982), Symstad et al. (2000), Dindal (1990) and Yeates et al. (1993a). Dry weight was chosen as the measure of pool size, including dry matter inputs.

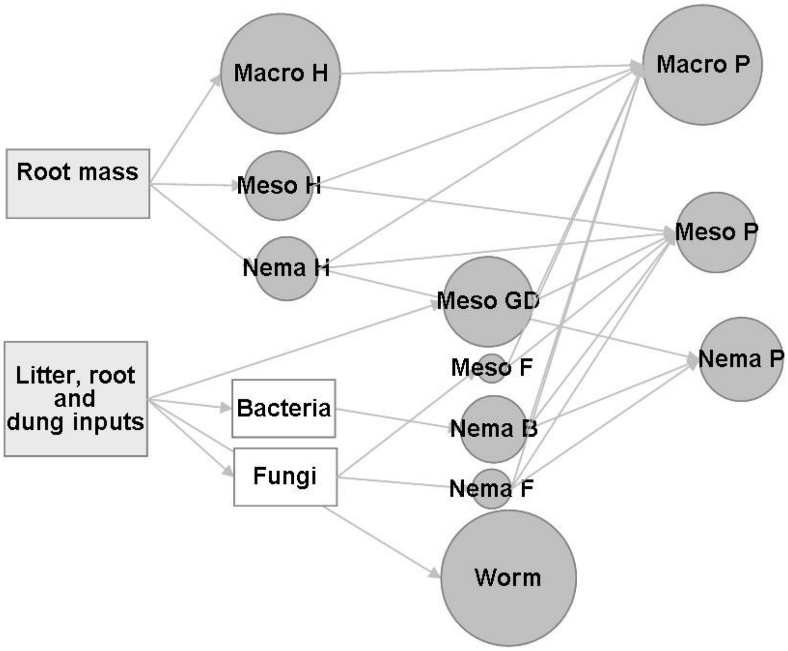


Fig. 1. Food web of selected soil faunal groups as applied in this study. Macrofauna (Macro), mesofauna (Meso) and nematode (Nema) herbivores (H) feed on plant material. Earthworms (Worm), general detritivores (GD), bacterial feeders (B) and fungal feeders (F) feed on detrital inputs and associated microflora. The macrofauna, mesofauna and nematodes are in turn consumed by predators (P) of each group. In this case circles represent the logarithm of the faunal biomass. Trophic groups were allocated and biomass calculated as indicated in Table 1.

To calculate faunal biomass a similar approach to that of Mulder et al. (2005) was used. The biomass values for each taxa used in the production of the food web are given in Table 1. The macrofauna were weighed at the time of sampling and converted to dry weight. Biomass values for mesofauna were determined from the literature. Biomass values for nematodes were calculated using the equation given in Andrássy where:

$$\text{Volume } (\mu m^3) = \text{Body width}^2 (\mu m) \times \text{Length } (\mu m) / 1700\,000$$

Table 1. The standing biomass of the described soil invertebrate populations was determined using the weights (µg dry wt.) given in the table below. To enhance versatility of the table it includes some taxa that were not encountered in the present study. Trophic groupings are also given.

Classification	Trophic group*	Individual weight	DM (%)	Source **	Classification	Trophic group*	Individual weight	Source **
MACROFAUNA***					NEMATODA****			
Earthworms[1]		Actual	15.0	1	Cephalobidae	B	0.0207	4
Coleoptera[2]	P/H	Actual	36.9	2	*Acrobeles*	B	0.0265	4
Diptera	P	Actual	25.4	2	*Cephalobus*	B	0.0105	4
Lepidoptera[3]	H	Actual	25.4		*Eucephalobus*	B	0.0109	4
Hemiptera	H	Actual	26.0	2	*Heterocephalobus*	B	0.0396	4
Chilopoda	P	Actual	26.5	2	*Nothacrobeles*	B	0.0145	4
Diplopoda	P	Actual	46.0	2	*Pseudoacrobeles*	B	0.0096	4
Gastropoda	H	Actual	16.6	2	*Zeldia*	B	0.0329	4
MESOFAUNA					Teratocephalidae	B	0.0092	6
Oribatida	GD	5		1	*Teratocephalus*	B	0.0092	6
Mesostigmata	GD	8		1	Rhabdolaimidae	B	0.0036	6
Other	GD	1		1	*Rhabdolaimus*	B	0.0036	6
Collembola	GD	3		1	Oncholaimoidae	B	0.4436	4
Diplura	GD	32		3	*Eurystomina*	B	0.4436	4
Protura	F	1		3	Plectidae	B	0.0266	4
Lepidoptera[3]	H	100			*Anaplectus*	B	0.0395	4
Coleoptera[4]	GD	156		3	*Plectus*	B	0.0325	4
Diptera[5]	GD	100		3	*Wilsonematidae*	B	0.0078	4
Hymenoptera	P	500		1	Leptolaimidae	B	0.0138	4
Psocoptera	GD	301		2	*Aphanolaimus*	B	0.0138	4
Hemiptera	H	81		2	Prismatolaimoidea	B	0.0097	4
Thysanoptera	H	7		2	*Prismatolaimus*	B	0.0097	4
Isopods	GD	186		2	Monhysteridae	B	0.0429	4
Amphipoda[6]	GD	200			*Monhystera*	B	0.0429	4
Arachnida	P	800		1	Chromadoridae	B		
Chilopoda	P	1900		1	Microbial feeding	B	0.0237	4 & 7
Diplopoda	GD	1400		1	Predacious	P	0.0115	4 & 7
Pauropoda	GD	1		3	Enoplidae	P	2.2070	4
Symphyla	GD	1		3	*Enoplolaimus*	P	1.8974	4
NEMATODA****					Enoplus	P	2.5166	4
Tylenchidae	H	0.0094		4	Ironidae	P	0.0188	4
Basiria	H	0.0072		4	*Ironus*	P	0.0188	4
Cephalenchus	H	0.0087		4	Tripylidae	P	0.1703	4
Coslenchus	H	0.0044		4	*Tripyla*	P	0.1703	4
Ecphyadophora	H	0.0011		4	Tobrilidae	P	0.2831	4
Malenchus	H	0.0034		4	*Tobrilus*	P	0.2831	4
Psilenchus	H	0.0255		4	Dorylaimidae	P	0.1925	4
Tylenchus	H	0.0154		4	*Prodorylaimus*	P	0.1944	4
Anguinidae	H	0.0530		4	*Discolaimus*	P	0.1082	4

Appendix One

Classification	Trophic group*	Individual weight	Source **	Classification	Trophic group**	Individual weight	Source **
Ditylenchus	H	0.0530	4	*Eudorylaimus*	P	0.2526	4
Meloidogynidae J2	H	0.0127	5	*Labronema*	P	0.2763	4
Heteroderidae & Meloidogynidae ♂	H	0.0351	5	*Laimydorus*	P	0.3622	4
Heteroderidae J2	H	0.0280	5	*Mesodorylaimus*	P	0.0902	4
Belonolaimidae	H	0.0221	4	*Pungentus*	H	0.0636	4
Tylenchorhynchus	H	0.0157	4	Aporcelaimidae	P	3.1855	6 & 8
Geocenamus	H	0.0211	4	*Aporcelaimellus*	P	0.3649	6 & 8
Nagelus	H	0.0296	4	*Sectonema*	P	6.0062	8
Hoplolaimidae	H	0.0325	4	Actinolamidae	P	0.4534	4
Helicotylenchus	H	0.0146	4	*Paractinolaimus*	P	0.5662	4
Hirschmanniella	H	0.0765	4	*Neoactinolaimus*	P	0.3407	4
Radopholus	H	0.0085	4	Longidoridae	H	0.5967	4
Rotylenchus	H	0.0302	4	*Xiphinema*	H	0.2057	4
Pratylenchidae	H	0.0064	4	*Paralongidorus*	H	0.7185	4
Pratylenchus	H	0.0064	4	*Longidorus*	H	0.8659	4
Criconematidae	H	0.0347	4	Belondiridae	H	0.0671	4
Criconema	H	0.0250	4	*Axonchium*	H	0.1252	4
Ogma	H	0.0445	4	*Belondira*	H	0.0538	4
Hemicycliophoridae	H	0.0450	4	*Dorylaimellus*	H	0.0224	4
Hemicycliophora	H	0.0450	4	Leptonchidae	F	0.1716	9
Tylenchulidae	H	0.0018	4	*Leptonchus*	F	0.1716	9
Gracilacus	H	0.0017	4	Aulolaimidae	B	0.0113	4
Paratylenchus	H	0.0019	4	*Aulolaimus*	B	0.0113	4
Aphelenchidae	F	0.0164	4	Tylencholaimidae	F	0.0229	4
Aphelenchus	F	0.0167	4	*Tylencholaimellus*	F	0.0212	4
Paraphelenchus	F	0.0161	4	*Tylencholaimus*	F	0.0246	4
Aphelenchoididae	F	0.0086	4	Nygolaimidae	P	0.0849	4
Ektaphelenchus	F	0.0146	4	*Nygolaimus*	P	0.0849	4
Aphelenchoides	F	0.0048	4	Mononchidae	P	0.2563	4
Seinura	P	0.0075	4	*Mylonchulus*	P	0.0958	4
Laimaphelenchus	F	0.0077	4	*Clarkus*	P	0.0844	10
Diplogastroididae	B	0.0710	4	*Coomansus*	P	0.7174	4
Diplogasteroides	B	0.0710	4	*Cobbonchus*	P	0.1278	4
Rhabditidae	B	0.0394	4	Anatonchidae	P	0.3204	4
Mesorhabditis	B	0.0394	4	*Miconchus*	P	0.4390	4
Bunonematidae	B	0.0051	4	*Iotonchus*	P	0.2017	4
Bunonema	B	0.0051	4	Alamidae	B	0.0435	4
Dilogasteridae	B	0.0629	4	*Alaimus*	B	0.0236	4
Mononchoides	B	0.0629	4	*Amphidelus*	B	0.0633	4
Panagrolaimidae	B	0.0342	4	Trichodoridae	H	0.0344	4
Panagrolaimus	B	0.0342	4	*Paratrichodorus*	H	0.0305	4
				Trichodorus	H	0.0382	4
				Diphtherophoridae	F	0.0192	4
				Diphtherophora	F	0.0192	4

[1] Wet weight/empty gut to dry weight/empty gut.[2] Dry matter % for Diptera used.[3] Coleoptera larvae herbivores, adult Coleoptera predators.[4] Weight for Staphlinidae larvae used.[5] Weight for Diptera larvae used.[6] Weight for Isopod used.

*H: herbivore, GD: general detrtivore, B: bacterial feeding, F: fungal feeding, and P: predatory and omnivorous.

**Source for weight: 1) Petersen and Luxton (1982), 2) Edwards (1967), 3) Axelsson et al. (1984), 4) Yeates and Boag (2006), 5) C.I.H (1972-1977), 6) Bongers (1988), 7) descriptions in various systematic compilations, 8) Wood (1973), 9) Yeates (1967), 10) Yeates (1987).

***Macrofauna weight: wet weight multiplied by dry matter (DM) %.

****Nematode mass was determined from published length and width measurements using the approach of Yeates and Boag (2003) and 25% dry matter (Yeates, 1979).

Calculations were based on nematode body length (adjusted for tail shape) and width as given by Yeates and Boag (2003) and converted to dry weight using Yeates (1979). This 'adult' weight was divided by a factor of 4.58 since on an annual average only 1/3 of total nematodes are adults (Yeates and Boag, 2003). Estimated masses of *Heterodera* and *Meloidogyne* were not adjusted in this manner as only juveniles and males are observed.

2. Calculation of potential dry matter returned to the soil

As food availability is a key factor regulating invertebrate abundance and their activity the potential organic inputs to the soil and the soil food web were calculated. Important sources of food to the soil food web include (a) plant litter (both aboveground and belowground), (b) dung inputs and (c) living plant roots. These are components of pasture production typically measured in agronomic field trials.

In the sites sampled for invertebrates, data on pasture dry matter production was provided by those running trials, using the 'trim' technique or by using a 'pasture plate meter' (Piggot, 1989). When information on pasture production was not available from the trial, pasture intake was estimated assuming that a standard stock unit consumes 550 kg DM/ha/yr and a standard dairy cow consumes 4500 DM/ha/yr and then applying a utilisation factor of 75% for sheep grazed pastures and 85% for dairy grazed pastures to calculate pasture production (www.maf.govt.nz).

a) *Dry matter from litter* was calculated using the relationship of Parsons et al. (1983) between grazing intensity and the partitioning of fixed carbon between shoot and root growth, respiration and animal intake. It was assumed that grazing occurred at a time optimal for pasture growth (i.e., at peak of pasture intake curve in Fig. 2 – unless grazing intensity was either considered low or high). Fig. 2 was scaled to match the peak of the pasture intake curve with the pasture intake of each site. An example of two contrasting locations, a sheep grazed pasture and a dairy grazed pasture is shown in Fig. 2. Potential litter to the soil food web is represented by the area with vertical lines in Fig. 2, the difference between total plant growth and pasture intake. Potential litter from plant roots is represented by the area with horizontal lines in Fig. 2. At a single site where fertiliser inputs were the same between treatments, treatments were plotted on the same graph. If fertiliser levels were different, treatments were plotted on separate graphs.

b) *Dry matter from dung* was calculated as 35% of pasture intake (Takahashi et al., 2007).

c) *Biomass of living roots* was estimated. Composite soil samples (20 cores, each 2.5 cm ø, 0–7.5 cm depth) were collected and crumbled into a hydropneumatic root washer, where soil was agitated using water with high pressure air bubbles. The soil was washed from the roots, roots and tillers towel dried, separated, dried at 60ºC, and weighed.

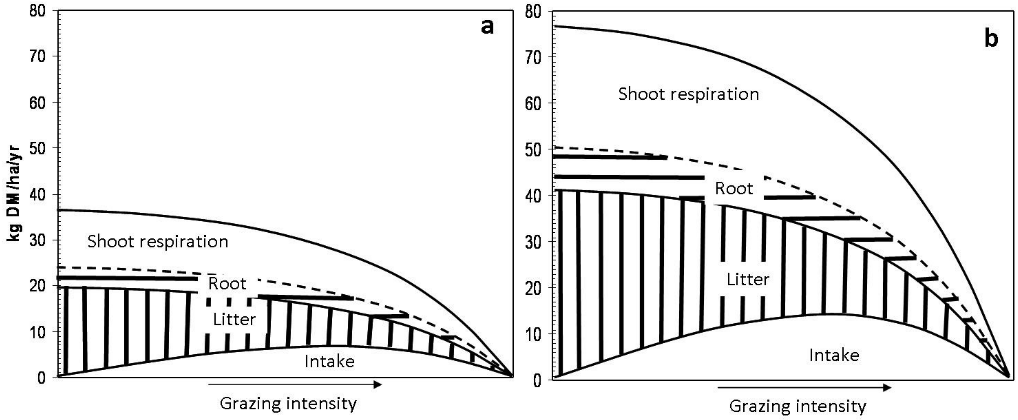


Fig. 2. Diagram showing the relationship between plant dry matter uptake and loss along a gradient of increasing grazing intensity. An example of (a) a sheep grazed pasture where pasture intake is lower than in (b) a dairy grazed pasture. Modified from Parsons et al. (1983) by scaling the vertical axis. Areas with vertical lines represent potential dry matter from aboveground plant (i.e., litter) to the soil food web and those with horizontal lines represent dry matter from roots to the soil. Pastures assumed to be grazed at the peak of the intake curve.

3. Quantification of soil pore size and shape

Habitable pore space is an important factor influencing the size and diversity of the invertebrate community. The pore size distribution was calculated separately for (a) water filled pores <60 µm in diameter (ø) and (b) for pores >50 µm ø.

a) For small pores (<60 µm ø) sieved soil which had been passed through a 2 mm sieve was saturated with distilled water. The 50 ml of saturated soil was placed in aluminium rings on ceramic plates and placed under tensions of 5, 10, 33, 50, 100, 300, or 1500 kPa and left to equilibrate until drainage stopped (Danielson and Sutherland, 1986). The soil was then removed, weighed, dried at 105°C and weighed again. From this the volume of water filled pores could be determined. The tensions equated to pore diameters of 60, 30, 10, 6, 3, 1 and 0.2 µm ø, respectively.

b) For larger pores (<50 µm ø) intact soil cores were collected in 15 cm ø PVC pipe, leaving 5 cm headspace to apply resin. To ensure minimal soil disturbance a lever press apparatus was used to collect the core (Fig. 3a). When topography prevented this a hand held fencepost rammer was used (Fig. 3b). Samples were collected when soil moisture was 40% or less to ensure penetration and curing of the resin. Plant material was trimmed to within 2 cm of the soil surface using handheld shears.

In the laboratory, any loose material at the soil surface was removed by suction to ensure pores at the surface could not block (Fig. 3c). The cores were then individually placed upside down on a workbench and the soil trimmed flush with the PVC tube using a large kitchen knife and loose material was removed by suction.

A capped, 5 cm length of 15 cm ø PVC pipe, filled with vermiculite, was bonded to the base of each core using silicon sealant. Foam rubber tape and a 5 cm section of car tyre inner tube were fitted around the outside of the bond to ensure the resilience of the seal (Fig. 3d). The cores were left at room temperature for 48 hours to allow the silicon sealant to set. A slow curing resin mixture (Table 2) containing ultraviolet fluorescent dye plus an opacifying agent was poured on the surface of each core to a depth of 5 cm, and topped up if the soil surface became visible as the resin flowed into the soil voids (Fig. 3e). The cores were then left at 4ºC for 24 hours to ensure optimum infiltration by the resin, before moving to room temperature where they were left standing for a minimum of 48 hours for the resin to set. Only cores in which the resin had cured and was visible at the base were processed further; the success rate was close to 90%.

Table 2. Resin mixture, not miscible with water, used for infiltration into soil cores. The components were thoroughly mixed at room temperature by vigorously shaking in a closed container. The resin mixture was applied to soil cores immediately after mixing.

			Part by weight
Resin	NZAA2[1]	Adhesive Technologies NZ Ltd.	1
Hardner	ADH400[1]	Adhesive Technologies NZ Ltd.	1
Opacifier	Epoxy pigment paste[1]	Adhesive Technologies NZ Ltd.	0.02
Dye	Oracet Yellow 8GF[2]	Chemiplas NZ	0.02

Once the resin had set the cores were cut with a drop saw (Fig. 3f) at the desired depths below the soil surface (2.5, 5, 8 and 12 cm). Before photographing, the sections were lightly washed with tap water to remove any smearing effects and then illuminated under ultraviolet light (Crompton 75W Blacklight Blue light bulb). Images of the exposed surface were captured using a PENTAX digital camera (K20D, DSLR with SIGMA 50 mm DG-Macro lens). The initial photographs (Fig. 3g) were captured in Adobe DNG RAW image format and later converted to a three colour binary image using Adobe Photoshop CS2®, with black pixels representing soil pores, white pixels representing soil solid, and grey pixels the outer part of the image not analysed (Fig. 3h). The outer 5 mm of the core image was removed to reduce any edge effects. Each pixel represented a 48 µm diameter patch on the original core.

The images were analysed using Solicon© analysis software (The University of Sydney, Cotton Research and Development Corporation) (Vervoort and Cattle, 2003). Images were described in terms of percent porosity and pore area (mm^2). Pore area was estimated using limbs of a 16-sided polygon. The pore area, of a certain size pore per square centimetre, was also analysed (mm^2/cm^2).

Relevant diameters include:

1. Pores >75 µm drain by gravity and accommodate roots (Brewer, 1964).
2. Nematode body widths tend to be <100 µm (Swift et al., 1979).
3. Acari and Collembola body widths tend to be <2000 µm (Swift et al., 1979). In the present pastoral systems a small oribatid is regarded as having a body width <175 µm, and a large oribatid having a body width >350 µm (body width being the soma, excluding legs).
4. Typical diameters of earthworm burrows for the epigeic *Lumbricus rubellus* are ~3 mm ø (body width 2–6 mm), the endogeic *Aporrectodea caliginosa* are ~2.5 mm ø (body width ~4 mm), and for the anecic *A. longa* are ~5 mm ø (body width 6–9 mm) (Lee, 1959; Springett, 1983).

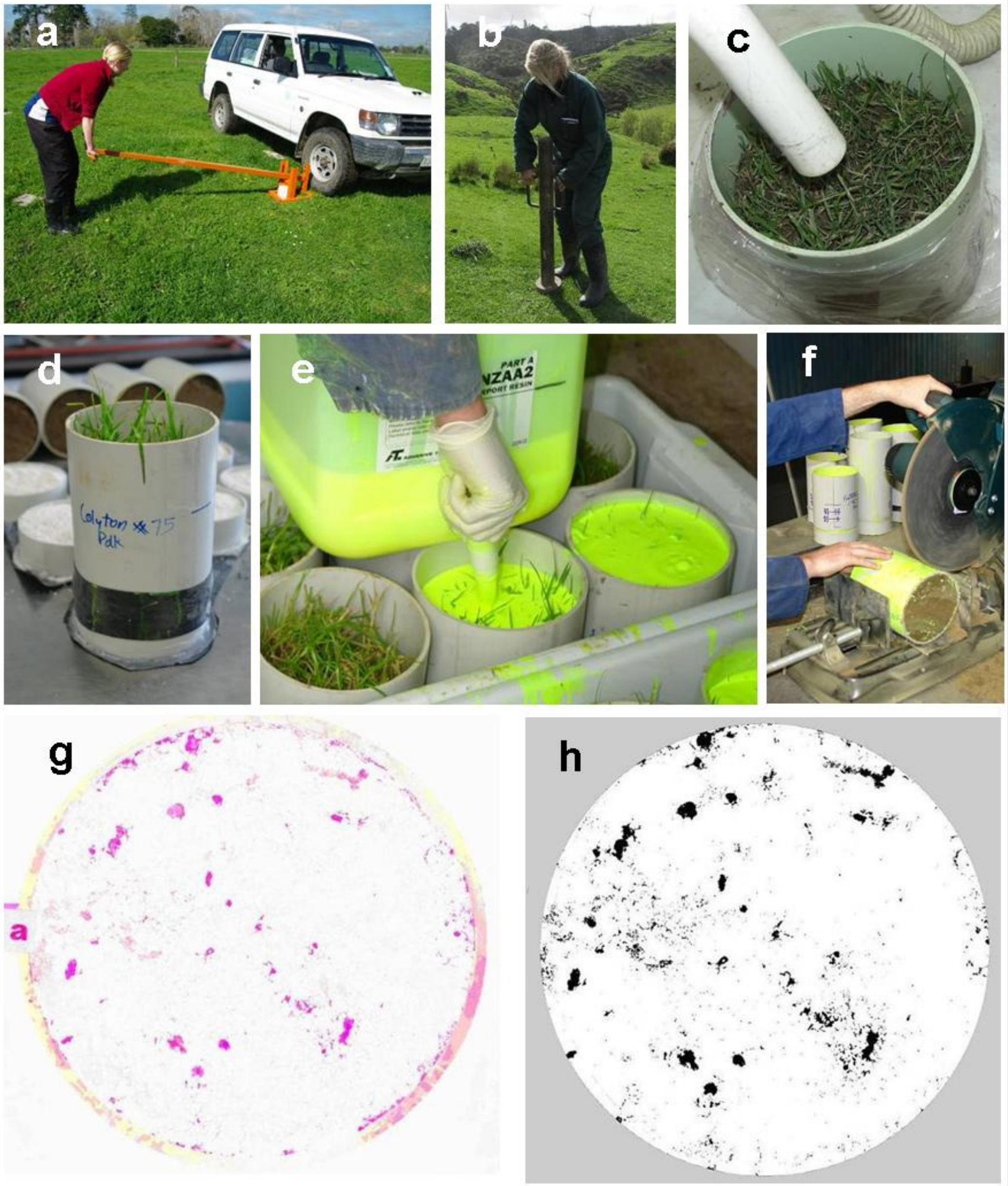
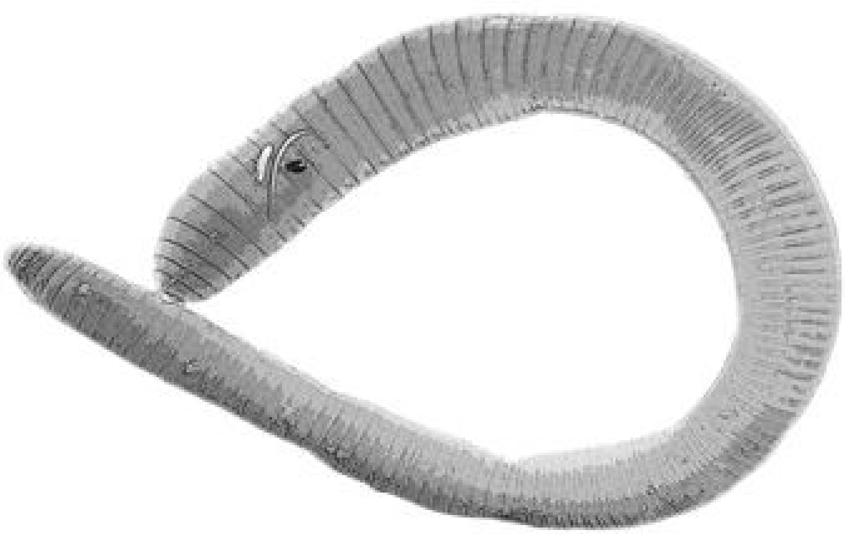


Fig. 3. From the field to the image. (a) Collecting a soil core using a lever apparatus. (b) Collecting a soil core using a hand held fence post rammer. (c) Suction removal of debris from soil surface of core. (d) Core before the application of resin. (e) Applying the resin. (f) Cutting the core with the drop saw. (i) Raw image of pores taken by camera (colours inverted). (h) The same image as converted to a 3-bit image for analysis in Solicon©.

Chapter Two:

Effects of dairy pasture intensification on invertebrates in two soils



Chapter One showed that pastoral intensification influences the invertebrate community. It is also known that soil type is important for the soil fauna. This chapter explores the response of invertebrates to pastoral management under two different soil types.

N.L. Schon, A.D. Mackay, M.A. Minor. Effects of dairy cow treading pressures and food resources on invertebrates in two soils.

Abstract

Pastoral intensification, defined by increasing dairy cow numbers and feed availability to cows, has differing effects on soil properties depending on soil type. It is often difficult to assess the effects of the same management practices on invertebrates on different soil types, as practices are generally adjusted to compensate for soil differences. A mosaic of two contrasting and co occurring soils offered a opportunity to examine the influence of management practices on soil invertebrates (macrofauna, mesofauna and nematodes). Treatments established on a well structured Andosol and poorly structured Gleysol included a legume based pasture grazed at 2.3 cows/ha, a nitrogen fertilised pasture grazed at 3.0 cows/ha and a nitrogen fertilised and maize supplemented pasture grazed at 3.8 cows/ha. We tested the hypothesis that within each invertebrate group, more intensive systems would be dominated by small, short lived organisms, with a relative increase in plant and bacterial feeding nematodes. We expected the magnitude of any response to be greater on the Gleysol.

Dairy cow treading on both soils resulted in an extremely low abundance of Oribatida (<13 000 ind./m^2), reflecting the low porosity measured in resin embedded cores (<3%). The Gleysol was characterised as having more pores >4 mm in diameter, and fewer pores <1 mm. These larger pores may have provided an important habitat for soil fauna, with similar abundances of soil invertebrates at the lowest stocking rate when compared with the Andosol. However, the detrimental effects of intensification were more pronounced on the Gleysol as habitable pores decreased. For example, Mesostigmata declined with stocking rate in the Gleysol soil, allowing Collembola abundances to recover to higher abundances. Nematode trophic groups behaved most predictably across both soil types. Nematode abundance, including plant feeding and bacterial feeding nematodes, increased from legume based to nitrogen fertilised pastures under both soil types, even though the clover cyst nematode, *Heterodera*, declined. The food web of standing faunal biomass showed that when the biomass of macrofauna herbivores was high (>2000 mg/m^2), mesofauna herbivores were low (<3 mg/m^2). There was some evidence of increased rate of nutrient cycling and lower maturity with intensification, as short lived organisms increased. Even though the more productive systems potentially have more organic matter returning to the soil, low faunal abundance and biomass would limit the incorporation of litter into the soil profile.

Introduction

Nitrogen (N) fertilisation to boost pasture growth of the traditional phosphorus (P) fertilised legume based pastures, with symbiotic nitrogen fixation, is now a feature of New Zealand pastoral agriculture. The lift in pasture productivity has often been accompanied by an increase in stocking rate and associated treading pressures leading to soil compaction (Singleton and Addison 1999). Soil compaction can impact on the composition of soil faunal communities by altering the size distribution and connectivity of the pore space. This influences both the organisms that can inhabit the pores as well as their trophic interactions (King and Hutchinson, 1976; Elliott et al., 1980; Bouwman and Arts, 2000; Nielsen et al., 2008). In contrast, increased food supply associated with increased soil fertility often stimulates the abundance of soil invertebrates (Yeates, 1976; Cole et al., 2005; Curry et al., 2008), particularly bacterial feeding, plant feeding and plant associated nematodes (Yeates and Bongers, 1999). The use of crops (e.g., maize silage, brassicas) to supplement the feed of grass fed livestock increases the deposition of urine and dung to the soil surface, and therefore the supply of carbon and plant available nutrients to the soil plant system (Ruess and Seagle, 1994). Increased rates of nutrient cycling can influence organism life history, with short lived organisms becoming dominant (Bongers and Bongers, 1998; Coja and Bruckner, 2006). Interestingly, while N fertilised legume based pastures are more productive, with increases in the potential inputs of carbon (i.e., litter) into the soil, recent data by Schipper et al. (2007) suggests a trend for losses, rather than gains of soil carbon in New Zealand pastoral soils.

It is often difficult to assess the impact of intensification practices, defined by increasing dairy cow numbers and feed availability to ruminants for milk production, on soil biota on different soil types. This is because different soils require different management practices and often have different stocking rates and fertiliser inputs. In New Zealand, different soils have formed in close proximity in a number of landscapes (Hewitt, 1993). One good example is in the Waikato, where rhyolitic alluvium was deposited in higher areas and formed well structured Andosol soil, while finer rhyolitic alluvium which was deposited in low lying areas of the alluvial plain has formed poorly structured Gleysol soils (Molloy, 1998). In both soils, porosity declines with intensive grazing, however, the Gleysol, with its high silt content, is more susceptible to compaction (Singleton and Addison, 1999). The Gleysol-Andosol mosaic in very close proximity provides a unique opportunity to investigate the effects of the same long term farm management practices on soil properties and processes and specifically on soil invertebrates, that otherwise is often confounded.

This study investigated the influence of intensification on soil invertebrates in two co occurring but very different soil types (Andosol and Gleysol). The three treatments explored are representative of current dairy management in New Zealand and include legume based pastures grazed at 2.3 cows/ha receiving P fertiliser; 3.0 cows/ha receiving P and N fertiliser; and 3.8 cows/ha P and N fertiliser and maize supplementation. All three treatments can be regarded as intensive, with high treading pressures and inputs to the soil through fertiliser additions, dung and urine deposition and maize supplementation. The hypothesis that soil invertebrates would become dominated by small, short lived organisms, in more intensive pastures with a relative increase in plant and bacterial feeding nematodes was tested. The hypothesis that the shift in the soil invertebrate community would be more profound on the poorly structured Gleysol soils, particularly for those organisms (such as Oribatida) which are sensitive to physical disturbance or changes in soil porosity was also tested.

Methods

Study sites

The study site was located on the DairyNZ, Scott Farm in the Waikato region of New Zealand (37°45'S 175°21'E). The trial site is at an altitude of 30 m, has an average air temperature of 14ºC and annual rainfall of 1200 mm. Rainfall was less (932 mm) than usual in the year leading up to the sampling (Fig. 1). The soils are classified as Andosol (FAO, 1988) (NZSC: Allophanic, Horotiu silt loam) (Hewitt, 1993) and Gleysol (NZSC: Gley, Te Kowhai silt loam). Both soils had predominantly been at about 20 mm available water (difference between 10 and 1500 kPa at 0–10 cm soil depth) in the month leading up to the sampling, with the Gleysol remaining wetter for longer after rainfall events. Pugging events are likely to occur more frequently on Gleysols as they have a lower plastic limit (Fig. 1), however pugging also occurs on Andosol soil and acts to decrease porosity (Singleton and Addison, 1999).

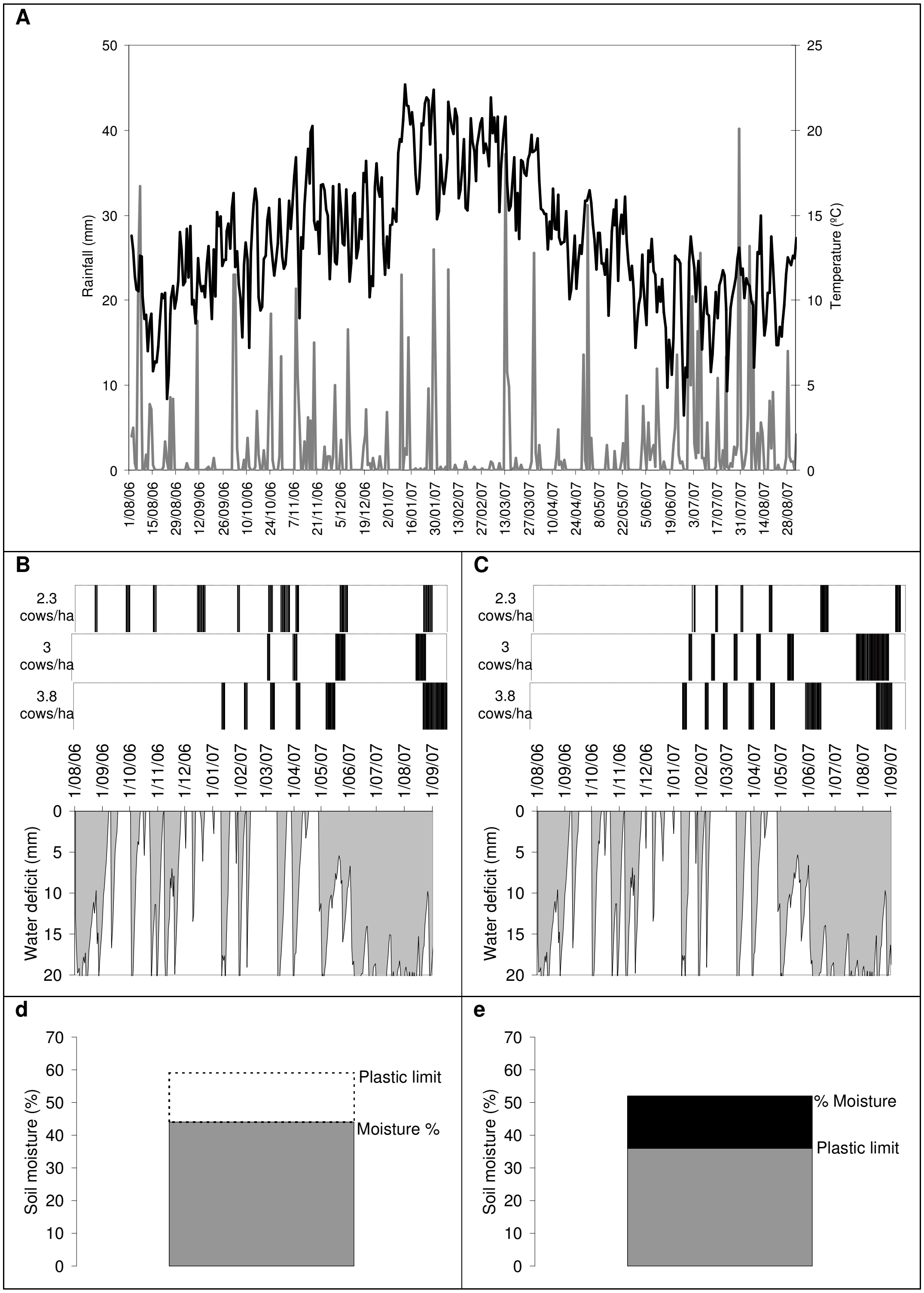


Fig. 1. (a) Daily air temperature (—) and rainfall (—) in Waikato, N.Z. from August 2006 to August 2007 (NIWA). Water balance showing water deficit (grey area), in each case grazing periods are shown in bars above the graph, for (b) Andosol, Horotiu silt loam and (c) Gleysol, Te Kowhai silt loam. Data from Sparling (2001). Soil moisture (% TDR) at time of sampling, with plastic limit (point of deformation) for (d) Andosol soil, where soil moisture was below its plastic limit and (e) Gleysol soil, where soil moisture was above its plastic limit.

Intensification treatments

The 'Resource Efficient Dairy' (RED) Trial began in 2000 and included three intensification treatment levels: 2.3, 3, and 3.8 cows/ha. Each treatment was operated as a self contained farmlet (varying in size from 6–9 ha), consisting of dairy cow herds of 21 cows rotationally grazed. Treatments were not replicated. In each treatment the two soil types occurred together and were not differentiated for either fertiliser application or stock management. Each treatment received the same application of maintenance fertiliser each year, including 50 kg P/ha/yr as superphosphate (Table 1). Nitrogen as urea (170 kg N/ha/yr) was applied to the 3 and 3.8 cows/ha treatments. The 3.8 cows/ha treatment also received maize supplements. Soil sampling was carried out in August 2007 (Southern Hemisphere winter). For further details on the trial see Jensen et al. (2005).

Table 1. Treatment properties and management inputs in dairy grazed pasture under three management intensities, Waikato, New Zealand (2007).

Stocking rate (cows/ha)	2.3	3.0	3.8
Live weight (kg/ha)[1]	1 150	1 500	1 900
INPUTS			
Phosphorus (superphosphate) (kg P/ha/yr)	50	50	50
Nitrogen (urea) (kg N/ha/yr)	0	170	170
Maize supplements (kg DM/ha/yr)	0	0	4600
PASTURE PARAMETERS (1000's kg DM/ha/yr)			
Pasture production[1]	12.2	15.9	14.7
Pasture intake[1]	10.4	13.5	12.5
DM returned in litter[2]	11.6	24.5	27.5
DM returned in dung[3]	3.6	4.7	5.9
DM returned in roots[2]	6.0	9.0	10.0
Total DM returned	21.2	38.2	43.5

[1] Standard cow: 450 kg live weight and consumes 4500 kg DM/yr. Pasture intake: 0.85 pasture production (www.maf.govt.nz). DM: Dry matter. Treading pressure of a cow 138 kPa (Greenwood and McKenzie, 2001).

[2] Calculated from Parsons et al. (1983).

[3] 0.35x of pasture intake (Takahashi et al., 2007).

Soil biological sampling

In each of the three intensification treatments soil samples were collected from two paddocks, each paddock being dominated by either Andosol or Gleysol soil. Five cores for macrofauna (15.5 cm ø, 0–15.5 cm depth), four soil cores for mesofauna (5 cm ø, 0–7.5 cm depth) and four composite soil samples for nematode (each comprising 5 cores 2.5 cm ø, 0–7.5 cm depth) were collected from each soil type in each treatment. Macrofauna were hand sorted (Wimbledon et al., 1996), mesofauna were extracted in a modified Berlese-Tullgren extractor, and nematodes extracted using a modified tray method as described by Yeates (1978). The Nematode Channel Ratio (NCR), Maturity Index (MI), Plant Parasitic Index (PPI) and ΣMaturity Index (ΣMI) were calculated (Bongers, 1990; Yeates, 1994, 2003). For details see Chapter 1.

The Shannon-Wiener diversity index (H'), Margalef's richness (SR) and Pielou's evenness (J') were calculated to describe the diversity of soil fauna (Yeates, 1984a; Ludwig and Reynolds, 1988).

Soil microbial biomass was measured using substrate induced respiration methods (for methodology refer to Chapter 1). Three soil samples (20 cores pooled, each core 2.5 cm ø, 0–7.5 cm deep) were collected from each soil type in each treatment.

Soil and pasture sampling

Soil temperature (Checktemp – Hanna Instruments, England) and moisture (TDR 300 Soil Moisture Probe – Spectrum Technologies, Inc., USA) at 0–10 cm depth were recorded in the field at the time of sampling. The mesofauna cores were subsequently analysed for soil pH (1:2.5 soil:water), Olsen P (Olsen et al., 1954), total nitrogen and total carbon (dry combustion using LECO-2000, LECO Equipment Corp., St. Joseph, USA). Bulk density was determined by collecting three intact soil cores (10 cm ø, 0–7.5 cm depth), drying (105ºC) and weighing.

Pasture species were determined from pasture samples collected using a 'trim' method (Piggot, 1989). Root biomass was determined using three soil samples (20 cores pooled, each core 2.5 cm ø, 0–7.5 cm deep) from each soil type, on each treatment. Samples were crumbled and washed through a hydropneumatic root washer until soil was removed. Samples were towel dried, roots and tillers were separated, dried at 60ºC and weighed.

Pore size distribution for pores <60 μm ø was determined using tension plates (see Chapter 1). Soil from each treatment was sieved (<2 mm) and saturated. Tensions of 10, 50, and 1500 kPa equated to water filled pore sizes of 30, 6, and 0.2 μm ø, respectively. Pores >50 μm ø were characterised using a fluorescent resin technique. Three 15 cm ø cores were collected from each soil type for 2.3 and 3.0 cows/ha in 2009. Methods are described in detail in Chapter 1. Briefly, the cores were impregnated with a fluorescent resin, and images of horizontal soil sections at 2.5 and 5 cm depths were analysed using Solicon© analysis software (The University of Sydney, Cotton Research and Development Corporation) (Vervoort and Cattle, 2003).

Statistical analysis

To test the hypothesis that there was no significant effect of pastoral intensification within soil type on the abundance of macrofauna, mesofauna, and microfauna the data were log (x+1) transformed and analysed using PROC MIXED in SAS v.9.1 (SAS Institute Inc., USA), using Satterthwaite degrees of freedom. To determine the trends resulting from increased pastoral intensification pressures, results were analysed for a $\geq$10% consistent increase or decrease from 2.3 cows/ha to 3.8 cows/ha. For each soil type a regression analysis was run using PROC REG in SAS v.9.1. The graphs and tables show untransformed arithmetic means. Least squares means were used to show treatment differences in a given soil in the tables. The error bars in figures represent standard errors of the means.

The farm system comparison had been in place for seven years at the time of sampling, with the same paddocks receiving the same treatment (i.e., 2.3, 3.0 and 3.8 cows/ha) throughout that period. At the treatment level, the paddocks are subsamples rather than replicates, and it had to be assumed that the differences between treatments can be attributed to the differences in long-term farm management. Large-scale experiments such as this can be difficult to replicate, but with caution, statistics can still be used (Oksanen, 2001). At the soil type level, the study has true replicates. Due to low replication a significance level of α=0.1 was chosen.

Results

Soil and pasture properties

The Gleysol had higher soil moisture, temperature, bulk density and Olsen P (Table 2) and lower soil total N than the Andosol. The sieved Gleysol is characterised as having more pores 0.2–30 µm ø than the Andosol (on average 37% vs. 19%, respectively). In sieved Andosol, there were more small pores (0.2–6 µm ø) at 2.3 cows/ha where larger pores (6–30 µm) were fewer. In both soils, 3.8 cows/ha had the highest percentage of pores 0.2–30 µm ø. In the resin embedded cores, the Andosols tended to have more pores <1 mm ø, while the Gleysol soils had more pores >4 mm ø at both treatments assessed (Fig. 2).

On both Gleysol and Andosol there was a decline in soil total C and soil total N with intensification (0–7.5 cm), even though it was calculated that more dry matter (and hence carbon) was potentially entering the soil food web (Tables 1 and 2). The pasture sward in all treatments on both soils was dominated by *Lolium perenne* (ryegrass), *Trifolium repens* (white clover) and *Poa annua* (annual poa).

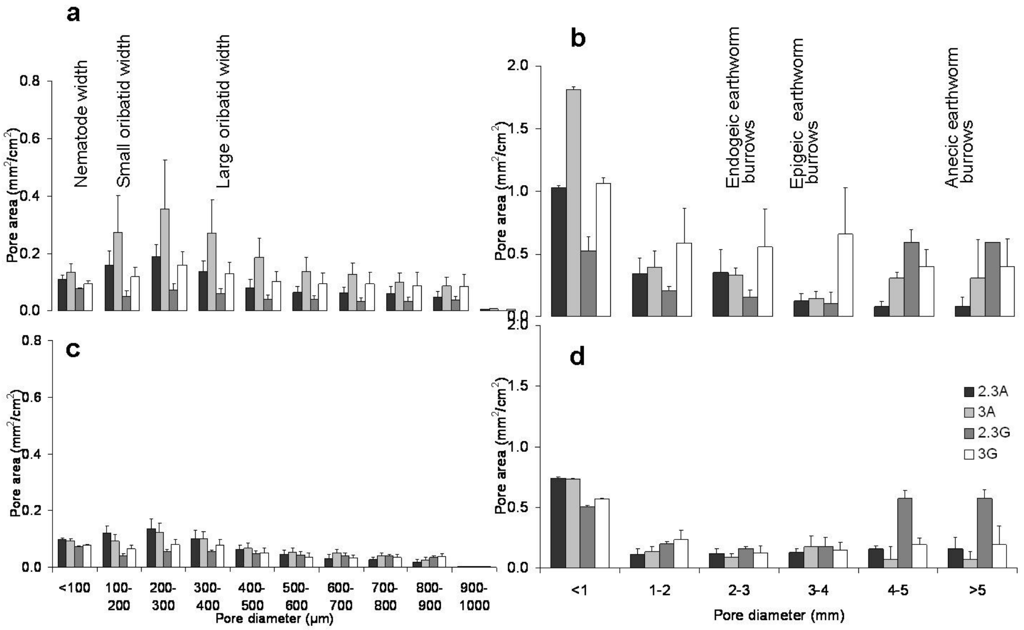


Fig. 2. Pore areas (mm^2/cm^2) over ranges of pore sizes as estimated from resin embedded cores from pastures at Waikato, New Zealand. (a) Pores <1 mm ø at 2.5 cm depth. (b) All pores (<1 to >5 mm ø) at 2.5 cm depth; the <1 mm bar is the sum of pores shown in (a). (c) Pores <1 mm ø at 5 cm depth. (d) All pores (<1 to >5 mm ø) at 5 cm depth; the <1 mm bar is the sum of pores shown in (c). Treatments include '2.3A': 2.3 cows/ha on Allophanic soil, '3A': 3.0 cows/ha on Allophanic soil, '2.3G': 2.3 cows/ha on Gley soil and '3G': 3.0 cows/ha on Gley soil.

Soil fauna

There was no significant effect of treatment on total earthworm and other macrofauna abundance in the Andosol (Table 3, Fig. 3). *Aporrectodea caliginosa* made up over 50% of the earthworm abundance in all treatments. The abundance of *A. longa* increased with intensification, while the other anecic species, *Lumbricus terrestris*, declined. The proportion of epigeic earthworm abundance was highest at 3.0 cows/ha where the proportion of endogeic abundance was lowest (Fig. 3).

There was a decline in earthworm abundance with intensification on the Gleysol (Table 3, Fig. 3). This reflected declines in both *A. caliginosa* and *L. terrestris*. Neither *A. rosea* nor *A. longa* were detected in the Gleysol. Other macrofauna, such as the clover root weevil, declined with intensification.

Table 2. Soil properties in dairy grazed pasture under three stocking rates on two soil types, Waikato, N.Z. (2007).

Soil type	Andosol				Gleysol			
Stocking rate (cows/ha)	2.3	3.0	3.8	T	2.3	3.0	3.8	T
Soil moisture (%)[1]	45	43	45		51	52	52	
Soil temperature (ºC)[1]	7.4	6.9	7.4		8.9	7.8	8.4	
Bulk density (Mg/m^3)[2]	0.69	0.67	0.70		0.75	0.79	0.76	
Porosity (% v/v of sieved soil)								
0.2–6 µm*	**14**^{a}	**9**^{b}	**12**^{b}		**13**^{a}	**10**^{b}	**17**^{c}	
6–30 µm*	**2**^{a}	**11**^{b}	**10**^{b}		**22**^{a}	**25**^{b}	**23**^{c}	
Porosity (intact cores from 2.5 cm depth)								
Porosity (%)	2	3	-		2	3	-	
Mean pore area (mm^2)	3.0	7.1	-		**18.3**	**8.9**	-	
Pores that fit <175 µm16-sided polygon (%)	23	19	-		12	13	-	
Pores that fit >350 µm16-sided polygon (%)	53	56	-		75	70	-	
Porosity (intact cores from 5 cm depth)								
Porosity (%)	1	1	-		2	1	-	
Mean pore area (mm^2)	6.5	4.3	-		13.9	6.1	-	
Pores that fit <175 µm16-sided polygon (%)	24	21	-		11	18	-	
Pores that fit >350 µm16-sided polygon (%)	53	57	-		78	66	-	
Microbial biomass (C/g soil)[2]	1098	1039	936	↓	762	1185	931	
pH[2]	6.1	5.7	6.2		6.1	5.9	5.7	
Olsen P (mg/L)[2]	34	31	53		37	52	67	↑
Total N (%)[2]	0.77	0.70	0.47	↓	0.52	0.47	0.46	↓
Total C (%)[2]	6.2	5.1	4.9	↓	8.1	7.4	5.0	↓
C:N ratio[2]	10.6	10.5	10.7		11.9	10.8	10.8	
HERBAGE COMPOSITION (%)								
Grass	87	77	80		80	63	97	
Legume	10	0	0.9		16	2	2	↓
Other (including weeds)	0.8	8	2		0	25	0.2	
Dead matter	2	15	17		4	10	0.8	
Root mass (g dry wt/m^2)[2]	224	214	143	↓↓	194	234	214	

[1] 0–10 cm depth.

[2] 0–7.5 cm depth.

T: consistent 10% change across stocking rates (↓ or ↑), ↑↑significant regression at $\alpha=0.1$.

[a,b,c] *P*-value significant at $\alpha=0.1$ (least squares means) for treatment effects in a given soil.

*Pores 0.2–6 µm ø retain mostly plant unavailable water and excludes most microorganisms, with no predation on bacteria. Pores 6–30 µm ø retain mostly plant available water and accommodate most bacteria and their predators (Brewer, 1964).

Total mesofauna abundance was negatively associated with intensification in the Andosol (Table 4, Fig. 3 and 4). This reflected a decline in Collembola and the elimination of aphids (Hemiptera). Consequently, there was a decrease in the proportion of general detritivores and herbivores, and an increase in the proportion of predators (largely Mesostigmata). Common Mesostigmata included Parasitidae, *Hypoaspis* and *Rhodacarellus silesiacus*. Oribatid abundance was low, with no Oribatida being detected at the higher stocking rate, 3.8 cows/ha. Only four Oribatid species were recovered. They were short lived, cosmopolitan species, either fungivorous or herbifungivores, with the exception of the larger, New Zealand endemic, omnivorous *Galumna rugosa.*

Table 3. Earthworms and macrofauna (0–15 cm soil) in dairy grazed pasture under three stocking rates on two soil types, Waikato, N.Z. (2007).

Soil type	Andosol				Gleysol				*P-value*	
Stocking rate (cows/ha)	2.3	3.0	3.8	T	2.3	3.0	3.8	T	*Soil*	*Soil*Tmt*
EARTHWORMS (ind./m^2)										
Lumbricus rubellus (Hoffmeister, 1843)	11	64	64	↑	95	106	53		*0.766*	*0.314*
Aporrectodea caliginosa (Savigny, 1826)	265	201	350		445	254	185	↓	*0.502*	*0.249*
Aporrectodea rosea (Savigny, 1826)	21	11	11	↓	0	0	0		***0.034***	*0.840*
Aporrectodea longa (Ude, 1885)	0	42	64	↑	0	0	0		***0.016***	*0.149*
Lumbricus terrestris (Linnaeus, 1758)	127	64	32	↓	74	74	53	↓	*0.398*	***0.066***
Total earthworms	424	382	519		615	435	291	↓	*0.328*	*0.150*
Earthworm biomass (g wet wt/m^2)	307	187	295		257	213	223		*0.532*	*0.798*
Anecic: total earthworm abundance	0.30	0.28	0.18	↓	0.12	0.17	0.18	↑	*0.559*	*0.293*
Anecic: total earthworm biomass	0.44	0.21	0.33		0.11	0.17	0.30	↑	*0.955*	*0.618*
SR	2.08	1.66	1.81		2.44	2.05	2.01	↓	*0.180*	*0.731*
J'	0.46	0.52	0.50		0.36	0.48	0.32		*0.785*	*0.801*
H'	0.74	0.84	0.81		0.58	0.77	0.51		*0.180*	*0.730*
OTHER MACROFAUNA (ind./m^2)										
Costelytra zealandica (White, 1846) larvae (Scarabaeidae, Coleoptera)	32	21	21		21	0	0		***0.085***	*0.511*
Click beetle larvae (Elateridae, Coleoptera)	21	0	0		0	11	0		*0.912*	*0.232*
Weevils (Circulionidae, Coleoptera)	85	106	477	↑↑	201	127	13	↓↓	*0.296*	***0.028***
Coleoptera (adult)	0	11	11	↑	11	0	0		*0.431*	*0.185*
Diptera larvae	42	11	0	↓	0	11	0		*0.308*	*0.269*
Gastropoda	11	0	0		0	0	0		*0.331*	*0.384*
Turbellaria	11	0	0		0	0	0		*0.331*	*0.384*
Total macrofauna	201	148	509		$\mathbf{233^{a}}$	$\mathbf{148^{a}}$	$\mathbf{13^{b}}$	↓↓	***0.014***	***0.071***
Macrofauna biomass (g wet wt/m^2)	11.0	8.8	14.4		$\mathbf{7.5^{a}}$	$\mathbf{1.4^{b}}$	$\mathbf{0.7^{b}}$	↓	***0.007***	*0.285*
SR	2.16	3.22	1.51		2.28	2.31	0		*0.211*	*0.113*
J'	0.27	0.17	0.09	↓	0.16	0.11	0	↓	*0.598*	*0.992*
H'	0.53	0.34	0.18	↓	0.31	0.21	0	↓	*0.113*	*0.994*

^{a,b,c}*P*-value significant at α=0.1 (least squares means) for treatment effects in a given soil.

T: consistent 10% change across stocking rates (↓ or ↑), ↑↑significant regression at α=0.1.

There was no significant effect of treatment on total mesofauna abundance in Gleysol (Table 4, Fig. 3 and 4). Total Acari, including Oribatida, did decline with intensification. Adult Oribatida were found solely at 2.3 cows/ha, and were dominated by *L. similis*. Collembola increased with increased intensification in the Gleysol, in contrast to the decrease in abundance in the Andosol. Among the soil mesofauna Symphyla were not found in the Gleysol and Astigmata were significantly less abundant in Gleysols. In both soils mesofauna diversity was greatest at 3.0 cows/ha, but at a given stocking rate it was always higher in the Andosol.

Total nematode abundance was not significantly influenced by treatment even though it increased from legume based to N fertilised pastures in the Andosol (Table 5, Fig. 3). A total of 33 taxa were recorded. Pastures receiving N fertiliser showed an increase in the relatively responsive bacterial feeding, Rhabditidae (CP1) and *Cephalobus* (CP2). Among plant feeding nematodes, there was a decline in *Heterodera trifolii* (clover-cyst nematode) under N fertilised pastures but at least a six-fold increase in *Pratylenchus* abundance from 2.3 to 3.8 cows/ha in both soils. *Monhystera* and *Aporcelaimus* also increased with intensification, whereas *Pungentus* decreased. Predator and omnivore abundance, driven by *Aporcelaimus*, increased from the legume-based to N fertilised pastures in the Andosol (Fig. 3). The maturity indices (MI, PPI and ΣMI) were not significantly influenced by treatment (Table 5).

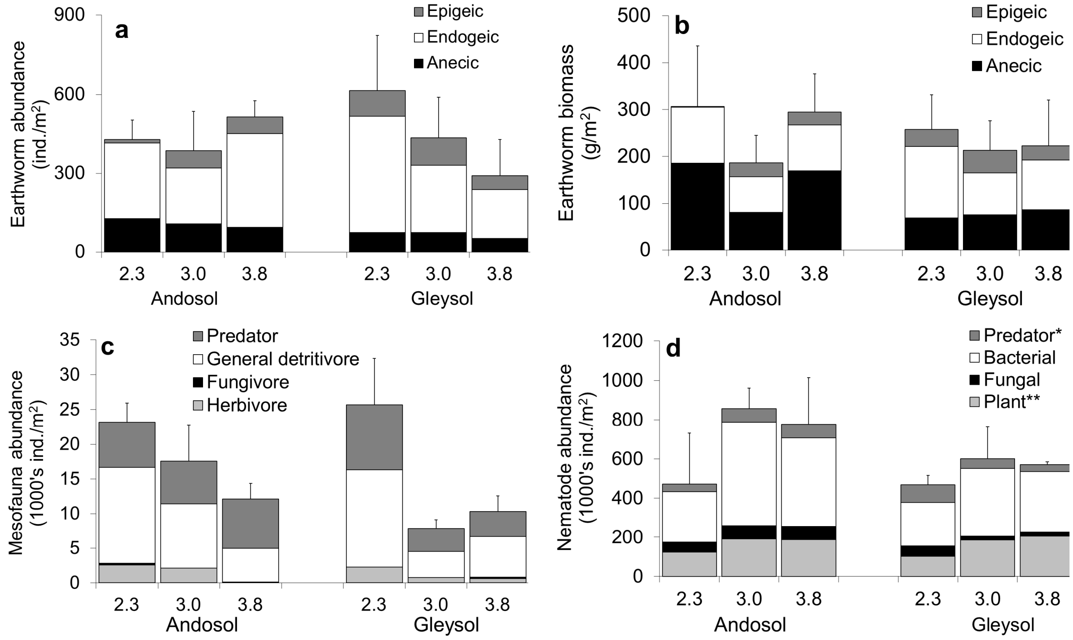


Fig. 3. Invertebrates under different grazing intensities (2.3, 3.0 and 3.8 cows/ha) in Andosol and Gleysol soil (0–7.5 cm soil depths) at Waikato, N.Z. (a) Abundance of earthworm functional groups, (b) biomass of earthworm functional groups, (c) abundance of mesofauna trophic groups and (d) abundance of nematode trophic groups.

*Predacious and omnivorous nematodes.

**Plant feeding and plant associated nematodes.

Total nematode abundance was not significantly influenced by treatment even though it increased from legume based to N fertilised pastures in the Gleysol (Table 5, Fig. 3). A total of 33 taxa were recorded. The proportion of plant feeding and plant associated nematodes increased under N fertilised pastures in the Gleysol. This largely reflected a nine-fold increase in Hoplolaimidae and five-fold increase in *Pratylenchus*, even though there was a decline in *H. trifolii* with N fertilisation as the legume content of the pasture sward was decreased (Table 2). Pastures receiving N fertiliser showed an increase in the Rhabditidae (CP1), and in *Pungentus*, *Aporcelaimus* and *Dorylaimus*, while the putative fungal feeder *Doryllium* decreased with intensification. The NCR increased from 0.81 at 2.3 cows/ha to 0.93 at 3.8 cows/ha. The abundance of predators and omnivores declined with intensification in the Gleysol (Fig. 3). The lowest population of *Aporcelaimus,* at 3.8 cows/ha in the Gleysol, contrasts with this treatment having the highest *Aporcelaimus* abundance in the Andosol. The MI was highest at 2.3 cows/ha (Table 5). *Aphelenchoides, Anaplectus* and *Dorylaimus* were found at the highest abundances in the Gleysol at 2.3 cows/ha, but was found at lowest abundance in the Andosol under the same treatment.

Table 4. Mesofauna and Oribatid species (0–7.5 cm soil) in dairy grazed pasture under three stocking rates on two soil types, Waikato, N.Z. (2007).

Soil type	Andosol				Gleysol				*P-value*	
Stocking rate (cows/ha)	2.3	3.0	3.8	T	2.3	3.0	3.8	T	*Soil*	*Soil*Tmt*
MESOFAUNA (1000's ind./m^{2})										
Tectocepheus sarekensis (Trägårdh, 1910)	0.3	0	0		0.3	0	0		*0.941*	*0.994*
Punctoribates punctum (Koch, 1839)	0	0.1	0		2.2	0	0		*0.375*	***0.065***
Galumna rugosa (Hammer, 1968)	0	0.3	0		0	0	0		*0.100*	*0.075*
Liebstadia similis (Michael, 1888)	0	0.1	0		**5.7**^{a}	**0**^{b}	**0**^{b}		*0.854*	***0.004***
Nymphs	1.1	3.4	0		4.1	0.1	0.1	↓	*0.963*	*0.513*
Oribatida (adult)	0.3	0.5	0		**8.0**^{a}	**0**^{b}	**0**^{b}		*0.928*	***0.006***
Total Oribatida	**1.4**^{a}	**3.9**^{b}	**0**^{a}		**12.1**^{a}	**0.1**^{b}	**0.1**^{b}		*0.860*	***0.004***
Astigmata	**0.3**^{a}	**1.1**^{b}	**1.8**^{b}	↑↑	0	0.6	0.1		***0.009***	*0.425*
Mesostigmata	4.1	4.4	4.8	↑	8.1	1.7	2.5		*0.235*	*0.909*
Prostigmata	1.7	0.9	0.3	↓	0.1	0.3	0.4	↑	*0.330*	*0.108*
Scutacaridae	0.1	0.4	0.5	↑	0.5	0.5	0.3	↓	*0.498*	*0.895*
Total Acari	7.5	10.8	7.4		**20.9**^{a}	**3.2**^{b}	**3.4**^{b}		*0.280*	***0.030***
Entomobryomorpha	5.2	3.3	1.3	↓	1.4	1.8	4.5	↑	*0.814*	*0.146*
Poduromorpha	**6.5**^{a}	**0.4**^{b}	**1.5**^{c}		0.1	0.9	0.5		*0.169*	***0.047***
Sminthuridae	0.4	0.4	0.1		0.3	0.3	0.6	↑	*0.783*	*0.407*
Total Collembola	12.1	4.1	2.9	↓↓	1.8	2.9	5.6	↑↑	*0.899*	*0.178*
Protura	0.3	0	0		0	0	0.3		*0.586*	***0.081***
Coleoptera	0.4	0.1	0.3		0.3	0	0.3		*0.676*	*0.615*
Diptera	0.3	0.3	1.3	↑	0.4	0.6	0.1		*0.713*	*0.749*
Formicidae	0.1	0	0		0	0	0		*0.331*	*0.387*
Hemiptera	2.7	0.1	0	↓	**1.8**^{a}	**0**^{b}	**0**^{b}		*0.986*	*0.559*
Thysanoptera	0	2.0	0.3		0.4	0.8	0.6		*0.264*	*0.639*
Arachnida	0	0	0		0	0	0.1		*0.331*	*0.387*
Chilopoda	0	0	0		0	0.3	0		*0.331*	*0.387*
Symphyla	0.1	0.1	0.3		0	0	0		*0.100*	*1.000*
Total mesofauna	23.4	17.6	12.1	↓	25.5	7.8	10.4		*0.369*	*0.506*
SR	4.3	5.3	5.5	↑	**4.3**^{a}	**6.2**^{b}	**5.5**^{b}		*0.462*	*0.230*
J'	0.45	0.53	0.47		0.41	0.49	0.44		*0.618*	*0.976*
H'	1.29	1.50	1.33		1.15	1.38	1.25		*0.159*	*0.991*

^{a,b,c}*P*-value significant at α=0.1 (least squares means) for treatment effects in a given soil.

T: consistent 10% change across stocking rates (↓ or ↑), ↑↑significant regression at α=0.1.

Table 5. Nematodes (1000'S ind./m^2in 0–7.5 cm soil) in dairy grazed pasture under three stocking rates on two soil types, Waikato, N.Z. (2007). CP groups, NCR, MI, PPI and ΣMI are also given.

Soil type	Andosol				Gleysol				*P-value*	
Stocking rate (cows/ha)	2.3	3.0	3.8	T	2.3	3.0	3.8	T	*Soil*	*Soil*Tmt*
NEMATODA										
Tylenchus	**30.8**^{a}	**111.6**^{b}	**101.8**^{b}		31.7	68.0	18.7		*0.134*	*0.183*
Cephalenchus	0	0	0		**0**^{a}	**5.1**^{b}	**0**^{a}		***0.069***	***0.047***
Heterodera juv.	32.3	19.1	18.9	↓	**24.5**^{a}	**0**^{b}	**5.1**^{c}		*0.261*	*0.319*
Meloidogyne juv.	0	2.7	4.7	↑	0	6.8	1.7		*0.999*	*0.999*
Tylenchorhynchus	3.1	5.4	7.1		2.9	0	3.4		*0.629*	*0.827*
Hoplolaimidae	20.0	16.3	23.7		15.9	91.7	144.1	↑↑	*0.792*	*0.324*
Pratylenchus	**3.1**^{a}	**13.6**^{b}	**18.9**^{b}		4.3	3.4	22.0		*0.546*	*0.165*
Paratylenchus	0	2.7	0		**0**^{a}	**5.1**^{b}	**0**^{a}		*0.506*	*0.636*
Aphelenchus	46.2	51.7	52.1		26.0	5.1	18.7		*0.166*	*0.303*
Aphelenchoides	0	8.2	2.4		4.3	1.7	3.4		*0.384*	***0.074***
Diplogaster	0	5.4	2.4		0	6.8	0		*0.617*	*0.739*
Rhabditidae	78.5	103.5	104.2	↑	49.1	112.1	115.3	↑	*0.856*	*0.990*
Dauerlarvae	6.2	2.7	11.8		0	35.7	13.7		*0.457*	***0.097***
Panagrolaimus	53.9	117.1	68.7		60.6	68.0	35.6		*0.466*	*0.490*
Cephalobus	**89.3**^{a}	**212.4**^{b}	**213.1**^{b}	↑	56.3	42.5	40.7	↓	***0.006***	*0.138*
Heterocephalobus	15.4	46.3	18.9		10.1	17.0	50.9	↑↑	*0.563*	*0.821*
Euteratocephalus	0	0	0		0	0	17.0		*0.337*	*0.397*
Acrobeles	6.2	8.2	4.7		0	0	0		***0.043***	*0.792*
Acrobeloides	0	0	0		1.4	1.7	0		*0.183*	*0.618*
Stegellata	0	5.4	2.4		0	0	0		*0.183*	*0.619*
Plectus	0	0	2.4		0	47.6	1.7		*0.228*	*0.240*
Anaplectus	0	5.4	9.5	↑	21.6	1.7	5.1		*0.331*	***0.064***
Plectid	0	5.4	0		0	0	0		*0.337*	*0.397*
Prismatolaimus	1.5	8.2	0		1.4	6.8	8.5	↑	*0.223*	*0.530*
Monhystera	7.7	8.2	11.8	↑	**18.8**^{a}	**1.7**^{b}	**15.3**^{a}		*0.587*	*0.480*
Chromadoridae	0	2.7	0		4.3	3.4	0	↓	*0.274*	*0.296*
Dorylaimus	0	10.9	9.5		26.0	6.8	3.4		*0.317*	***0.057***
Eudorylaimus	6.2	5.4	7.1		15.9	1.7	8.5		*0.531*	*0.479*
Pungentus	30.8	16.3	11.8	↓	21.6	3.4	10.2		*0.900*	*0.510*
Aporcelaimus	29.3	40.8	49.7		28.9	23.8	8.5		*0.225*	*0.288*
Doryllium	4.6	10.9	9.5		**21.6**^{a}	**11.9**^{a}	**1.7**^{b}	↓↓	*0.628*	*0.359*
Clarkus	1.5	13.6	4.7		15.9	15.3	15.3		***0.051***	*0.680*
Prionchulus	0	0	0		**2.9**^{a}	**0**^{b}	**0**^{b}		***0.069***	***0.047***
Alaimidae	0	0	2.4		0	3.4	1.7		*0.600*	*0.716*
Trichodoridae	3.1	5.4	0		0	0	0		*0.182*	*0.618*
Diphtherophora	0	0	2.4		0	0	0		*0.3330*	*0.397*
Total nematodes	471.2	865.8	776.6		467.5	599.7	569.8		*0.770*	*0.467*
SR	4.8	5.0	5.5		5.1	5.1	5.7	↑	*0.912*	*0.436*
J'	0.64	0.64	0.63		0.72	0.62	0.61	↓	*0.533*	***0.092***
H'	2.32	2.32	2.30		**2.62**^{a}	**2.24**^{b}	**2.22**^{b}	↑↑	*0.553*	***0.097***
NCR	0.84	0.88	0.87		**0.81**^{a}	**0.95**^{b}	**0.93**^{c}		*0.182*	*0.192*
Maturity groups (%)										
CP1	29	26	24	↓	23	37	29		*0.954*	*0.491*
CP2	**42**^{a}	**54**^{b}	**54**^{b}	↑	36	33	27	↓	***0.058***	*0.279*
CP3	13	8	10		12	19	35	↑↑	*0.207*	*0.119*
CP4	10	7	6	↓	**22**^{a}	**7**^{b}	**7**^{b}	↓↓	*0.451*	***0.085***
CP5	7	5	6		6	4	1	↓	*0.176*	*0.353*
MI	1.45	1.56	1.53		**1.88**^{a}	**1.28**^{b}	**1.18**^{b}	↓	*0.393*	***0.011***
PPI	0.77	0.54	0.65		0.62	0.77	1.08	↑	*0.257*	*0.244*
Σ MI	2.22	2.10	2.18		2.51	2.05	2.25		*0.467*	*0.515*

^{a,b,c}*P*-value significant at α=0.1 (least squares means) for treatment effects in a given soil.

T: consistent 10% change across stocking rates (↓ or ↑), ↑↑ significant regression at α=0.1.

Seinura, Tobrilus, Dorylaimellus were only detected in one treatment at <2000 ind/m^2 so are not included in table.

The food web showed macrofauna predators absent only from the highest stocking rate under the Gleysol (Fig. 4). Further, it highlighted the decline in nematode predators from 2.3 to 3.8 cows/ha in the Gleysol. Total faunal biomass was higher under the Andosol in comparison with the Gleysol for 2.3 and 3.8 cows/ha. The biomass of fungal feeding nematodes was low in all treatments and is not included.

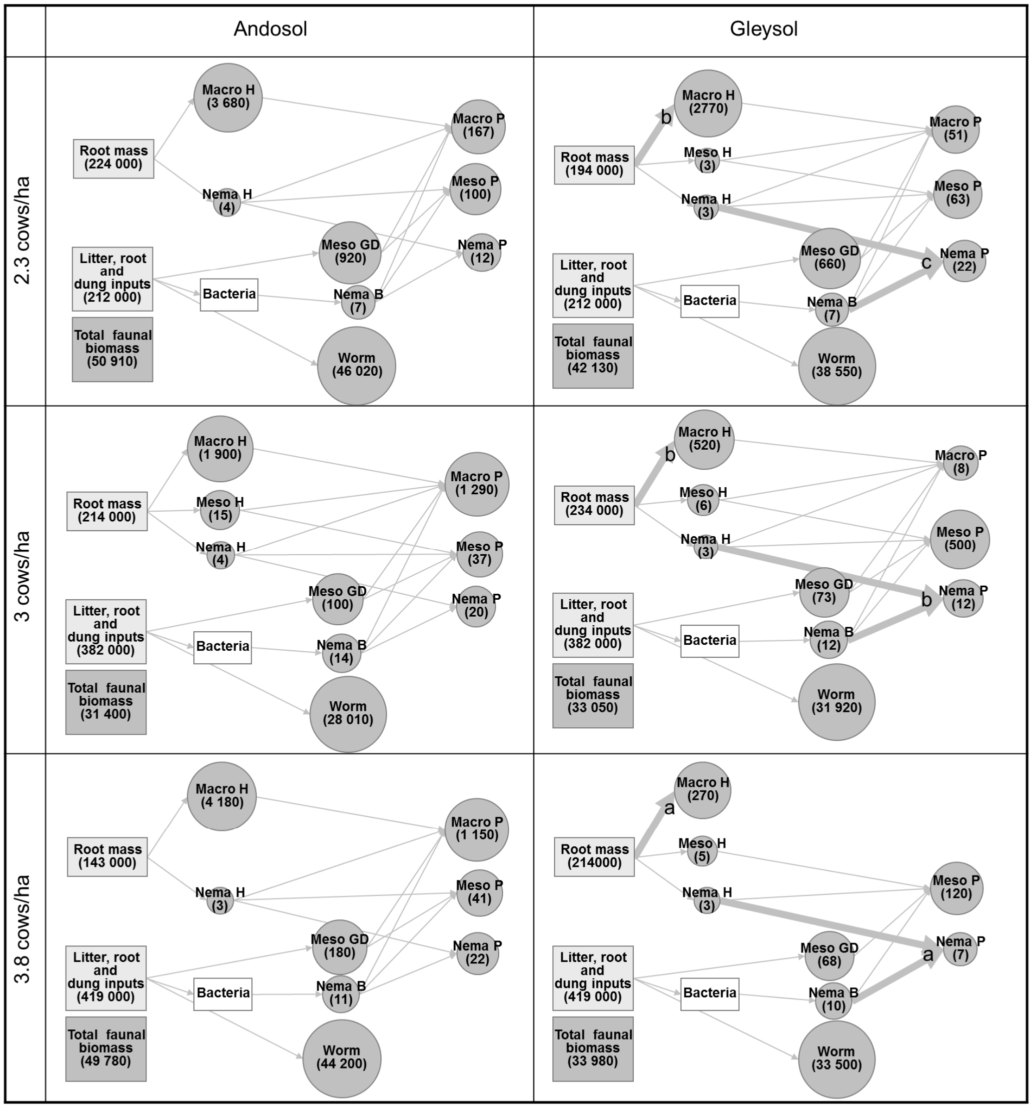


Fig. 4. Food webs of selected soil faunal groups at 0–7.5 cm soil depth under different pasture management regimes and soil types, Waikato, N.Z. Food web and calculations after Hunt (1987) and Mulder et al. (2005). Resource inputs are given in mg dry weight/m^2. Macrofauna (Macro), mesofauna (Meso) and nematode (Nema) herbivores (H) feed on plant material. Earthworms (Worm), mesofauna general detritivores (GD) and nematode bacterial feeders (B) feed on detrital inputs and associated microflora. The macrofauna, mesofauna and nematodes are in turn consumed by predators (P). Circle areas represent the log biomass of the fauna, actual biomass (dry weight mg/m^2) given in parenthesis. Biomass calculated as described in Chapter 1. Trophic groups with biomass <1.5 mg dry weight/m^2 were excluded. Wide arrow and $^{a,\,b}$ given in the arrow head indicate significant difference at α=0.05 within the functional group to which the arrows lead.

Discussion

In both Andosol and Gleysol soils, soil porosity was low (3% for resin impregnated pores >50 µm ø on both soils), and lower than macroporosity reported by Singleton and Addison (1999) for the same soil type. Macroporosity, defined as pores >30 µm ø (Greenwood and McKenzie, 2001), of less than 10% has been shown to have negative impacts on pasture productivity, with such values not being uncommon for New Zealand pastures (Sparling and Schipper, 2004). The low porosity in the current intensively managed pastures may have contributed to low oribatid abundance in both soils (0–4000 ind./m^2 in Andosol, and 0–12 100 ind./m^2 in Gleysol, Fig 4). Oribatida have previously been shown to be sensitive to treading (King and Hutchinson, 1980; Cole et al., 2008; Schon et al., 2008) and as the treading pressure of cows is double that of sheep (Greenwood and McKenzie, 2001), there may be negative consequences of dairy grazed pastures on Oribatida communities even at low stocking rates. Due to their low abundance, it is difficult to make inferences about any selective pressure on their body size due to changes in habitable pore space (Elliott et al., 1980).

The Gleysol soil, with its structural vulnerability and susceptibility to treading due to more days above its plastic limit (Hewitt and Shepherd, 1997; Singleton and Addison, 1999) and higher bulk density, is potentially a less favourable habitat for soil organisms compared with the Andosol. Even though soil porosity was similar in both soils, the distribution of pore sizes differed. The Andosol had more, smaller (<1 mm ø) pores than the Gleysol (Fig. 2), these pores may be occupied by mesofauna and nematodes (body widths <2 mm, but often <1 mm in these pastoral soils). The Gleysol had more, larger pores (>4 mm ø) which are probably a product of wetting and drying processes that contribute to cracking (Greenwood and McKenzie, 2001) rather than biological activity. For example, while the decline in pores >4 mm ø reflected a decline in earthworm abundance, dominant *A. caliginosa* burrows are ~2.5 mm (Springett, 1983). In the Gleysol, where there was a reduction of pores <1 mm diameter, larger pores (>4 mm) appear to provide an important habitat for soil invertebrates, with earthworm, mesofauna and nematode abundances being similar at the lowest stocking rates in both soils.

Habitable pore space was affected by management, with the negative influences of intensification being more pronounced in the Gleysol where there was a decline in mean pore size and faunal predators (Table 2, Fig. 4). Juvenile earthworms are reported to be more sensitive than adults to trampling effects (Cluzeau et al., 1992). That there were fewer juveniles at higher stocking rates in the Gleysol (data not shown) is likely a result of increased treading pressures. This resulted in a similar earthworm biomass at all stocking rates in the Gleysol. Neither *A. longa* nor *A. rosea* were detected in the Gleysol, suggesting that the soil environment was too difficult to function and survive in.

The high abundance of Mesostigmata at low stocking rates in Gleysol is likely to be a result of the presence of more large pores which are preferred by the Mesostigmata, Parasitidae and *R. silesiacus* (Koehler, 1999). Mesostigmata declined from legume based to N fertilised pastures as the mean pore size declined, agreeing with Koehler (1999) that they can be sensitive to compaction, although Cole et al. (2008) suggested their abundance may be more influenced by food availability. Predation by Mesostigmata may have contributed to low Collembola abundance in this soil (Fig. 5). As Mesostigmata abundance declined with intensification in Gleysols, Collembola populations were able to recover.

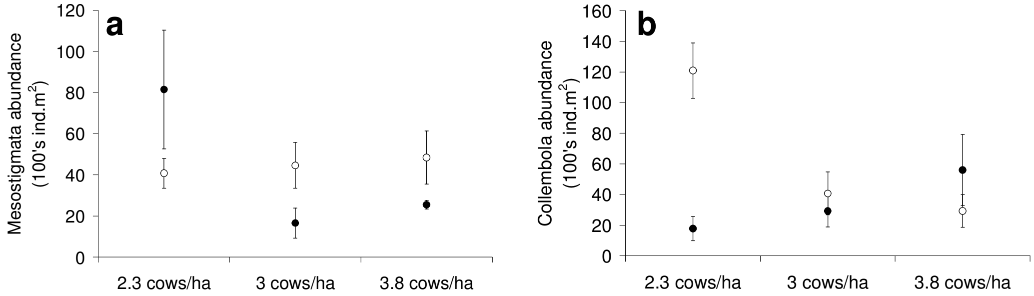


Fig. 5. Change in abundance of soil mesofauna with intensification for Andosol (○) and Gleysol (●) soils at Waikato, N.Z. (0–7.5 cm soil depth). (a) Mesostigmata and (b) Collembola.

We found two anecic earthworm species showing opposite trends in abundance under Andosols, *A. longa* increased with increased stocking rates, whereas *L. terrestris* decreased. This may reflect the poor competitiveness of *L. terrestris* under field conditions as described by Butt (1998). Further, the more permanent vertical burrows of *L. terrestris* in comparison to *A. longa* (with burrowing activities having similarities to those of endogeic earthworms (Felten and Emmerling, 2009)), may be more susceptible to treading damage. There was also evidence of a decline in *L. terrestris* abundance in the Gleysol.

In response to greater dry matter inputs, there was an increase in the relative dominance of the bacterial pathway over the fungal pathway in the soil food web (reflected in the NCR) under N fertilised pastures on the Gleysol. The greater abundance of bacterial feeding nematodes under N fertilised pastures may have a positive influence on the availability of plant nutrients (Bardgett et al., 1999). In these N fertilised pastures, DairyNZ Limited (2009) reported greater leaching to the environment than the legume based pastures.

As a result of N fertiliser stimulated herbage growth, there was an increase in the abundance and biomass of plant feeding and plant associated nematodes in both soils (Fig. 3). The increase in plant feeding and plant associated nematodes largely reflects an increase in Hoplolaimidae, whose feeding may not have significant effects on herbage production (Yeates, 1984b), although leakage of microbe available nutrients from roots may be significant (Yeates et al., 1999). Even though increased pasture growth is not reflected in root mass on the Andosol (Table 2), the decrease in root mass with intensification may be a reflection of increased clover root weevil (*Sitona lepidus*) abundance and other herbivory (Gerard et al., 2007; Yeates et al., 2009) (Table 3) or root turnover (Barker et al., unpublished 1998). This increase in the clover root weevil is noteworthy because it occurred despite the application of N fertiliser at the two higher stocking rates, with such treatments having reduced legumes in a recent trial reported by Gillingham et al. (2008). In contrast, the clover cyst nematode, *H. trifolii* declined. The high biomass of macrofauna herbivores (>2000 mg/m^2) were associated with very low biomass of mesofauna herbivores (<3 mg/m^2) (Fig. 4).

Nematodes behaved predictably across both soils, increasing as productivity increased. While their assemblages were different under both soils, the general response of nematode trophic groups was similar. The importance of both productivity and soil type has also been observed by Yeates (1980, 1984a). The change in nematode trophic group abundance was dependent on soil type. In the present study, nematode abundance was similar in legume based pastures on both soil types. However, that there was a smaller increase in nematode abundance to N fertilised pastures in the Gleysol (particularly bacterial feeding nematodes, Fig. 3), may be a reflection of fewer habitable pores for nematodes. Additionally, there is some evidence that nematodes are affected by a certain amount of stock treading, their abundance increasing from 2.3 to 3.0 cows/ha, before decreasing to 3.8 cows/ha (Fig. 3). A decrease in nematode abundance was found under sheep grazing (10, 20 and 30 sheep/ha, with 23 kg P/ha/yr) on a gleyed podzol in Australia by King and Hutchinson (1976). In contrast, Yeates (1976) found an increase in nematode abundance with increased sheep stocking rate and phosphate application on a silt loam in New Zealand (14.8 and 22.2 sheep/ha, with 11 and 45 kg P/ha/yr). These three studies illustrate that the response to treading (a stocking rate of 20 sheep/ha corresponds to live weights of 1100 kg/ha), is dependent on both soil type and fertiliser application. Further, predatory nematodes, which may increase as food resources increase, but have also been reported to be sensitive to compaction (Yeates, 1987), increased in the Andosol but decreased in the Gleysol.

Plant litter and dung on the soil surface can be incorporated and mixed in the soil through invertebrate activity and the treading actions of grazing ruminants. Despite potentially more organic matter available for incorporation into the soil profile with intensification, lower abundances of litter incorporating earthworms, Collembola and Oribatida (Fig. 3) may collectively have contributed to a decline in soil C (Table 2). Schipper et al. (2007) also reported losses of soil C in intensive grazed pasture systems. Litter left on the surface may be quickly oxidised and lost as carbon dioxide.

Conclusion

As management of pastoral systems is intensified, there is increased food availability for soil invertebrates through increased plant growth and dung deposition. On a single farm with a mosaic of contrasting soil types, soil invertebrates were influenced by both soil type and intensification. Soil invertebrates had a similar abundance at the lowest stocking rate on both soils, even though the Gleysol was expected to be a less favourable habitat for the soil invertebrates under uniform management. However, the influence of treading was more pronounced in Gleysol, with earthworm and Mesostigmata abundance declining with intensification in Gleysol. Nematodes behaved most predictably on both soil types. Nematode abundance (including bacterial feeding and plant feeding) increased from legume-based to N fertilised pastures as herbage productivity increased. The increase in the relative abundance of bacterial feeding nematodes was reflected in a higher NCR in the Gleysol. The maturity of the nematode assemblage was lower under N fertilised pastures, where N losses to the environment were apparently greater.

This study supports the importance of soil characteristics in influencing the invertebrate community. Further, it reinforces the need for further studies exploring the relationship between soil invertebrates and soil physical properties.

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Chapter Three:

Soil invertebrates and their contribution to nitrogen mineralisation on four soils under organic and conventional dairy management

Chapters 1 and 2 have shown that invertebrates respond to pastoral management. This chapter explores whether organic dairy management has a positive influence on the invertebrate community.

N.L. Schon, A.D. Mackay, M.J. Hedley, M.A. Minor. Soil invertebrates and their contribution to nitrogen mineralisation on four soils under organic and conventional dairy management.

Abstract

Organic management aims to promote soil biological activity and, with certification restrictions on nutrients and other inputs into the pastoral system, to reduce the environmental impact of pastoral agricultural systems. To test whether organic management stimulates soil biological activity, invertebrates (macrofauna, mesofauna and microfauna) were collected from four paired commercial organically and conventionally managed dairy farms on different soil types (Allophanic, Pallic, Recent and flooded Recent). Food webs were constructed, and rates of invertebrate mediated nitrogen (N) mineralisation calculated.

The organic dairy operations examined used fewer nutrient inputs and had lower stocking rates than their paired conventional farms. This translated into lower calculated pasture production and less available plant litter entering the soil food web and was reflected in lower abundance of herbivorous nematodes and mesofauna. Associated with higher legume contents of organic pastures were greater numbers of clover root weevil (*Sitona lepidus,* 295 vs. 234 ind./m^2) and clover cyst nematode (*Heterodera trifolii,* 25.6 x10^3 vs. 0 ind./m^2). Despite the lower plant litter inputs into the organic system, earthworm biomass was higher (particularly in the Recent and flooded Recent soils), suggesting that under conventional management the physical condition of the soil, as influenced by stock treading pressures, was more important for invertebrate activity and their influence on N mineralisation than was food supply. This can be demonstrated by examining earthworm biomass in the paired farms with the largest (Recent, 486 vs. 308 g/m^2) and smallest differences in stocking rate (Pallic, 377 vs. 376 g/m^2). Further evidence for this comes from examining nematodes, as despite microbial biomass increasing, there was a trend of decreasing microbial feeding, predatory and omnivorous nematodes as treading pressure increased. The contribution of fungal feeding nematodes to decomposition and N mineralisation was low in all pastures, and was more influenced by the soil type than by management. Nitrogen mineralisation was higher in organic systems, with earthworms contributing the most (24–98 kg N/ha/yr). As the physical loading on the soil increased under conventional management, the ability of the soil to provide soil services (i.e., N mineralisation and litter decomposition) became compromised. In this study organic management on four soils stimulated biological activity by reducing the physical pressure on the soil, despite lower dry matter inputs into the soil food web.

Introduction

The long term sustainability of intensive pastoral systems is being questioned, with increasing concerns about the environmental impacts associated with the losses of soil structure and function and the leakage of nutrients from beyond the root zone (Doran and Zeiss, 2000; Mackay, 2008). Organic agriculture is seen by some as a more sustainable option, one that reduces the environmental impacts of pastoral management through strict limitations on fertiliser and other inputs, with the aim of promoting biological cycles and production systems. Yeates et al. (1997) and Mulder et al. (2003) found faunal abundance and activity to be positively associated with organic pasture management. Enhanced activity of soil invertebrates such as earthworms, mesofauna and nematodes provides support for soil processes and services such as nutrient supply and nitrogen mineralisation (Hunt et al., 1987; Bardgett and Chan, 1999; Cole et al., 2004; Fonte et al., 2007). However, not all studies have shown a consistent response to organic management. For example, Parfitt et al. (2005) found no evidence of increased biological activity under organic management.

Organic practices which may stimulate soil invertebrates include: the use of organic fertilisers and limited nitrogen inputs to stimulate legume contribution to the sward; reduced stocking rates and associated lower treading pressure on the soil; and the use of non agrichemical practices in the control of pests and weeds (Edwards and Lofty, 1982; Clapperton et al., 2002; Hole et al., 2005; Cole et al., 2008). All these actions may potentially encourage soil invertebrates, but limiting the use of nitrogen fertiliser will reduce pasture growth and the amount of litter and dung entering the soil food web. Several studies have reported increases in soil fauna, especially earthworms and nematodes, in response to increased food availability (Yeates, 1976b; Zyromska-Rudzka, 1977; Cole et al., 2005; Oliver et al., 2005; Sjursen et al., 2005; Curry et al., 2008). The reduced availability of food resources may help explain the lack of a consistent soil invertebrate response to organic management in comparison with conventional pastoral systems.

This study examined the influence of organic management on soil invertebrates and their simulated role in nitrogen mineralisation. Recognising that the response of the soil fauna to changes in organic and conventional management may also differ with soil type, the comparison included four paired commercial organic and conventional dairy farms on different soils with varying managements in a region under similar climate. Each of the four organic operations was certified and supplied milk to an organic processor. The potential food resources and soil physical condition were also explored in relation to food webs of invertebrates standing biomass.

Methods

Study sites

Four organic dairy farms on four different soils, one Allophanic and three sedimentary soils, NZSC: Allophanic, Pallic, Recent and a flooded Recent soil (Hewitt, 1993), FAO: Andosol, Luvisol and Fluvisol (FAO, 1988) were selected in the Manawatu region, New Zealand. Conventional farms in close proximity and on the same soil type were sampled alongside the organic farms. The organic farms were all certified to meet the requirements of BioGro New Zealand (BioGro, 2001). Table 1 summarises management practices, fertiliser inputs, stocking rates and pasture production levels of all eight farms. Sites which were sampled on one of the paired farms on the Recent soil, both conventional and organic sites, had been affected by flooding and alluvial deposition in February 2004. All samples were collected in July 2007 from two paddocks on each farm.

Soil biological sampling

Four cores for macrofauna (15.5 cm ø, 0–15.5 cm deep), four soil cores for mesofauna (5 cm ø, 0–7.5 cm deep), and two composite soil samples for nematodes (each comprising 5 cores 2.5 cm ø, 0–7.5 cm deep) were collected from each farm. Macrofauna were hand sorted (Wimbledon et al., 1996), mesofauna were extracted in a modified Berlese-Tullgren extractor as described by Schon et al. (2008), and nematodes extracted using a modified tray method as described by Yeates (1978). The Nematode Channel Ratio (NCR), Maturity Index (MI), Plant Parasitic Index (PPI) and ΣMaturity Index (ΣMI) were calculated (Bongers, 1990; Yeates, 1994, 2003).

The Shannon-Wiener diversity index (H'), Margalef's richness (SR) and Pielou's evenness (J') were calculated to describe the diversity of soil fauna (Yeates, 1984; Ludwig and Reynolds, 1988).

Soil microbial biomass was measured as substrate induced respiration. Two composite soil samples (20 cores pooled, each core 2.5 cm ø, 0–7.5 cm deep) were collected from each farm. Samples were sieved to <2 mm and the amount of CO_2

respired in two hours was estimated by collecting 25 ml gas in a syringe and empting into a preevacuated Exetainer®, for methodology refer to Chapter 1.

Table 1. Site properties and management inputs in dairy grazed pasture under organic (O) and conventional (C) management, Manawatu, New Zealand (2007). Being within 40 km of each other all sites had similar rainfall in the year preceding sampling (850 mm) and mean annual air temperature (13.5°C).

Soil type FAO	Andosol		Luvisol		Fluvisol		Fluvisol	
Soil type NZSC	Allophanic		Pallic		Recent		flooded Recent	
Soil series	Kiwitea		Tokomaru		Manawatu		Manawatu	
Soil texture	sandy silt		silt loam		sandy loam		sandy loam	
Management	O	C	O	C	O	C	O	C
Latitude	40°03'S	40°08'S	40°23'S	40°23'S	40°19'S	40°20'S	40°20'S	40°20'S
Longitude	175°47'E	175°45'E	175°36'E	175°36'E	175°44'E	175°41'E	175°40'E	175°40'E
Stocking rate (cows/ha)[1]	1.8*	2.9	2.1	2.3	1.0*	3.4*	1.6	3.3
Live weight loading (kg/ha)[1]	970	1 450	1 050	1 150	580	1 650	800	1 650
INPUTS								
Inorganic fertiliser used	Yes[a]	Yes[b]	No	Yes[d]	No	Yes[h]	No	Yes[f]
Compost fertiliser used[2]	No	No	Yes[c]	No	No[g]	No	Yes[e]	No
PASTURE PARAMETERS (1000's kg DM/ha/yr)								
Pasture production [1]	8.5	13.6	9.9	10.8	4.7	16.0	7.5	15.5
Pasture intake[1]	7.2	11.6	8.4	9.2	4.0	13.6	6.4	13.2
DM from litter[3]	9.8	15.4	10.6	12.8	6.0	18.4	8.6	17.8
DM from dung[4]	2.5	4.1	2.9	3.2	1.4	4.8	2.2	4.6
DM from roots[3]	4.0	7.0	4.0	4.0	3.0	8.0	3.0	7.0
Total DM	16.3	26.5	17.5	20.0	10.4	31.2	13.8	29.4

[1] Standard cow (450 kg live weight) consumes 4500 kg DM/yr (www.maf.govt.nz). DM: Dry matter. Treading pressure of a dairy cow is 138 kPa and a sheep is 65 kPa (Greenwood and McKenzie, 2001). Pasture intake: 0.85x pasture production.

[2] Type of fertiliser used: [a] RPR; [b] RPR and SustainN; [c] chicken manure and compost tea; [d] SSP and Urea; [e] Liquid fish, Probatase, Compost; [f] DAP and AMSULF; [g] no fertiliser used, [h] SSP and SustainN

[3] Calculated from Parsons et al. (1983).

[4] 0.35x animal intake (Takahashi et al., 2007).

*Other types of animals (heifers, calves, sheep, goats) were present on these pastures; the stocking rates were converted to "standard cows".

Soil food webs were constructed after Hunt et al. (1987) and Mulder et al. (2005). Nitrogen mineralisation was calculated ($N_{min,}$ mg N/m^2/yr, Eqn. 1) following De Ruiter et al. (1993) using the standing faunal biomass (B, mg dry weight/m^2) for invertebrates and their annual natural death rates (D_{nat}) and death rates by predation (D_{pred}). For each invertebrate trophic interaction nitrogen mineralisation was influenced by feeding rate which was calculated using assimilation efficiency (E_{ass}), production efficiency (E_{prod}) and organism C:N ratio for both prey (CN_{prey}) and predators (CN_{pred}), for which values from De Ruiter et al. (1993) were used. When calculating nitrogen mineralisation for macrofauna predators, information given for mesofauna predators was used.

Eqn. 1 $$N_{min} = E_{ass} \cdot (1/CN_{prey} - E_{prod}/CN_{pred}) \cdot (D_{nat} \cdot B + D_{pred}/E_{ass} \cdot E_{prod})$$

Soil and pasture sampling

Soil temperature (Checktemp, Hanna Instruments, UK) and moisture (TDR 300 Soil Moisture Probe, Spectrum Technologies Inc., USA) at 0–10 cm depth were recorded in the field at the time of sampling. After extracting the mesofauna, the cores were subsequently analysed for soil pH (1:2.5 soil:water), Olsen P (Olsen et al., 1954), total nitrogen and total carbon (dry combustion using LECO-2000, LECO Equipment Corp., USA). Bulk density was determined by collecting three intact soil cores (10 cm ø, 0–7.5 cm depth), drying (105ºC) and weighing.

Pasture species were determined from pasture samples collected using a 'trim' method (Piggot, 1989). Root biomass was determined using two composite soil samples (20 cores pooled, each core 2.5 cm ø, 0–7.5 cm deep) from each farm. Samples were crumbled and washed through a hydropneumatic root washer until soil was removed. Samples were towel dried, roots and tillers were separated, dried at 60ºC and weighed.

Pore size distribution for pores <60 µm was determined using tension plates (see Chapter 1). Soil was sieved (<2 mm) and saturated. Tensions of 10, 50, and 1500 kPa equated to pore sizes of 30, 6, and 0.2 µm ø, respectively.

Statistical analysis

The effects of management (organic vs. conventional) on abundance of macrofauna, mesofauna, and nematodes, and other measured variables were analysed using PROC MIXED in SAS v.9.1 (SAS Institute Inc., USA). Prior to analysis the abundance data were log (x+1) transformed. The effect of soil type was also analysed, with the two Recent soils (Recent, and Recent influenced by flooding) treated as separate soils. The graphs and tables show untransformed arithmetic means. The error bars in figures represent standard errors of the means. Due to low replication a significance level of α=0.1 was chosen.

Results

Soil bulk density (P=0.0001) and microbial biomass (P=0.009) were influenced by soil type (Table 2). Bulk density and the number of pores 0.2–30 µm ø in sieved soil were highest in the Pallic soil. Soil bulk density was lowest in the Allophanic soil. Often there were interactions between soil type and management, for example pores 0.2–6 µm ø were more abundant under organic management in three out of four soils. Soil moisture was higher, and temperature lower, under organic than conventional management on all soils, except the Pallic (*P*=0.0001).

Table 2. Soil and herbage properties in dairy grazed pastures under organic (O) and conventional (C) management, Manawatu, N.Z. (2007)

Soil type	Allophanic		Pallic		Recent		flooded Recent	
Management	O	C	O	C	O	C	O	C
Soil moisture (%)[1]	**53**	**35**	34	38	**55**	**41**	**46**	**35**
Soil temperature (ºC)[1]	**8**	**9.3**	12	12	**11**	**12**	**11**	**12**
Bulk density (Mg/m^3)[2]	0.69	0.69	0.96	0.93	0.83	0.86	0.94	0.92
Porosity (% v/v of sieved soil)								
0.2–6 µm*	17	18	**8**	**10**	**21**	**19**	**14**	**17**
6–30 µm*	11	11	**49**	**39**	**12**	**10**	10	10
Microbial biomass (µg C/g soil)[2]	1201	1895	2085	1612	1495	2333	1195	1637
pH[3]	6.0	6.0	6.0	5.7	5.7	6.0	6.1	5.9
Olsen P (mg/L)[2]	12	23	47	102	48	20	32	55
Total N (%)[2]	0.78	0.90	0.42	0.47	0.48	0.44	0.45	0.49
Total C (%)[2]	8.1	8.6	4.4	5.4	4.8	4.5	4.7	5.0
C:N ratio[2]	10.5	9.5	10.6	11.6	10.0	10.1	11.0	10.7
HERBAGE COMPOSITION (%)								
Grass	79	84	86	84	70	78	75	83
Legume	10	1	1	2	2	0	**4**	**2**
Other (including weeds)	4	0	1	1	3	4	2	1
Dead matter	7	15	12	13	24	18	19	14
Roots (g dry wt/m^2)[2]	512	443	474	484	432	454	464	464

[1] 0–10 cm depth.

[2] 0–7.5 cm depth.

*Pores 0.2–6 µm ø retain mostly plant unavailable water, and excludes most microorganisms with no predation on bacteria. Pores 6–30 µm ø retain mostly plant available water and accommodate most bacteria and their predators (Brewer, 1964).

Bold font indicates management effect within soil type significant at α=0.1.

Soil type influenced abundances of earthworms (*P*=0.026, Table 3), other macrofauna (*P*=0.011), mesofauna (*P*=0.002, Table 4) and nematodes (Table 5). In the well structured Allophanic soil there were few herbivorous macrofauna and earthworm abundance was low (Fig. 1). Among nematodes, plant feeding *Tylenchus* (*P*=0.082) and fungal feeding *Diphtherophora* (*P*=0.043) were more abundant in the Allophanic soil. Bacterial feeding *Cervidellus* and Alaimidae were only detected in Allophanic soils. *Meloidogyne* was more abundant in the Recent and Recent flooded soil where *Doryllium* (*P*=0.011) was less abundant (Table 5).

Fertiliser and nutrient inputs were lower under organic management. All conventional farms applied N as fertiliser, while N was applied only on some organic farms and this was as organic fertilisers. With the exception of the Recent soil, the lower fertiliser inputs under organic management were reflected in lower Olsen P and total N values (Table 2). The organic dairy farms had lower stocking rates than the conventional farms (on average 1.6 cows/ha under organic management, 2.9 cows/ha under conventional). There was a corresponding reduction in the live weight loading on the soil (Table 1).

Table 3. Earthworms and other macrofauna abundance (ind./m^2) and biomass (g wet wt/m^2) in dairy grazed pastures under organic (O) and conventional (C) management at 0–15 cm soil depth, Manawatu, N.Z. (2007).

Soil type	Allophanic		Pallic		Recent		flooded Recent		*P-value*		
Management	O	C	O	C	O	C	O	C	*Mngmt*	*Soil*	*Soil* Mngmt*
EARTHWORMS											
Lumbricus rubellus^1	**113**	**26**	113	53	119	53	73	79	***0.034***	*0.804*	***0.088***
Aporrectodea caliginosa^2	318	364	722	550	689	715	497	225	*0.597*	***0.009***	*0.930*
Aporrectodea rosea^2	**146**	**99**	66	33	**154**	**0**	0	13	***0.010***	***0.001***	***0.025***
Octolasion cyaneum^2	13	0	7	0	0	0	7	0	***0.090***	*0.797*	*0.797*
Aporrectodea longa^3	**0**	**172**	106	119	185	142	265	60	***0.079***	***0.001***	***0.001***
Total earthworms	590	662	1014	755	1147	911	841	378	*0.598*	***0.026***	*0.960*
Earthworm biomass	170	356	377	376	486	308	696	279	*0.902*	*0.409*	*0.570*
Anecic: total earthworm											
Abundance	**0**	**0.29**	0.12	0.17	0.17	0.19	0.31	0.16			
Biomass	**0**	**0.58**	**0.30**	**0.54**	0.42	0.37	0.58	0.47			
SR	**1.7**	**1.85**	1.4	1.6	1.4	1.5	**1.4**	**2.16**	*0.178*	*0.374*	***0.056***
J'	0.60	0.51	0.51	0.48	**0.57**	**0.34**	0.43	0.53	***0.005***	*0.117*	***0.035***
H'	**0.96**	**0.82**	0.82	0.78	**0.92**	**0.55**	0.70	0.86	*0.187*	*0.139*	***0.056***
MACROFAUNA											
Wiseana cervinata^4 larvae (Hepialidae)	0	0	7	0	13	0	0	7	*0.304*	*0.545*	*0.159*
Costelytra zealandica^5 larvae (Scarabaeidae)	40	7	0	0	0	0	0	0	*0.461*	***0.029***	*0.650*
Click beetle larvae (Elateridae)	0	7	0	0	13	0	13	7	*0.394*	*0.308*	*0.308*
Weevils (Circulionidae)*	66	40	437	325	205	166	470	404	*0.956*	***0.004***	*0.934*
Other Coleoptera (adult)	0	0	0	7	0	13	0	0	*0.164*	*0.574*	*0.574*
Gastropoda	0	0	7	13	26	0	0	0	*0.872*	*0.158*	*0.489*
Cicadidae (Hemiptera)	0	0	0	7	20	0	20	0	*0.143*	*0.465*	***0.124***
Total macrofauna	106	53	450	351	278	179	503	417	*0.526*	***0.011***	*0.911*
Macrofauna biomass	7	2	16	9	36	4	16	7	***0.052***	***0.064***	*0.739*
SR	1.08	1.08	0.21	0.83	**2.58**	**0.68**	0.7	0.65	*0.459*	*0.448*	*0.225*
J'	0.04	0.04	0.01	0.10	**0.20**	**0.04**	0.07	0.04	*0.436*	*0.331*	***0.078***
H'	0.09	0.09	0.02	0.19	**0.39**	**0.08**	0.14	0.08	*0.444*	*0.321*	***0.076***

*Predominantly clover root weevil (*Sitona lepidus*).

Bold font indicates management effect within soil type significant at α=0.1.

^{1}Hoffmeister (1843), ^{2}Savigny (1826), ^{3}Ude (1885), ^{4}Walker (1865), ^{5}White (1846).

Independent of soil type, soil fauna appeared to respond to changes in stock live weight loading and the amount of calculated dry matter potentially entering the soil food web (Fig. 2). Calculated from stocking rate, litter inputs to the soil were higher under conventional than organic management.

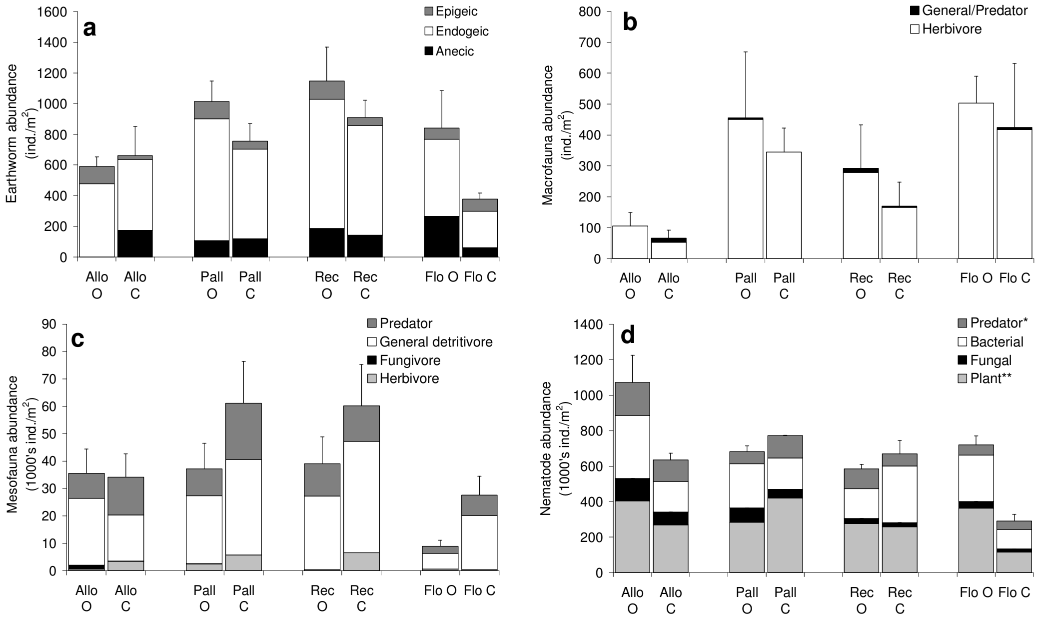

Fig. 1. Invertebrates under organic and conventional management in the Manawatu, N.Z. (a) Abundance of earthworm functional groups, (b) abundance of macrofauna trophic groups, (c) abundance of mesofauna trophic groups, and (d) abundance of nematode trophic groups. Allo: Allophanic, Pall: Pallic, Rec: Recent, Flo: flooded Recent. O: organic and C: conventional.
*Predacious and omnivorous nematodes.
**Plant feeding and plant associated nematodes.

Total earthworm abundance showed no significant response to management, but tended to decline as dry matter input to the soil food web increased (i.e., conventional management) (Fig. 2). Further, earthworm diversity and the abundance of *Lumbricus rubellus* and *Aporrectodea rosea* were lower under conventional management. *Octolasion cyaneum* was not detected under conventional pastures. *Aporrectodea longa* was more abundant under organic management in Recent soils, but more abundant under conventional management in the Pallic soil (Table 3). *A. longa* was absent from the conventional farm on Allophanic soil. Other macrofauna had a higher biomass under organic management, where there tended to be a higher abundance of the clover root weevil (*S. lepidus*) (Fig. 1, Table 3).

Management had a significant influence on mesofauna abundance, which was higher under conventional management (*P*=0.063, Table 4). While Collembola abundance tended to increase with stock live weight loading, Oribatid abundance tended to decrease (Fig. 2). For some mesofauna taxa the absence of overall management effect reflected the opposing trends between organic and conventional management in different soil types. For example, Collembola, Poduromorpha (*P*=0.003) were more abundant under organic management in Allophanic soils, but more abundant under conventional management in the three other soil types (Table 4).

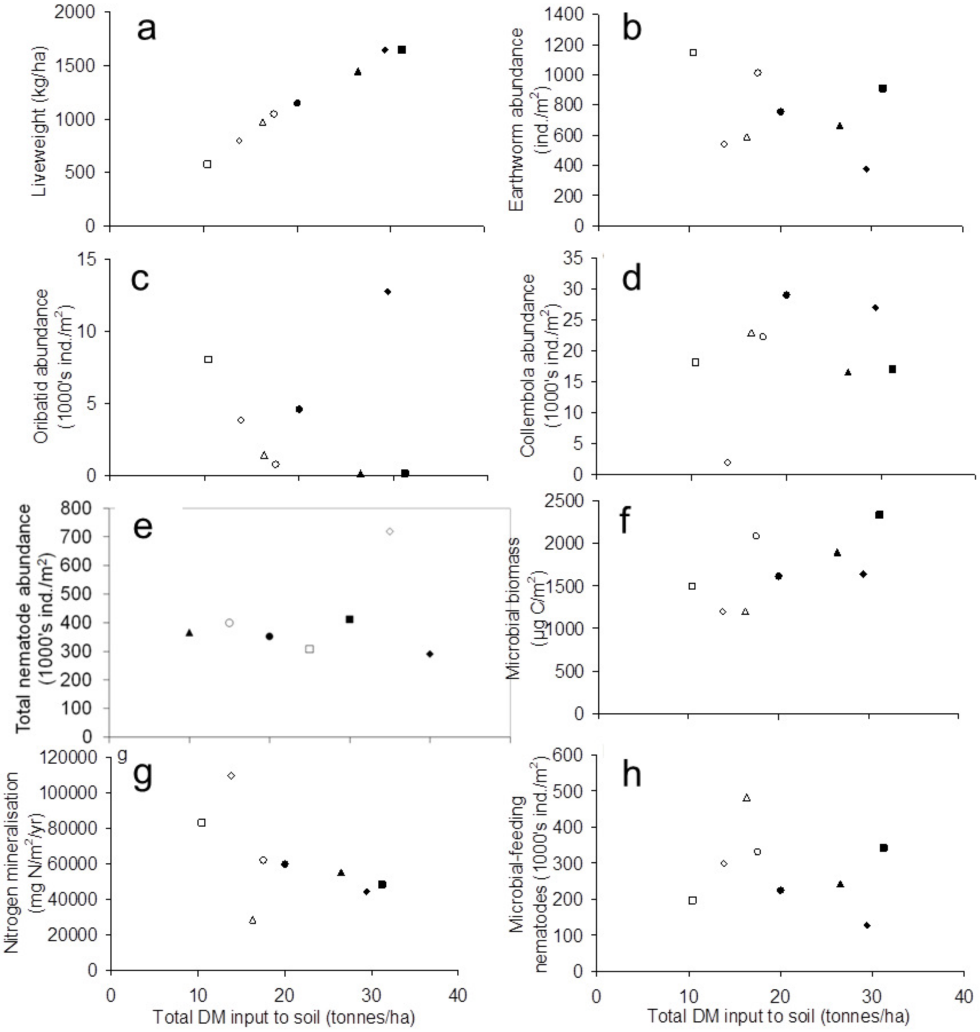

Fig. 2. Calculated dry matter (DM) input to the soil plotted against (a) live weight loading, (b) earthworm abundance, (c) Oribatida abundance, (d) Collembola abundance, (e) nematode abundance, (f) microbial biomass, (g) calculated nitrogen mineralisation and (h) microbial feeding nematode abundance. Hollow symbols are organic, solid symbols are conventional. △▲: Allophanic; ○●: Pallic, □■: Recent; ◇◆: Recent flooded.

There was a significant interaction between management and soil type/location for nematode abundance. Total nematode abundance tended to be higher under organic management in the Allophanic and the Recent flooded soils (Table 5). Between 24 and 32 taxa were found within a particular soil. Among nematodes, clover cyst nematode *Heterodera* (*P*=0.002) and predatory *Clarkus* (*P*=0.018) were more abundant under organic management in all soils in which they were detected.

Table 4. Mesofauna and Oribatida (1000's ind./m^2) in dairy grazed pastures under organic (O) and conventional (C) management at 0–7.5 cm soil depth, Manawatu, N.Z. (2007).

Soil type	Allophanic		Pallic		Recent		flooded Recent		*P-value*		
Management	O	C	O	C	O	C	O	C	*Mngmt*	*Soil*	_Soil* Mngmt_
MESOFAUNA											
Oppiella nova (Oudemans, 1902)	0	0	0.1	0.8	0.6	0	0	0	*0.965*	*0.107*	*0.398*
Ramusella sp.1	0	0	0	0	1.5	0	0	0	*0.327*	*0.410*	*0.410*
Setobates scheloribatoides (Ramsay, 1966)	0.5	0	**0.3**	**3.6**	3.7	12.5	**3.4**	**0**	*0.202*	***0.010***	***0.018***
Nymphs	0.4	0	0.1	0.3	1.8	0.3	0.1	0.1	*0.255*	*0.601*	*0.322*
Oribatida (adult)*	1.0	0.1	0.6	4.3	6.2	12.5	**3.7**	**0**	*0.195*	***0.018***	***0.066***
Total Oribatida	1.4	0.1	0.8	4.6	8.0	12.7	3.8	0.1	*0.196*	***0.084***	*0.168*
Astigmata	0.1	0.1	1.7	1.3	0.8	0.9	0	2.5	*0.543*	*0.313*	*0.832*
Mesostigmata	3.9	7.1	7.4	17.3	9.7	8.2	2.3	7.0	*0.959*	*0.196*	*0.812*
Prostigmata	4.6	1.3	0.5	2.4	1.1	3.4	0	0.1	*0.254*	***0.001***	*0.544*
Scutacaridae	0.4	1.9	1.0	0.5	0.1	0.5	0	0.1	*0.167*	*0.136*	*0.986*
Total Acari	10.1	10.6	11.2	25.8	18.0	25.5	6.0	9.8	*0.591*	***0.044***	*0.777*
Entomobryomorpha	17.7	15.5	21.3	21.1	15.4	26.7	1.9	13.9	*0.129*	***0.016***	*0.267*
Poduromorpha	**2.5**	**0.3**	**3**	**7.1**	0	0.3	0	1.9	***0.041***	***0.028***	***0.007***
Sminthuridae	2.5	0.8	0.8	0.6	**2.4**	**0**	0	0.4	*0.491*	*0.254*	*0.100*
Neelipleona	0.1	0	0	0.1	0.3	0	0	0.9	*0.929*	*0.997*	*0.288*
Total Collembola	22.9	16.6	22.3	29.0	18.0	26.9	1.9	17.1	***0.092***	***0.013***	***0.077***
Protura	1.4	0.1	0.1	0	0	0	0	0	*0.491*	*0.297*	*0.876*
Coleoptera	0.1	0.4	0.6	0.1	0.5	0.3	0	0.1	*0.923*	*0.386*	*0.375*
Diptera	0	3.1	0.3	0	0	0.1	0.3	0.1	*0.563*	*0.843*	***0.115***
Hemiptera	0.1	0	0.9	0.1	0	0	0	0	*0.252*	*0.081*	*0.704*
Thysanoptera	0.5	3.4	1.7	5.6	0.4	6.6	0.6	0.4	***0.104***	*0.915*	*0.435*
Chilopoda	0	0	0	0.1	**0.1**	**0.3**	0	0	*1.00*	***0.086***	*0.553*
Total mesofauna	35.1	34.1	37.1	60.9	37.3	60.0	8.8	27.5	***0.063***	***0.002***	*0.496*
SR	3.7	3.6	3.6	3.2	3.6	3.5	6.6	4.3	***0.070***	***0.002***	*0.285*
J'	0.35	0.44	0.42	0.44	0.45	0.48	0.37	0.27	*0.716*	***0.007***	*0.117*
H'	0.98	1.23	1.16	1.22	1.25	1.33	1.02	0.74	*0.704*	***0.007***	*0.109*

*Oribatid species low in abundance (<500 ind./m^2) and not reported in the table, include: *Tectocepheus sarekensis* (Trägårdh, 1910) and *Achipteria* sp. in Allophanic soil, *Microppia minus* (Paoli, 1908) and *Ramusella* sp.2 in Pallic soil, *Platynothrus peltifer* (Koch, 1839) and *Liebstadia similis* (Michael, 1888) in Recent soil.

Bold font indicates management effect (within soil type) significant at α=0.1.

Table 5. Nematodes (1000's ind./m^2) in dairy grazed pastures under organic (O) and conventional (C) management at 0–7.5 cm soil depth, Manawatu, N.Z. (2007).

Soil type	Allophanic		Pallic		Recent		flooded Recent		*P-value*		
Management	O	C	O	C	O	C	O	C	*Mngmt*	*Soil*	Soil* Mngmt
Tylenchus	116.8	108.6	**78.5**	**134.6**	**65.5**	**53.1**	98.4	39.4	*0.202*	***0.082***	*0.110*
Cephalenchus	19.5	3.1	27.3	20.7	22.8	23.2	3.4	4.4	*0.735*	*0.289*	*0.858*
Heterodera juv.	**68.2**	**0**	10.2	0	**17.1**	**0**	**6.8**	**0**	***0.002***	*0.494*	*0.494*
Meloidogyne juv.	0	3.1	0	0	5.7	3.3	6.8	13.1	*0.551*	***0.051***	*0.816*
Tylenchorhynchus	0	0	**0**	**6.9**	0	10.0	13.6	7.3	*0.154*	*0.407*	*0.445*
Hoplolaimidae	73.0	3.1	**17.1**	**151.9**	**51.2**	**43.1**	149.3	4.4	*0.118*	*0.297*	*0.114*
Pratylenchus	14.6	34.1	**133.1**	**72.5**	45.6	86.3	30.5	26.3	*0.338*	*0.258*	*0.391*
Criconemoides	0	0	0	0	0	3.3	0	0	*0.347*	*0.441*	*0.441*
Paratylenchus	24.3	6.2	0	6.9	5.7	10.0	6.8	8.8	*0.478*	*0.777*	*0.895*
Aphelenchus	73.0	31.0	40.9	24.2	22.8	23.2	17.0	17.5	*0.629*	*0.276*	*0.829*
Aphelenchoides	0	3.1	13.6	10.4	2.8	0	0	0	*0.580*	*0.150*	*0.397*
Seinura	0	0	6.8	10.4	0	3.3	6.8	4.4	*0.703*	*0.545*	*0.901*
Diplogaster	0	0	0	0	0	10.0	0	1.5	*0.199*	*0.588*	*0.588*
Rhabditidae	29.2	24.8	64.8	17.3	**22.8**	**82.9**	108.6	29.2	*0.273*	*0.608*	*0.298*
Dauerlarvae	112.0	9.3	**27.3**	**0**	0	29.9	**10.2**	**0**	*0.349*	*0.798*	*0.302*
Panagrolaimus	126.6	62.0	54.6	65.6	65.5	96.2	91.6	42.4	*0.267*	*0.592*	*0.278*
Cephalobus	53.6	40.3	**51.2**	**62.1**	39.9	29.9	10.2	27.7	*0.483*	*0.600*	*0.580*
Heterocephalobus	4.9	0	6.8	10.4	**0**	**29.9**	**17.0**	**0**	*0.965*	*0.793*	*0.193*
Cervidellus	4.9	21.7	0	0	0	0	0	0	*0.925*	*0.194*	*0.999*
Stegellata	0	0	0	0	2.8	0	0	0	*0.347*	*0.441*	*0.441*
Plectus	4.9	0	10.2	10.4	8.5	10.0	**10.2**	**0**	*0.146*	*0.396*	*0.240*
Anaplectus	0	0	0	0	8.5	0	0	1.5	*0.930*	*0.594*	*0.331*
Prismatolaimus	0	0	0	0	5.7	0	0	0	*0.347*	*0.441*	*0.441*
Monhystera	14.6	9.3	34.1	10.4	14.2	26.5	3.4	7.3	*0.574*	*0.748*	*0.367*
Chromadoridae	0	0	0	0	0	3.3	0	0	*0.347*	*0.441*	*0.441*
Tobrilus	0	0	3.4	0	5.7	13.3	0	0	*0.635*	*0.344*	*0.822*
Dorylaimus	38.9	21.7	27.3	48.3	**57.0**	**19.9**	**10.2**	**0**	***0.001***	***0.001***	***0.001***
Eudorylaimus	29.2	18.6	10.2	24.2	22.8	3.3	6.8	1.5	*0.834*	*0.437*	*0.466*
Pungentus	53.6	62.0	17.1	24.2	48.4	19.9	**23.7**	**0**	***0.001***	***0.0001***	***0.0002***
Aporcelaimus	77.9	80.7	20.5	44.9	11.4	29.9	23.7	42.4	*0.262*	*0.301*	*0.446*
Longidorus	**0**	**49.6**	0	3.5	14.2	6.6	17.0	11.7	*0.123*	*0.200*	*0.249*
Dorylaimellus	34.1	0	0	0	0	0	**6.8**	**0**	*0.196*	*0.594*	*0.594*
Doryllium	34.1	34.1	**27.3**	**13.8**	2.8	0	13.6	0	*0.172*	***0.011***	*0.639*
Clarkus	38.9	3.1	0	0	**14.2**	**0**	**6.8**	**0**	***0.018***	***0.069***	*0.328*
Alaimidae	4.9	3.1	0	0	0	0	0	0	*0.996*	*0.193*	*1.00*
Diphtherophora	19.5	3.1	0	0	0	0	6.8	0	*0.148*	***0.043***	*0.497*
Total nematodes	1071.0	635.9	682.4	773.1	583.7	670.2	719.2	290.6	***0.070***	***0.072***	***0.070***
SR	4.7	5.0	5.0	4.9	5.1	5.0	5.0	5.8	***0.079***	***0.081***	***0.076***
J'	0.72	0.71	0.72	0.70	0.76	0.71	0.67	0.61	*0.173*	***0.081***	*0.882*
H'	2.63	2.57	2.61	2.55	2.76	2.59	2.43	2.23	*0.169*	***0.078***	*0.871*
NCR	0.73	0.71	0.76	0.78	0.86	0.93	0.85	0.86	*0.683*	*0.106*	*0.914*
Maturity groups (%)											
CP1	25	15	22	11	15	33	**29**	**25**	*0.763*	*0.693*	*0.455*
CP2	30	35	40	39	33	31	25	38	*0.255*	*0.343*	*0.378*
CP3	16	7	24	30	22	24	30	18	*0.431*	*0.145*	*0.505*
CP4	19	22	12	14	**25**	**6**	**9**	**1**	***0.040***	***0.005***	***0.022***
CP5	10	20	3	6	4	5	7	19	***0.043***	***0.042***	*0.505*
MI	1.67	1.64	1.24	1.20	1.32	1.13	0.98	1.40	*0.804*	*0.172*	*0.570*
PPI	**0.94**	**1.34**	1.12	1.46	1.38	1.06	1.39	1.09	*0.820*	*0.901*	*0.212*
ΣMI	2.60	2.98	2.36	2.65	2.70	2.19	2.37	2.49	*0.738*	*0.417*	***0.283***

Bold font indicates management effect (within soil type) significant at α=0.1.

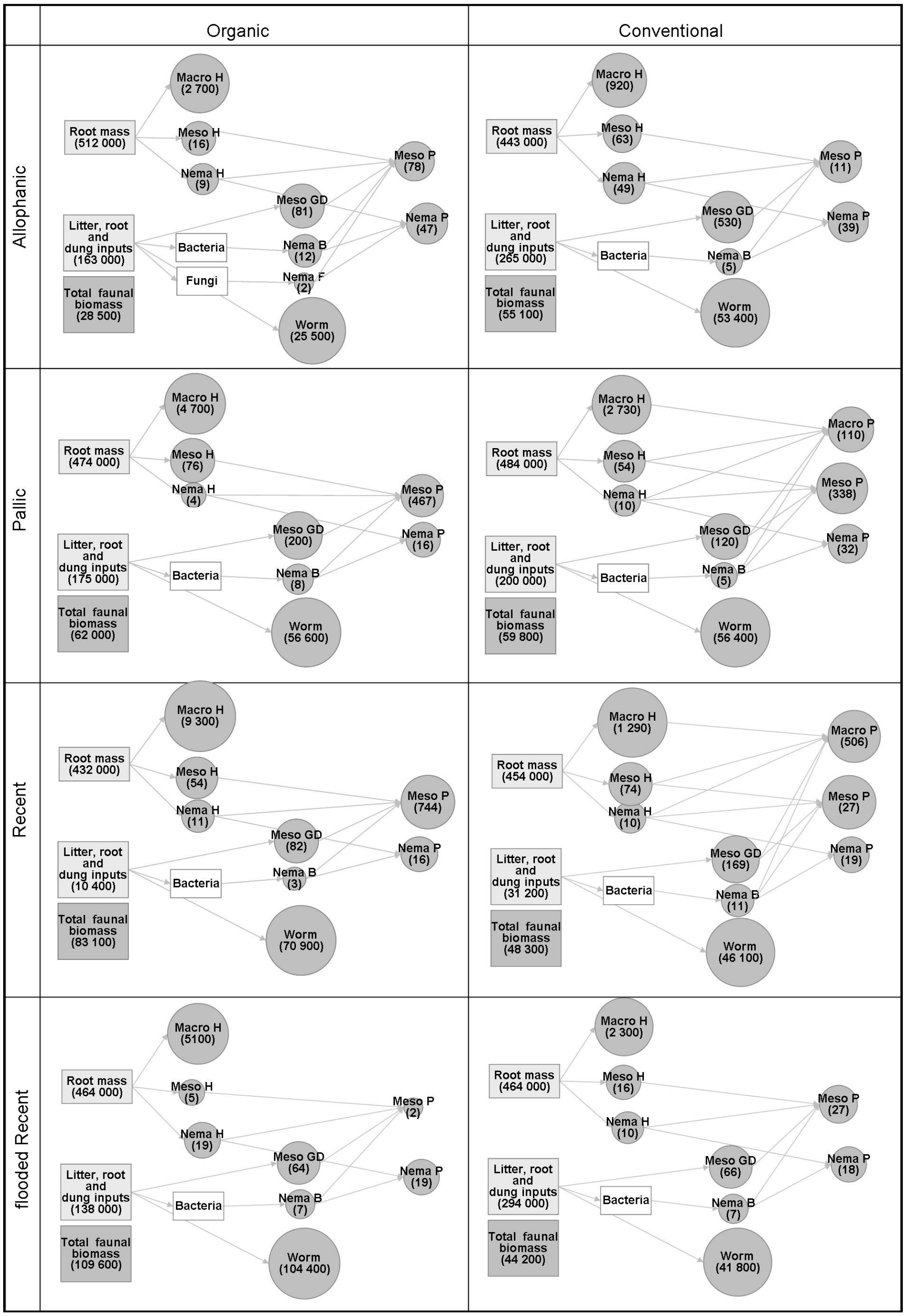

Fig. 3. Food webs of selected soil faunal groups in four soils under different pasture management regimes, Manawatu, New Zealand. Food webs and biomass calculation derived from Hunt (1987) and Mulder et al. (2005). Resource inputs are given in mg dry weight/m^2. Macrofauna (Macro), mesofauna (Meso) and nematode (Nema) herbivores (H) feed on plant material. Earthworms (Worm), mesofauna general detritivores (GD) and nematode bacterial feeders (B) feed on detrital inputs and associated microflora. The macrofauna, mesofauna and nematodes are, in turn, consumed by predators (P). Circle areas represent the log biomass of the fauna, actual biomass (dry weight mg/m^2) given in parentheses. Biomass calculated as described in Chapter 1. Trophic groups with biomass <1.5 mg dry weight/m^2 were excluded.

The total standing biomass in the soil food web varied, mostly reflecting changes in earthworm biomass (Fig. 3). Total faunal biomass ranged from 28 500 mg dry weight/m^2 under organic management in Allophanic soil where *A. longa* was absent to 104 400 mg dry weight/m^2 under organic management in Recent flooded soil where the biomass of *A. longa* was dominant. Fungal feeding nematodes were low in biomass in all soils (<1.5 mg dry weight/m^2) except under organic management in the Allophanic soil where they were found to have a biomass of 2 mg dry weight/m^2. Fig. 4 shows calculated contribution of the invertebrates within the decomposer food web to N mineralisation. Earthworms had the highest biomass and were also calculated to have the largest contribution to N mineralisation.

Discussion

Plant material is an important source of food to the soil food web, so any change in pasture production affects the soil food web (Yeates, 1976b; Zyromska-Rudzka, 1977; Yeates, 1980; Cole et al., 2005; Oliver et al., 2005; Sjursen et al., 2005; King and Hutchinson, 2007; Curry et al., 2008). Based on livestock numbers, pasture growth was calculated to be lower under organic than conventional management, where there was a trend of lower biomass of plant feeding and plant associated nematodes (i.e., *Longidorus* and *Tylenchorhynchus*), and herbivorous mesofauna (Fig. 3). Total biomass of herbivorous fauna was, however, higher under organic management, with higher abundances of the clover root weevil (*S. lepidus*) and the clover cyst nematode (*H. trifolii*) observed across all soil types. Soil type influenced only absolute abundances, with a seven-fold difference in clover root weevil abundance across the soils (from 40 ind./m^2 in Allophanic to 470 ind./m^2 in flooded Recent). The higher clover root weevil and the clover cyst nematode abundance in organic systems reflected the higher proportion of legumes there, and might reflect the greater dependence of organic pastures on legume growth and biological N fixation (Table 1).

The lower nutrient and dry matter inputs into the soil food web in the organic dairy operations (Table 1) were expected to have a negative influence on decomposing invertebrates and, in turn, on their contribution to N mineralisation. In particular, it is earthworms, with their high biomass, which have large influences on soil properties (Cole et al., 2006). In this study, total earthworm abundance increased as the dry matter entering the soil food web decreased (Fig. 2). This suggests that, in these soils, the impact of stock treading from higher live weight loading was more of a determinant of earthworm abundance than available food resources. Similar results have been reported by Lambert (1986) and Curry et al. (2008). This conclusion is supported by the findings of no difference in earthworm biomass between the two farm systems on the Pallic soil, where live weight loadings were similar. Because earthworm biomass had a large influence on calculated N mineralisation, their lower biomass in the more productive pastures was associated with lower rates of N mineralisation (Fig. 4).

The positive influence of organic management on biological activity and N mineralisation was most pronounced in the Recent soil, where the differences in stocking rates between organic and conventional management were largest. In the Recent soil, where earthworm abundance and biomass was high, the stocking regime was more diverse, including dairy cows, goats and sheep. Hence, these pastures were associated with low live weight loading and treading pressures (the treading pressure of sheep is about half that of cows (Greenwood and McKenzie, 2001)). Similar patterns were observed in the flooded Recent soil. There, the application of organic composts may have been an additional valuable source of food input to the soil food web (Edwards and Lofty, 1982; Curry, 1987) which may explain the higher abundance of earthworms and nematodes under organic management in this soil. Under these pastures on a flooded Recent soil the abundance of *A. longa* was high, and its deep burrowing ability makes it less vulnerable to flooding than endogeic *A. caliginosa,* as observed by Ausden et al. (2001) in various soils in England. In the well structured Allophanic soil, which may be more resistant to compaction than the sedimentary soils (Hewitt and Shepherd, 1997), earthworm biomass was higher in conventional dairy grazed pastures. Here, where distance between the paired farms was large (~8 km), large anecic *A. longa* were absent, likely due to their patchy distribution within New Zealand (Springett, 1992).

Under less intensive organic systems in European soils, both Yeates et al. (1997) and Mulder et al. (2003) observed a relative increase in the fungal decomposition pathway. In this study contribution of fungal-feeding nematodes to N mineralisation was lower than that for bacterial feeding nematodes (Fig. 4), and the relative contribution of bacterial feeding nematodes and fungal feeding nematodes was more influenced by the soil type than by management (NCR, Table 5). As the calculated dry matter potentially entering the soil food web increased, soil microbial biomass increased (except in the Pallic soil) (Fig. 2). However, the abundance of microbial feeding nematodes and larger predatory and omnivorous nematodes which feed on them decreased, suggesting that even though their food resources were increasing, such nematodes may be more affected by the impact of livestock on their physical environment (Yeates, 1976b, 1980; Bouwman and Arts, 2000).

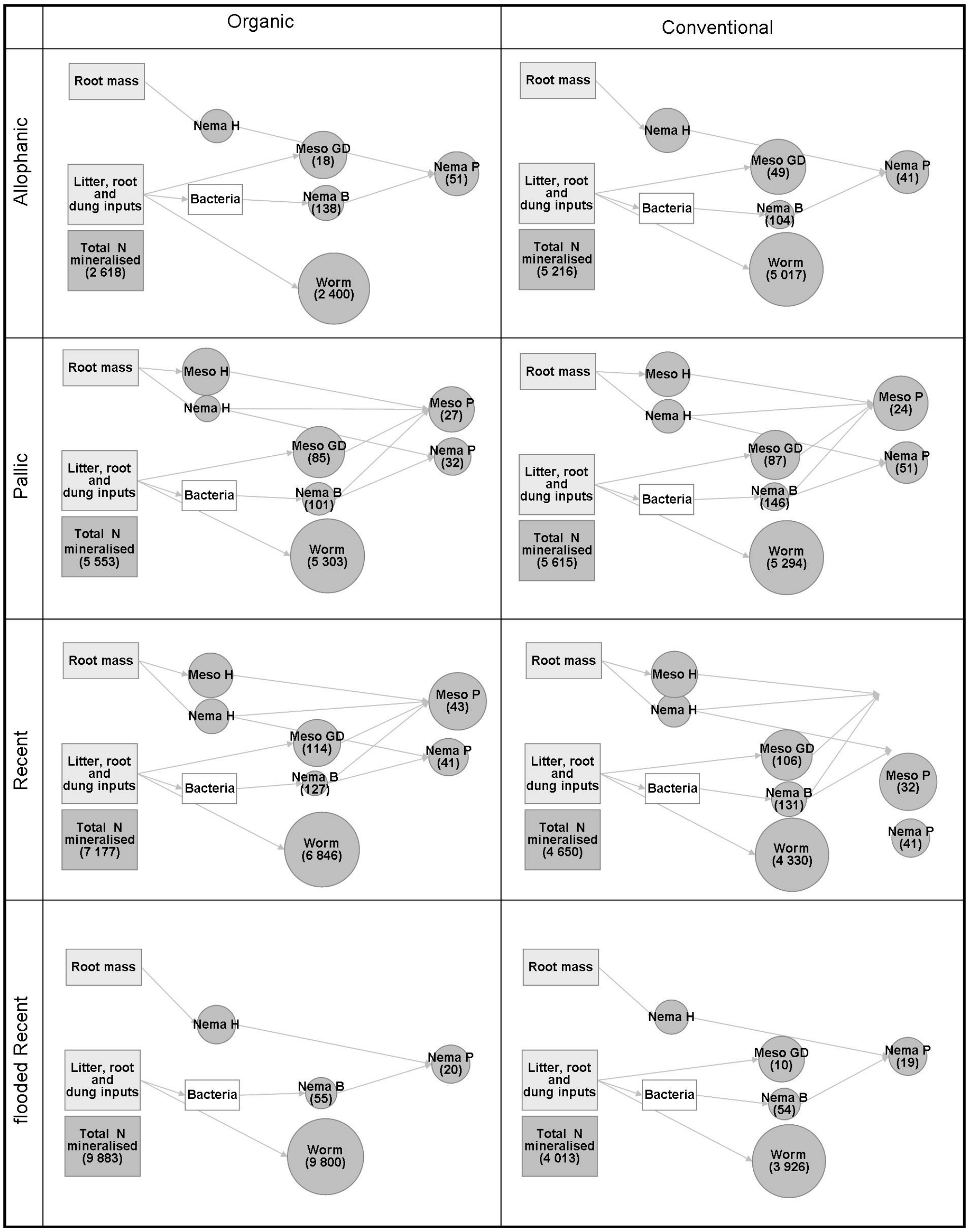

Fig. 4. Calculated nitrogen mineralisation in the components of the food webs under different pasture management regimes, Manawatu, New Zealand. Modified after Hunt (1987) and De Ruiter et al. (1993). For details see Fig. 3. Circle areas represent the log biomass of the fauna, with contribution to N mineralisation (mg N/m^2/yr) given in parentheses. Only trophic groups contributing more than 10 mg N/m^2 are shown.

The soil mesofauna showed little response to increases in dry matter input to the soil surface. Detritus feeding Oribatida were low in abundance in this study (<13 000 ind./m^2) supporting previous findings that they are sensitive to physical disturbance such as dairy cow treading (Cole et al., 2008; Schon et al., 2008). This was in contrast to the same Pallic soil where Acari were more abundant under organic management (Kelly et al., 2006). In comparison with Oribatida, detritus feeding Collembola were more abundant in all soils, and would have contributed more to N mineralisation. Collembola abundance fluctuates throughout the year, and they may be less susceptible to physical disturbance due to their more *r*-selected life strategies (greater ability to colonise new environments) and jumping ability (Curry, 1994; Norton, 1994). Mesostigmata, which prey on Collembola (Koehler, 1999), were positively associated with Collembola but contributed little to the calculated N mineralisation (Fig. 3).

Of the invertebrates identified in this study, earthworms were calculated to have the largest contribution to N mineralisation, consuming 1090–4455 kg of N/ha/yr and mineralising 24–98 kg N/ha/yr (Fig. 4). This value assumes that the community composition and activity of the earthworms remained the same throughout the year, even though it is likely that they contribute more to N mineralisation during the spring and autumn months, aestivating during the drier summer months (Yeates, 1976a; Edwards and Bohlen, 1996). The mesofauna and nematodes were calculated to contribute 0.8 to 3.3 kg N/ha/yr, and even though nematodes had a lower biomass (5–65% of mesofauna biomass), their faster turnover rates meant that mesofauna and nematodes contributed equally to N mineralisation. Significant amounts of N are also mineralised by bacteria, fungi and protozoa. De Ruiter et al. (1993) reported a contribution of up to 90% by bacteria, fungi and protozoa in arable systems where earthworm abundance was low, with similar rates reported by Hunt et al. (1987) in a short grass prairie without consideration of earthworms. Assuming similar rates, bacteria, fungi and protozoa may be expected to mineralise up to 30 kg of N/ha/yr in this study. The studied dairy grazed pastures may require up to 500 kg N/ha/yr, with only 50–90 % of the mineralised N taken up by plants (Elgersma et al., 2000). This means that about 1000 kg N/ha/yr may be mineralised in these pastures, with the activity of invertebrates making up only a small proportion of this. Higher faunal biomass under less intensive organic management translates into greater N mineralisation (Fig. 3), suggesting that despite potentially more litter entering the soil food web under conventional management, conventional systems are less efficient at decomposition and mineralisation, as they may be compromised by higher livestock loading.

Conclusion

The present study highlights that increased stock treading pressure on soil invertebrates has a negative impact on calculated N mineralisation rates. This can be demonstrated by examining the paired farms with the largest (Recent and flooded Recent soils) and smallest differences in stocking rates (Pallic). In the Recent and flooded Recent soils the high earthworm biomass under organic management was associated with high N mineralisation rates. The contribution of fungal feeding nematodes to decomposition and N mineralisation was low in all pastures, and was more affected by the soil type than by management. Reliance on legumes in the organic pastures stimulated the clover root weevil and the clover cyst nematode. Across all four soils there was a positive response on the invertebrate community under organic management, with its lower live weight loading, despite lower dry matter inputs into the soil food web.

This organic conventional comparison highlights the diverse practices employed by land managers. To better understand the effects of organic management, factors such as fertiliser application and stocking regime need to be considered in any analysis**.**

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Chapter Four:

Soil fauna in ungrazed and sheep grazed pastures under organic and conventional management on hill country

Chapter Three observed a positive responsive of organic dairy management on the soil fauna mostly in relation to reduced fertiliser application and stocking rates. This chapter explores the influence of an organic sheep system on the soil fauna in study where fertiliser application and stocking rates between the conventional and organic systems are the same. An ungrazed pasture was also included in the sampling to determine if the invertebrate diversity and abundance between the conventional and organic systems represented the limits in the potential invertebrate community that could be sustained in this soil and climate.

N.L. Schon, A.D. Mackay, M.A. Minor. Soil fauna in ungrazed and sheep grazed pastures under organic and conventional management on hill country.

Abstract

Organic pasture management is a broad term associated with legume based pasture production, mixed livestock grazing and certification restrictions on nutrient inputs, and pest and weed control. These are all factors which influence the environment of soil invertebrates. In this study, soil macrofauna, mesofauna and microfauna were collected from duplicate 11 and 20 year old organic and conventional sheep grazed systems. Both systems had the same reactive phosphate rock (33 kg P/ha/yr) and stocking rate (12 su/ha) regimes. Two ungrazed sites which had not received any nutrient inputs for 20+ years were also sampled.

The ungrazed pastures had a higher proportion of fungal feeding than bacterial feeding nematodes than the sheep grazed pastures (NCR: 0.64 vs. 0.90). The ungrazed pastures had more species endemic to New Zealand such as the earthworm *Octochaetus multiporus*, and Oribatida *Metabelba obtusus, Lanceoppia jacoti, Galumna rugosa, Zygoribatula novazealandica, Setobates scheloribatoides* and *Nesopelops punctatus*, with twice as many large Oribatida (36% vs. 18%). The introduction of fertiliser and stock grazing resulted in fewer endemic species, more earthworms (318 vs. 853 ind./m^2) and nematodes (682.4 $x10^3$ vs. 1158.6 $x10^3$ ind./m^2). This resulted in a higher biomass of soil fauna. The soil fauna in the organic and conventional grazed pastures had similarities between them and had common differences with the ungrazed pasture.

While fertiliser regime and sheep stocking rates were the same in organic and conventional systems, sheep live weight was lower under organic management. This resulted in reduced pasture intake and increased the amount of litter available to the soil food web, stimulating *Lumbricus rubellus* abundance (191 vs. 106 ind./m^2). Total earthworm abundance was lower under organic management (763 vs. 943 ind./m^2), resulting in a lower faunal biomass in the soil food web. In the organic pastures, where pasture growth was lower than under conventional management, the abundance of plant feeding nematodes was lower and macrofauna predators were absent. The farmlet that had been under organic management for 20 years had more Oribatida than the farmlet that had been under organic management for only 11 years, which may be in response to reduced earthworm burrowing.

There was little evidence of increased biological activity under organic management in sheep grazed pastures, suggesting that observed responses to organic management are more likely to be the result of restrictions placed on nutrient inputs, limiting production levels and stocking rates.

Introduction

There is an increasing concern about the long term sustainability of intensive pastoral systems (Doran and Zeiss, 2000; Mackay, 2008). Issues of concern include declining physical properties of the soil (Greenwood and McKenzie, 2001; Sparling and Schipper, 2004), loss of soil carbon (Bellamy et al., 2005; Schipper et al., 2007), increased nitrogen leaching (Ledgard, 2001), and the loss of soil biodiversity (Wardle, 1999; Schon et al., 2008). Degradation of pastoral systems may lead to further intensification to maintain productivity. There is a growing recognition that there is a limit to continued intensification of pastoral systems (Parfitt et al., 2008).

Organic agriculture continues to be advanced as a viable and sustainable alternative to conventional agriculture, reducing the environmental impacts of agricultural practices, and providing 'clean green' produce to the population. As in many countries, only a very small percentage of New Zealand's agricultural land is under organic management (Willer and Yussefi, 2007), yet interest remains high in the potential economic and environmental benefits of expanding certified organic production from the pastoral industry. Organic pastoral production systems emphasise legume based pasture production, mixed livestock and grazing management practices, and are characterised by strict limits on plant nutrient inputs, imported feed supplements, and the use of agrochemicals in the control of pests and weeds. All these practices are believed to be beneficial to soil invertebrates (Hole et al., 2005). With enhanced activity of soil invertebrates, such as earthworms, mesofauna and nematodes, benefits to soil services such as nutrient cycling can be seen (Bardgett and Chan, 1999; Cole et al., 2004; Fonte et al., 2007). A number of studies have found soil fauna to be positively influenced by organic management in permanent pastures (Yeates et al., 1997; Mulder et al., 2003); in both these studies the organic production systems had lower ruminant stocking rates than the conventional systems. Yeates et al. (1997) found increases in the dominance of fungal feeding nematodes over bacterial feeding nematodes with organic management, as represented in the Nematode Channel Ratio (NCR). In Chapter 4 it was observed that the NCR was more influenced by soil type than lower fertiliser applications and stocking rates. Another study by Parfitt et al. (2005) did not show any measurable benefits of organic management for soil fauna; in their study, organic systems had the same stocking rate and the same animal type as conventional systems, but different levels of soil fertility and nutrient inputs. These differences illustrate one of the challenges of comparing organic and conventional pastoral systems, which is that of controlling stocking rate and fertiliser use, as both practices directly affect soil fauna (Hassink et al., 1993; Wardle et al., 1998; Nielsen et al., 2008). Controlling variables, such as grazing and fertiliser regimes, when assessing organic systems offers the opportunity to explore more closely the underlying impact of organic management on soil invertebrate community, while avoiding the compounding effects of management.

In this study we compared the influence of an organic and conventional sheep production system on the soil invertebrate community, under conditions where the major management variables influencing soil fauna (i.e., animal type and stocking rate, nutrient inputs, and pasture management) were the same in both systems. Both systems were legume based pastures grazed *in situ* by sheep year round. One replicate of the two production systems was established in 1987 and the other in 1997. Adjacent areas in pasture that had not been grazed for over 20 years were included in the study, to provide an indication of the soil fauna present under conditions where no fertiliser had been applied, there was no defoliation or livestock treading. Organic management is generally believed to be “better” for the soil and the environment and it is expected to positively influence soil invertebrates, including encouraging fungal feeding nematodes, reflective of a fungal based decomposition pathway. We investigated the differences in the invertebrate communities under organic and conventional pasture systems similar in stocking rate and fertiliser regime.

Methods

Study sites

The study was carried out at the AgResearch Hill Country Research Station, Ballantrae, Manawatu region, New Zealand (40°18'S 175°50'E). The Research Station is located 300 m above sea level, with an average air temperature of 12°C and an annual rainfall of 1270 mm. Temperature and rainfall were above average in the year preceding sampling. The soils are classified as Luvisol (FAO, 1988) (NZSC: Pallic, Ngamoka silt loam) (Hewitt, 1993), with silt loam texture (42 % sand, 40% silt and 18% clay). Pastures are dominated by the low fertility grass species *Agrostis capillaris* (browntop) and *Anthoxanthum odoratum* (sweet vernal), with grazed pastures also containing a small percentage of *Lolium perenne* (ryegrass) and *Trifolium repens* (white clover) (Nie et al., 1997; Mackay et al., 2006).

Four self contained, grazed experimental farmlets (each approximately 18 ha fenced into approximately 30 paddocks) were sampled. Two farmlets were established in 1987, one under organic and the other under conventional management. In 1996, another pair of organic and conventional farmlets was established, creating a replicated systems comparison. Within each farmlet, areas were fenced off (~0.1 ha), which had been neither grazed by domestic animals nor fertilised since 1987.

The organic farmlets were certified to meet the requirements of BioGro New Zealand (BioGro, 2001), which prohibits the routine use of drenches, vaccines and antibiotics, except when the animals' welfare is at risk. Risk animals are identified, treated and subsequently quarantined. History of the organic and conventional farm systems sampled in this study are described in detail by Mackay et al. (2006) and summarised in Table 1. Briefly, the organic and conventional farmlets received the same fertiliser inputs, reactive phosphate rock (33 kg P/ha/yr as RPR, a water insoluble fertiliser) and elemental sulphur (26 kg S/ha/yr), and were stocked at the same rate (12 stock units/ha) by sheep. A 'stock unit' is a 'standard sheep' which consumes 550 kg dry matter per year (www.maf.govt.nz). The major difference between the organic and conventional farmlets was that on the conventional farmlets**,** prior to lambing, sheep received a 100-day Ivermectin® bolus for control of intestinal parasites and a 7-in-1 vaccine mix for protection against clostridial diseases. Further, on the conventional farmlets lambs received a PK-antitet for protection against *Clostridium perfringens* and *C. tetani* at docking in October and five to seven anthelmintic drenches (21–28 days) from weaning in December until June of the following year; sheep were spray-dipped (Diflubenzuron®) or pour-on-treated (Cypermethrin®) once or twice a year for protection against ectoparasites.

Soil biological sampling

Soil fauna at all six sites (two ungrazed, two organic and two conventional) were sampled in July 2007 (Southern Hemisphere winter). At each of the four grazed sites, samples were collected from both low (0–12°) and medium (13–25°) slope classes, all slopes east facing. The two ungrazed sites were flat. At low slopes, 0–7.5 and 7.5–15 cm soil depths were sampled, but at medium slope only 0–7.5 cm depth was sampled.

Five cores for macrofauna (15.5 cm ø, 0–15.5 cm depth), four soil cores for mesofauna (5 cm ø) and two composite soil samples for microfauna (nematodes) (each sample consisted of 5 cores, each 2.5 cm ø) were collected from each site and slope class. Macrofauna were hand sorted (Wimbledon et al., 1996), mesofauna extracted in a modified Berlese-Tullgren funnel, for more details see Schon et al. (2008). Nematodes were extracted by the modified tray method described by Yeates (1978). The Nematode Channel Ratio (NCR), Maturity Index (MI), Plant Parasitic Index (PPI) and ΣMaturity Index (ΣMI) were calculated (Bongers, 1990; Yeates, 1994, 2003).

The Shannon-Wiener diversity index (H'), Margalef's richness (SR) and Pielou's evenness (J') were calculated to describe the diversity of soil fauna (Yeates, 1984; Ludwig and Reynolds, 1988).

Table 1. Treatment properties in hill country pasture under ungrazed, organic, and conventional management in Manawatu, New Zealand.

Management	Ungrazed	Organic	Conventional
Stocking rate (stock unit/ha)	0	12	12
Live weight (kg/ha)[1]	0	660	720
Treading pressure of single sheep (kPa)[2]	0	65	71
Farmlet size (ha) (each farmlet)		18	18
INPUTS			
Phosphorus (reactive phosphate rock) (kg P/ha/yr)	0	33	33
Other management inputs	–	–	Ivermectin and vaccinations
PASTURE PARAMETERS (kg DM/ha/yr with kg N/ha/yr in parentheses**)			
Pasture production[3]	n.d	8800	9592
Pasture intake[4]	n.d	6600	7194
DM from litter[5]	14 500 (348)	12 400 (397)	10 800 (346)
DM from dung[6]	0 (0)	2 100 (44)	2 300 (48)
DM from roots[5]	2 500 (60)	4 000 (128)	4 000 (128)
Total DM	17 000 (408)	18 500 (569)	17 100 (522)

[1] Standard sheep at organic 55 kg live weight and at conventional 60 kg (Mackay et al., 2006).

[2] Following Greenwood and McKenzie (2001).

[3] Assuming one stock unit consumes 550 kg DM/yr. DM: Dry matter. Pasture production at low slope 46% and medium slope 31% of these values (Lambert et al., 1983).

[4] 0.75x pasture production.

[5] Calculated from Parsons et al. (1983).

[6] 0.35x of animal intake (Takahashi et al., 2007). Dung to low slopes: 60%, and medium slopes: 30% (Saggar et al., 1990).

**N% in herbage from Parfitt et al. (2009) and dung from Lovell and Jarvis (1996).

Soil and pasture sampling

Soil microbial biomass was measured using substrate induced respiration methods. Two soil samples (each sample consisted of 20 cores, each 2.5 cm ø) were collected from each site and slope class. Samples were sieved to <2 mm and the amount of CO_2 respired in two hours was estimated by collecting 25 ml gas in a syringe and empting into a preevacuated Exetainer®, for methodology refer to Chapter 1.

At the time of sampling, soil temperature (Checktemp – Hanna Instruments, England) and moisture (TDR 300 Soil Moisture Probe – Spectrum Technologies, Inc., USA) at 0–10 cm depth were recorded in the field. The soil from mesofauna cores was subsequently analysed for soil pH (1:2.5 soil:water), Olsen P (Olsen et al., 1954), total nitrogen and total carbon (dry combustion using LECO-2000 – LECO Equipment Corp., St. Joseph, USA). Bulk density was determined by collecting three intact soil cores (10 cm ø, 0–7.5 cm depth), drying (105ºC) for 24 hours and weighing.

Root biomass was determined by collecting two soil samples (each sample consisted of 20 cores, each 2.5 cm ø) from 0–7.5 cm depth at each site and slope class. Samples were crumbled and washed through a hydropneumatic root washer until the soil was removed. Samples were towel dried, roots and tillers were separated before being dried at 60ºC for 24 hours and weighed.

Pore size distribution for pores <60 µm ø was determined using tension plates (see Chapter 1). Tensions of 10, 50, and 1500 kPa equated to water filled pore sizes 30, 6, and 0.2 µm ø, respectively. Pores >50 µm ø were characterised using a fluorescent resin technique. Two 15 cm ø cores were collected from each site and slope class when soil was <40% moisture. The cores were impregnated with a fluorescent resin, and images of horizontal soil sections at 2.5, 5, 8 and 12 cm depths were analysed using Solicon© analysis software (The University of Sydney, Cotton Research and Development Corporation) (Vervoort and Cattle, 2003). Images were described in terms of percent porosity and pore area (mm^2). Pore area was estimated using limbs of a 16-sided polygon. In Fig. 1 this is given as pore area of certain size pore per square centimetre of image analysed (mm^2/cm^2).

Statistical analysis

To test the hypothesis that there was no significant effect of management (grazed vs. ungrazed, and organic vs. conventional) at each slope and depth, on the abundance of soil fauna, the data were analysed using PROC NPAR1WAY in SAS v.9.1 (SAS Institute Inc., USA) using a series of orthogonal contrasts. The graphs and tables show untransformed arithmetic means. In figures error bars are the standard error of the mean. Due to low replication at the farmlet level, $P<0.1$ was used as level of significance at that level; otherwise $P<0.05$ was used.

Results

Ungrazed vs. grazed management

Grazed pastures had significantly higher Olsen P, pH and lower C:N ratio than the ungrazed pastures (Table 2). At 0–7.5 cm depth, soil total N (P=0.064) and soil total C (P=0.165) were greater in grazed pastures, while total N and C were higher under ungrazed than grazed management at 7.5–15 cm soil depths (0.30% vs. 0.28%, and 3.84% vs. 2.99%, respectively). While porosity measured on sieved soil or resin embedded sections was not significantly different between ungrazed and grazed pastures (Table 2), soil pores did tend to be larger in ungrazed pastures. In resin embedded soils at 2.5 cm depth, the average pore area was 9.6 mm^2/cm^2 for ungrazed pastures and 4.5 mm^2/cm^2 for grazed pastures (Table 2), with an increase in pores >5 mm diameter (Fig. 1).

Table 2. Soil properties in ungrazed (U), organic (O) and conventional (C) hill country pastures at low slopes, Manawatu, N.Z. (2007).

Management	U	O	C	*P-value*	
				O vs. C	*Grazed vs. U*
Soil moisture (%)^1	42.0	48.0	38.0	***0.083***	*0.864*
Soil temperature (°C)^1	8.0	8.0	7.6	*0.110*	*0.730*
Bulk density (Mg/m^3)^2	0.73	0.63	0.75	***0.083***	*0.308*
Porosity (% v/v of sieved soil)					
6–30 µm*	11	12	10	*0.105*	*0.823*
0.2–6 µm*	9	13	13	*0.500*	***0.009***
Porosity (intact cores from 2.5 cm depth)					
Porosity (%)	13	12	10	*1.0*	*0.838*
Mean pore area (mm^2)	9.6	3.7	5.2	*0.248*	*0.838*
Pores that fit <175 µm 16-sided polygon (%)	12	15	13	*0.773*	*0.540*
Pores that fit >350 µm 16-sided polygon (%)	66	63	67	*1.0*	*0.414*
Porosity (intact cores from 12 cm depth)					
Porosity (%)	6	2	4	*0.149*	*0.307*
Mean pore area (mm^2)	4.0	1.6	2.2	*0.564*	*0.103*
Pores that fit <175 µm 16-sided polygon (%)	22	29	23	*0.386*	*0.221*
Pores that fit >350 µm 16-sided polygon (%)	48	40	47	*0.240*	*0.540*
pH^2	5.1	5.4	5.4	*1.0*	***0.064***
Olsen P (mg/L)^2	12	68	63	*1.0*	***0.064***
Total N (%)^2	0.36	0.57	0.51	*0.121*	***0.064***
Total C (%)^2	4.78	6.22	5.58	*0.121*	*0.165*
C:N ratio^2	13.2	10.9	11.0	*1.0*	***0.064***
Microbial biomass (µg C/g soil)^2	869	991	1642	***0.083***	*0.173*
Roots mass (g dry wt/m^2)^2	605.3	767.9	753.5	*0.557*	*0.487*

^{1}0–10 cm depth.

^{2}0–7.5 cm depth.

*Pores 0.2–6 µm ø retain mostly plant unavailable water and exclude most microorganisms, with no predation on bacteria. Pores 6–30 µm ø retain mostly plant available water and accommodate most bacteria and their predators (Brewer, 1964).

The New Zealand endemic species *Octochaetus multiporus* was found only in the ungrazed pastures, significantly influencing the percentage of anecic earthworms (Fig. 2). Earthworm abundance was significantly lower in ungrazed pastures in comparison to the grazed (318 ind./m^2 vs. 853 ind./m^2), while earthworm diversity was significantly higher in the ungrazed pastures (Table 3). The relative abundance of general detritivores (e.g., Amphipoda) was significantly higher in the ungrazed pastures (Table 3). Herbivorous, *Wiseana cervinata* (porina) and *Costelytra zealandica* (grass grub) juvenile abundance was low at all sites, but their wet biomass was high (4.9 g/m^2 and 6.4 g/m^2; 0 g/m^2 and 1.3 g/m^2, grazed and ungrazed, respectively).

Table 3. Macrofauna in ungrazed (U), organic (O) and conventional (C) hill country pastures at low slopes, 0–15 cm soil depth, Manawatu, N.Z. (2007).

Management $^{\#}$	U	O	C	*P-value*	
				O vs. C	*Grazed vs. U*
EARTHWORMS (ind./m^2)					
Lumbricus rubellus (Hoffmeister, 1843)	21	191	106	*0.644*	***0.015***
Aporrectodea caliginosa (Savigny, 1826)	244	567	837	***0.086***	***0.0007***
Aporrectodea longa (Ude, 1885)	0	5	0	*0.779*	*0.779*
Octochaetus multiporus (Beddard, 1885)	53	0	0	*1.0*	***0.0001***
Total earthworms (ind./m^2)	318	763	943	*0.129*	***0.0004***
Earthworm biomass (g wet wt/m^2)	192	227	278	*0.199*	*0.114*
Anecic: total earthworm abundance	0.17	0.01	0.0	*0.317*	***0.0001***
Anecic: total earthworm biomass	0.60	0.02	0.0	*0.317*	***0.0001***
SR	1.88	1.19	1.08	*0.129*	***0.0004***
J'	0.41	0.28	0.20	*0.359*	***0.044***
H'	0.56	0.39	0.28	*0.359*	***0.044***
Distribution (% abundance)					
Peregrine	83	100	100	*1.0*	***0.0001***
New Zealand endemic	17	0	0	*1.0*	***0.0001***
MACROFAUNA (ind./m^2)					
Wiseana cervinata (Walker, 1865) larvae (Hepialidae, Lepidoptera)	5	37	16	*0.258*	*0.271*
Costelytra zealandica (White, 1846) larvae (Scarabaeidae, Coleoptera)	0	11	0	*0.368*	*0.779*
Click beetle larvae (Elateridae, Coleoptera)	21	21	16	*0.682*	*0.998*
Weevils (Curculionidae, Coleoptera)	21	58	111	*0.155*	*0.213*
Coleoptera (adult)	11	0	0	*0.126*	*0.126*
Noctuidae (Lepidoptera)	0	0	11	*0.126*	*0.596*
Gastropoda	5	0	0	*0.368*	***0.082***
Cicadidae (Hemiptera)	11	0	5	*0.342*	***0.052***
Amphipoda	85	0	0	***0.0008***	***0.0003***
Chilopoda (Myriapoda)	5	0	0	*0.368*	***0.082***
Turbellaria	0	0	5	*0.368*	*0.779*
Total macrofauna (ind./m^2)	164	127	165	*0.667*	*0.667*
Macrofauna biomass (g wet wt/m^2)	14.5	15.6	7.6	*0.732*	*0.732*
SR	3.31	3.30	2.20	*0.941*	*0.941*
J'	0.16	0.13	0.10	*0.878*	*0.878*
H'	0.38	0.32	0.25	*0.878*	*0.878*

Total mesofauna abundance at 0–7.5 cm depth was not significantly influenced by grazing (Table 4). However, there was a marked difference between organic and conventional management (see below). Among Oribatida, New Zealand endemic species (*Metabelba obtusus, Lanceoppia jacoti, Galumna rugosa, Zygoribatula novazealandica, Setobates scheloribatoides* and *Nesopelops punctatus*) made up a larger proportion of the total community in ungrazed in comparison to the grazed sites (Table 5). *L. jacoti*, *Lanceoppia* sp., *Oppiella nova* and *G. rugosa* were found only at the ungrazed sites. The percentage of large Oribatida (body width >350 µm) at the ungrazed sites was 36%, twice that of the grazed sites (18%). Total mesofauna abundance declined with depth, from 102 000 ind./m^2 in ungrazed and 89 000 ind./m^2 in grazed at 0–7.5 cm, to 16 000 ind./m^2 in ungrazed, and 26 000 ind./m^2 in grazed pastures at 7.5–15 cm (Table 6).

Table 4. Mesofauna in ungrazed (U), organic (O) and conventional (C) hill country pastures at low slopes, 0–7.5 cm soil depth, Manawatu, N.Z. (2007).

Management	U	O	C	*P-value*	
				O vs. C	*Grazed vs. U.*
MESOFAUNA (1000's ind./m^2)					
Oribatida	61.7	67.5	19.2	***0.027***	*0.142*
Astigmata	0.6	0.3	0.1	*0.263*	*0.487*
Mesostigmata	17.4	19.8	18.8	*0.370*	*0.951*
Prostigmata	1.0	0.6	1.7	*0.161*	*0.874*
Scutacaridae	0.2	1.1	0.3	*0.775*	*0.284*
Total Acari	80.9	89.4	40.0	*0.172*	*0.540*
Entomobryomorpha	10.3	19.0	8.7	*0.103*	*0.927*
Poduromorpha	1.1	5.3	3.2	*0.474*	*0.975*
Sminthuridae	0.3	1.1	0.2	*0.227*	*0.269*
Neelipleona	0.5	0.1	0.1	*1.0*	*0.120*
Total Collembola	12.2	25.5	12.1	*0.141*	*0.830*
Protura	0.8	0.3	0.5	*0.808*	*0.391*
Lepidoptera	0	0.1	0	*0.317*	*0.480*
Coleoptera	2.0	0.9	0.9	*0.627*	*0.165*
Diptera	0.1	0.1	0.3	*0.107*	*0.165*
Hymenoptera	0.1	0	0	*1.0*	*0.157*
Psocoptera	0.1	0	0	*1.0*	*0.157*
Hemiptera	0.1	0.1	0.3	*0.239*	*0.462*
Thysanoptera	4.1	2.9	4.9	*0.340*	*0.853*
Isopoda	0.1	0	0	*1.0*	*0.157*
Amphipoda	0.1	0	0	*1.0*	***0.041***
Arachnida	0.1	0.1	0	*0.317*	*0.609*
Chilopoda	0.6	0.1	0.2	*0.264*	*0.747*
Pauropoda	0.1	0.1	0	*0.317*	*0.609*
Symphyla	0.1	0.2	0	*0.317*	*0.655*
Total mesofauna	101.5	119.5	59.3	*0.248*	*0.391*
SR	4.36	4.42	4.85	*0.248*	*0.391*
J'	0.38	0.36	0.43	*0.707*	*0.320*
H'	1.19	1.20	1.37	*0.115*	*0.690*

The abundance of nematodes was significantly lower in ungrazed than in grazed pastures (0.7 x10^6 vs. 1.2 x10^6 ind./m^2, P=0.068, Table 7) at 0–7.5 cm soil depth but not at 7.5–15 cm (Table 6).The decline in nematode abundance from 0–7.5 cm to 7.5–15 cm, was lower in the ungrazed system. Ungrazed pastures had a higher percentage of fungal feeding nematodes in the top 0–7.5 cm (Fig. 2), resulting in a lower NCR (0.64 vs. 0.90, P=0.004). *Heterodera trifolii,* a clover root feeding nematode, was found only in grazed pastures where legumes were more abundant (Nie et al., 1997). Plant feeding *Paratylenchus* (112 000 vs. 38 000 ind./m^2), bacterial feeding *Cephalobus* (45 000 vs. 19 000 ind./m^2) and *Plectus* (18 000 vs. 7000 ind./m^2), fungal feeding *Doryllium* (18 000 vs. 4000 ind./m^2) and predatory *Tripyla* (4000 vs. 500 ind./m^2) and *Nygolaimus* (18 000 vs. 1000 ind./m^2) were in greater abundance in ungrazed than in grazed pastures at 7.5–15 cm depth.

The food web of ungrazed pastures had a lower faunal biomass (Fig. 3). All macrofauna trophic groups were present under ungrazed pastures, with macrofauna predators not being detected under organic pastures.

Table 5. Oribatid mites in ungrazed (U), organic (O) and conventional (C) hill country pastures at low slopes, 0–7.5 cm soil depth, Manawatu, N.Z. (2007).

Management	U	O	C	*P-value*	
				O vs. C	*Grazed vs. U*
ORIBATIDA (1000's ind./m^2)					
Platynothrus peltifer (Koch, 1839)	0.4	1.2	0.6	*0.448*	*0.390*
Metabelba obtusus (Hammer, 1966)	1.3	0	0.1	*0.317*	*0.166*
Lanceoppia jacoti (Hammer, 1968)	3.4	0	0	*1.0*	***0.041***
Lanceoppia sp.	1.0	0	0	*1.0*	***0.0001***
Microppia minus (Paoli, 1908)	0.1	3.4	0.5	*0.629*	*0.380*
Multioppia sp.	0.1	0.8	0.2	*0.538*	*0.931*
Oppiella nova (Oudemans, 1902)	1.6	0	0	*1.0*	***0.0006***
Ramusella sp.	2.6	0.3	1.7	*0.371*	*0.609*
Achipteria sp.	6.1	5.2	0.8	***0.009***	*0.138*
Minunthozetes semirufus (Koch, 1841)	19.6	16.0	1.8	*0.673*	*0.067*
Punctoribates punctum (Koch, 1839)	0.1	0.8	0.1	*0.189*	*0.412*
Galumna rugosa (Hammer, 1968)	8.7	0	0	*1.0*	***0.041***
Oribatella sp.	0	0.4	0	*0.317*	*0.480*
Liebstadia similis (Michael, 1888)	6.2	13.1	2.2	*0.195*	*0.475*
Zygoribatula novazealandica (Hammer, 1967)	0	0	0.1	*0.317*	*0.480*
Setobates scheloribatoides (Ramsay, 1966)	0.1	0.8	0	*0.317*	*0.655*
Nesopelops punctatus (Hammer, 1966)	0	1.1	0.1	*0.441*	*0.201*
Total oribatid (adult)	51.4	43.2	8.0	***0.074***	*0.358*
Nymphs	10.3	24.4	11.2	*0.494*	*0.500*
SR	4.67	5.75	5.98	*0.223*	*0.337*
J'	0.37	0.35	0.28	*0.401*	*0.462*
H'	1.07	1.00	0.82	*0.401*	*0.426*
Oribatid body width (%)					
Width <175 µm	47	48	52	*0.597*	*0.951*
Width 175–350 µm	17	35	30	*0.594*	*0.781*
Width >350 µm	36	17	18	*0.293*	*0.690*

Table 6. Soil mesofauna and nematodes (1000’s ind./m^2) in ungrazed (U), organic (O) and conventional (C) hill country pastures at low slopes, 7.5–15 cm soil depth, Manawatu, N.Z. (2007).

Management	U	O	C	*P-value*	
				O vs. C	*Grazed vs. U*
Total mesofauna	15.9	17.6	35.0	***0.046***	*0.298*
Oribatida	1.7	5.0	8.3	*0.290*	*0.517*
Mesostigmata	8.8	10.1	15.2	*0.495*	*0.624*
Acari	12.0	16.2	26.2	*0.172*	*0.270*
Collembola	1.2	0.7	4.0	*0.146*	*0.686*
Thysanoptera	1.5	0.6	3.6	*0.507*	*0.923*
Total nematodes	447.3	469.0	327.3	*0.564*	*1.000*
Bacterial feeding	98.4	77.6	78.9	*0.564*	*0.699*
Fungal feeding	22.4	16.0	1.5	*0.564*	*0.699*
Plant and plant associated	281.8	329.7	191.9	*0.387*	*0.439*
Predator and omnivore	44.7	55.3	54.9	*0.773*	*0.439*

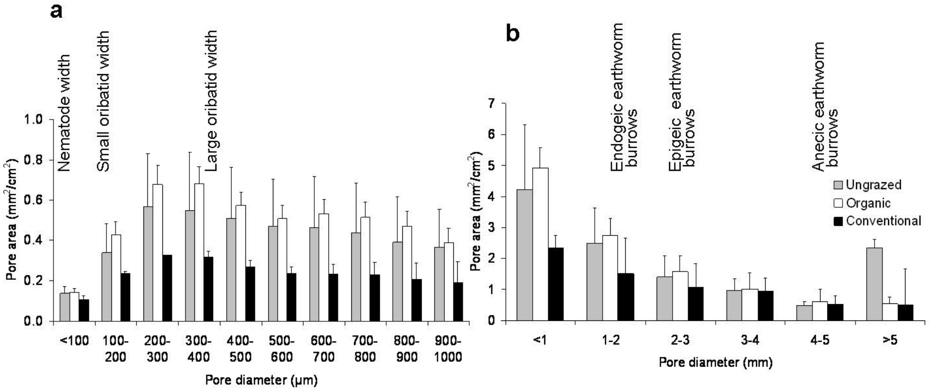

Fig. 1. Pore areas (mm^2/cm^2) over ranges of pore sizes as estimated from resin embedded cores at 2.5 cm depths from pastures under ungrazed and grazed (organic or conventional) managements, Manawatu, New Zealand, 2007. (a) Pores <1 mm ø and (b) All pores (<1 to >5 mm ø); the <1 mm bar is the sum of pores shown in (a).

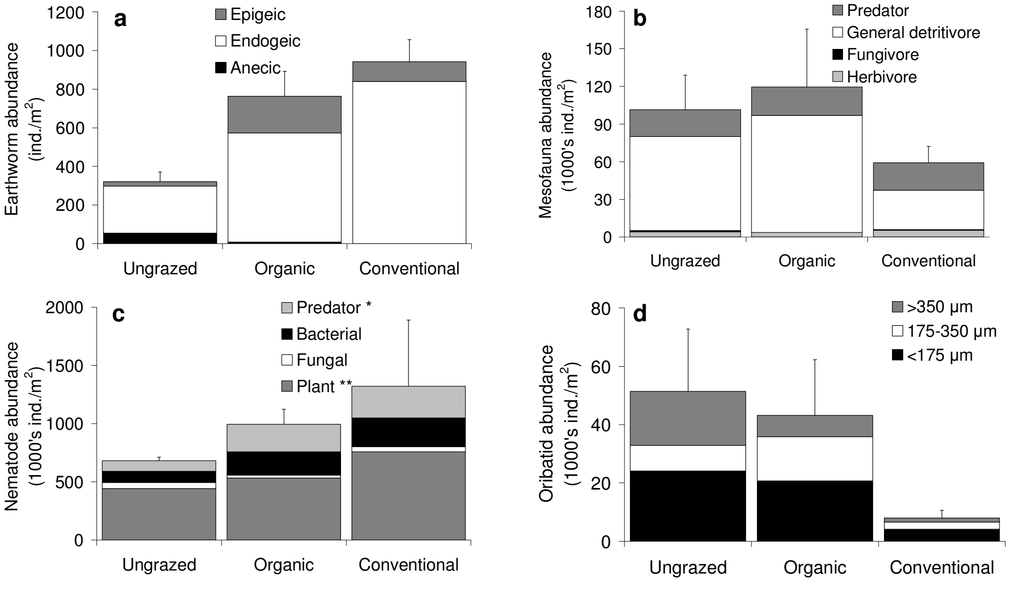

Fig. 2. Invertebrates under ungrazed, organic and conventionally grazed pastures at 0–7.5 cm soil depth at Manawatu, New Zealand (2007). (a) Abundance of earthworm functional groups, (b) abundance of mesofauna trophic groups, (c) abundance of nematode trophic groups, and (d) abundance of oribatid body widths.

*Predacious and omnivorous nematodes.

**Plant feeding and plant associated nematodes.

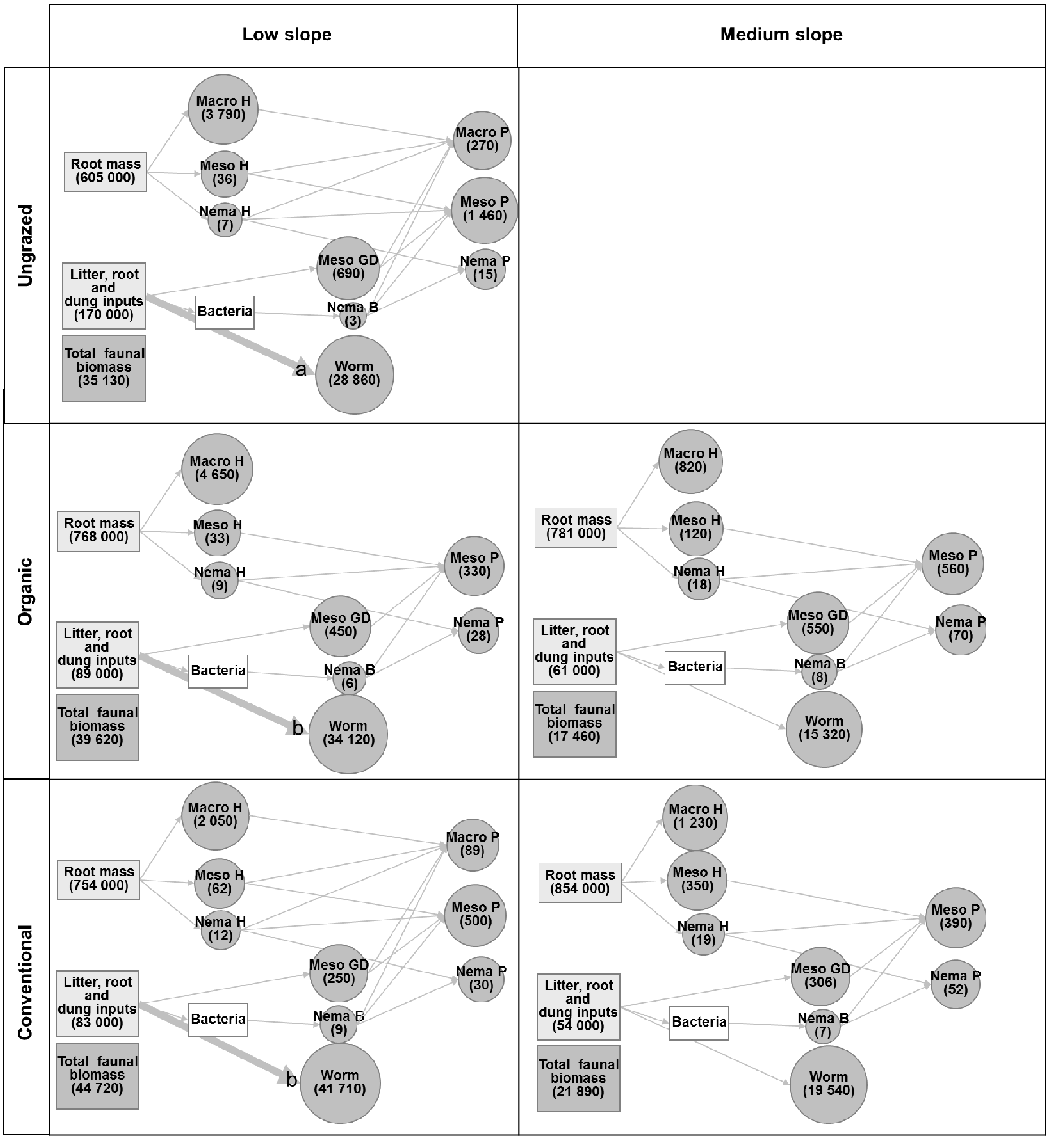

Fig. 3. Food-webs of selected soil faunal groups under ungrazed and grazed (organic or conventional) managements at low and medium slopes at 0–7.5 cm soil depth at Manawatu, New Zealand, 2007. Food webs and biomass calculation derived from Hunt (1987) and Mulder et al. (2005). Resource inputs are given in mg dry weight/m^2. Macrofauna (Macro), mesofauna (Meso) and nematode (Nema) herbivores (H) feed on plant material. Earthworms (Worm), mesofauna general detritivores (GD) and nematode bacterial feeders (B) feed on detrital inputs and associated microflora. The macrofauna, mesofauna and nematodes are in turn consumed by predators (P). Circle areas represent the log biomass of the fauna, actual biomass (dry weight mg/m^2) given in parenthesis. Biomass calculated as in Chapter 1.Trophic groups with biomass <1.5 mg dry weight/m^2 were excluded. Wide arrow and $^{a,\,b}$ given in the arrow head indicate significant difference at α=0.05 within the functional group to which the arrows lead.

Organic vs. conventional management

While soil moisture and temperature at sampling were higher under organic management, there was little difference in soil chemistry (Table 2). Bulk density was 20% lower under organic than under conventional pastures. Resin embedded cores showed organic soils to have more pores than conventional soils at 2.5 cm depth, with the amount of pores <5 mm diameter being similar to ungrazed soils (Fig. 1). Microbial biomass was higher under conventional management.

Total earthworm abundance was not significantly influenced by management, but *Aporrectodea caliginosa* abundance was significantly lower under organic management (Table 3). The organic pastures had a higher proportion of epigeic earthworms (i.e., *Lumbricus rubellus*) (Fig. 2).

Total mesofaunal abundance was not significantly influenced by management (119 000 vs. 59 000 ind./m^2). A higher proportion of both Acari and Collembola in 0–7.5 cm than in 7.5–15 cm were found under conventional management (Table 6, Fig. 4). Among mesofauna trophic groups, predators made up 19% under organic and 37% under conventional management (0–7.5 cm), even though predator abundance was similar (Fig. 2). There was a far larger decline in mesofauna abundance with depth under organic management (18 000 ind./m^2 at 7.5–15 cm depth) than under conventional (35 000 ind./m^2 at 7.5–15 cm depth). Herbivorous Thysanoptera were more abundant under conventional management at both depths.

Among Acari, Oribatida showed a pattern similar to the total mesofauna, with significantly higher abundance in organic pastures (P=0.027, Table 5, Fig. 2). *Platynothrus peltifer*, *Minunthozetes semirufus*, *Achipteria* sp. (P=0.009) and *Liebstadia similis* were more abundant under organic management (Table 5). Fungivores and herbifungivores were the dominant feeding groups at 0–7.5 cm (Fig. 2). The abundance of Oribatida decreased with soil depth (Table 6), with large Oribatida species (body width >350 μm) found only at 0–7.5 cm depth.

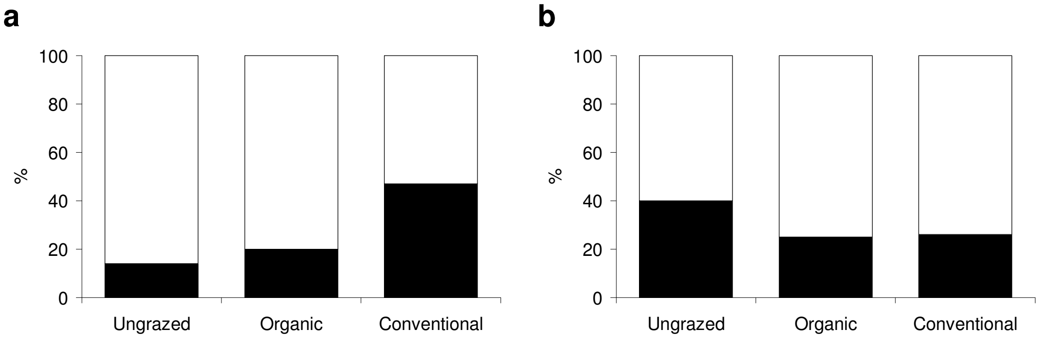

Fig. 4. Percent abundance of (a) Acari and (b) nematodes in 0–7.5 cm (□) and 7.5–15 cm (■) soil depths at low slopes in Manawatu, N.Z. (2007).

Table 7. Nematodes in ungrazed (U), organic (O) and conventional (C) hill country pastures at low slopes, 0–7.5 cm soil depth, Manawatu, N.Z. (2007).

Management	U	O	C	*P-value*	
				O vs. C	*Grazed vs. U*
NEMATODES (1000’s ind./m^2)					
Tylenchus	73.1	95.0	115.0	*0.773*	*0.700*
Cephalenchus	19.9	22.2	27.2	*0.386*	*0.632*
Ditylenchus	8.9	0	0	*1.0*	*0.264*
Heterodera juv.	0	12.7	27.2	*0.767*	*0.248*
Tylenchorhynchus	0	0	6.1	*0.317*	*0.417*
Hoplolaimidae	186.1	205.8	314.8	*0.387*	*0.114*
Pratylenchus	57.6	133.0	51.5	*1.0*	*0.809*
Paratylenchus	99.7	88.7	224.0	***0.043***	*0.167*
Aphelenchus	15.5	6.3	6.1	*0.850*	*0.866*
Aphelenchoides	0	6.3	3.0	*0.850*	*0.654*
Rhabditidae	26.6	25.3	63.6	*0.885*	*0.929*
Dauerlarvae	8.9	0	15.1	*0.131*	*0.318*
Panagrolaimus	17.7	41.2	93.8	*0.248*	*0.183*
Cephalobus	8.9	69.7	42.4	*0.317*	*0.427*
Heterocephalobus	0	6.3	0	*0.317*	*0.417*
Teratocephalus	0	3.2	0	*0.317*	*0.417*
Plectus	6.6	57.0	66.6	*0.767*	*0.397*
Anaplectus	0	6.3	6.1	*0.850*	*0.654*
Pakira	2.2	0	3.0	*0.317*	*0.531*
Prismatolaimus	0	0	3.0	*0.317*	*0.417*
Monhystera	4.4	0	6.1	*0.131*	*0.318*
Tripyla	0	6.3	6.1	*0.850*	*0.654*
Tobrilus	2.2	0	3.1	*0.317*	*0.531*
Dorylaimus	13.3	28.5	3.1	*0.850*	*0.866*
Mesodorylaimus	2.2	12.7	18.2	*0.508*	*0.680*
Eudorylaimus	33.2	44.3	54.5	*0.386*	*0.417*
Labronema	0	0	3.0	*0.317*	*0.417*
Pungentus	24.4	44.3	66.6	*0.773*	*0.176*
Aporcelaimus	4.4	12.7	6.1	*0.741*	*0.908*
Dorylaimellus	0	6.3	0	*0.317*	*0.417*
Doryllium	35.5	12.7	24.2	*0.539*	*0.397*
Nygolaimus	0	9.5	0	*0.317*	*0.417*
Clarkus	4.4	9.5	24.2	*0.166*	*0.302*
Iotonchus	4.4	15.8	27.2	*0.508*	*0.680*
Cobbonchus	2.2	0	12.1	*0.317*	*0.417*
Alaimidae	15.5	6.3	0	*0.317*	*0.531*
Trichodoridae	4.4	6.3	0	*0.317*	*0.531*
Total nematodes	682.4	994.3	1322.8	*0.564*	***0.068***
SR	5.81	5.54	4.24	*1.0*	*0.893*
J'	0.53	0.59	0.48	*1.0*	*1.0*
H'	2.00	2.23	1.81	*0.557*	*0.425*
NCR	0.64	0.89	0.90	*0.772*	*1.0*
Maturity groups (%)					
CP1	8	7	13	*0.564*	*0.794*
CP2	35	36	38	*0.387*	*0.794*
CP3	36	36	31	*0.387*	*0.602*
CP4	20	17	16	*0.564*	*0.192*
CP5	1	4	2	*0.773*	*0.794*
MI	0.91	0.95	0.73	*1.0*	*1.0*
PPI	1.81	1.80	1.31	*0.773*	*0.296*
ΣMI	2.72	2.76	2.04	*1.0*	*0.296*

Nematode abundance was similar under organic than under conventional management at 0–7.5 cm and 7.5–15 cm soil depths (Table 6 and 7). At 0–7.5 cm depth, the proportion of nematodes in the feeding groups was similar under both managements and thus the NCR was similar. The proportion of plant feeding and plant associated nematodes was high (over 50%) under both regimes, due to the high abundance of Hoplolaimidae and *Paratylenchus.*

The food web under organic management had a lower faunal biomass than conventional (Fig. 5). Macrofauna predators were only detected in conventional pastures.

Influence of slope

The influence of slope (low vs. medium) was investigated at 0–7.5 cm soil depth. Soil moisture, pH and fertility (Olsen P, total N and C) were all lower on medium slopes (Table 2 and 8). Both bulk density and soil porosity were higher on medium slopes. Earthworm abundance decreased from low to medium slope; at medium slopes there were about 50% fewer earthworms (Tables 3 and 8). In contrast mesofauna and nematode abundance increased from low to medium slope (Tables 4, 7 and 8). At medium slopes, Acari were more abundant in organic pastures, reflecting Mesostigmata (Table 8). The oribatid mite *Tectocepheus velatus sarekensis* was only found on medium slopes, where oribatid diversity was greater (data not shown).

Table 8. Soil properties and fauna (1000's ind./m^2) in organic (O) and conventional (C) hill country pastures at medium slopes, 0–7.5 cm soil depth, Manawatu, N.Z. (2007).

Management	O	C	*P-value*
			O vs. C
Bulk density (Mg/m^3)	0.76	0.83	***0.001***
Olsen P (mg/L)	19.8	27.4	***0.021***
Total N (%)	0.38	0.34	***0.021***
Total C (%)	4.8	4.6	***0.021***
Total earthworms *	0.4	0.5	*0.235*
Total mesofauna	138.7	133.9	*0.796*
Oribatida	61.2	37.6	*0.156*
Mesostigmata	24.7	15.3	***0.081***
Acari	106.2	67.6	*0.156*
Collembola	14.5	19.9	*0.245*
Thysanoptera	16.0	45.0	*0.799*
Total nematodes	1838.8	1384.1	*0.248*
Bacterial feeding	318.3	247.4	*0.387*
Fungal feeding	46.1	59.5	*0.564*
Plant and plant associated	1114.1	829.8	*0.387*
Predator and omnivore	381.2	253.6	*0.248*

*Earthworms 0–15 cm soil depth.

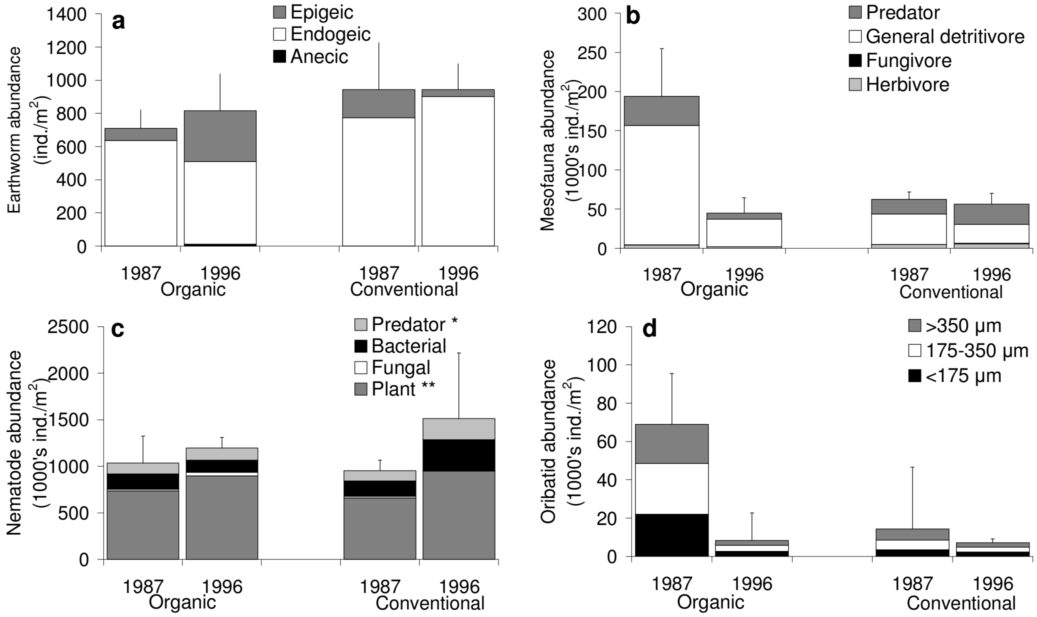

Fig. 5. Invertebrates in organic and conventional farmlets established in 1987 and 1996 at 0–7.5 cm soil depth at Manawatu, New Zealand (2007). Formatted to illustrate differences between farmlets established in 1987 and 1996. (a) Abundance of earthworm functional groups, (b) abundance of mesofauna trophic groups, (c) abundance of nematode trophic groups, and (d) abundance of oribatid body widths.
*Predacious and omnivorous nematodes.
**Plant feeding and plant associated nematodes.

The food web on medium slopes had a lower faunal biomass than on low slopes, as earthworm biomass decreased (Fig. 3). Macrofauna predators were not detected on medium slopes.

Discussion

The undisturbed, ungrazed pastures, with no stock treading and no fertiliser inputs had a relatively low contribution of bacterial feeding over fungal feeding nematodes (NCR 0.64 at ungrazed vs. 0.90 under conventional), reflecting the lower soil N fertility (soil C:N ratio 13.2 at ungrazed vs. 11.0 under conventional grazing). Other authors (Mulder et al., 2003; Yeates, 2003), have also reported lower NCR values in low fertility pastures. While calculated plant litter input to the soil in the ungrazed pastures was higher than in the grazed pastures (Table 1), the likely low N content of the ungrazed pasture litter (2009), reduced the total nutritional value of the litter to the soil. Correspondingly, the abundance of earthworms and nematodes, which tend to reflect food availability (Lambert, 1986; Curry and Baker, 1998; Paoletti, 1999; Curry et al., 2008; Mulder et al., 2008), was lower in ungrazed pastures, although their communities were more diverse. New Zealand endemic earthworms (*O. multiporus)* and Oribatida (*M. obtusus, L. jacoti, G. rugosa, Z. novazealandica, S. scheloribatoides* and *N. punctatus*) were more abundant in these undisturbed, ungrazed soils. In the absence of stock treading in the ungrazed pastures, soil porosity (pores greater than 50 μm) was higher than in the sheep grazed pastures, with a larger average pore size and twice as many large oribatid species (36% with body widths >350 μm), confirming that Oribatida are indeed sensitive to changes in soil structure (Cole et al., 2008).

Organic and conventional grazed pastures had more similarities in soil fauna, and common differences with the ungrazed pastures. Both had fewer New Zealand endemic species. Both were characterised by higher abundances of earthworms and nematodes, particularly plant feeding nematodes, reflecting higher root biomass. The higher earthworm abundance in the grazed pastures may have offset the negative effects of sheep treading through their burrowing, even though there was no improvement in soil porosity.

Organic systems are often associated with mixed livestock grazing management practices and, with certification restrictions on nutrient inputs. Effectively this generally reduces pasture production and stocking rates in comparison with conventional management. In this study, fertiliser inputs, animal type, stocking rates, and live weight were the same at the start of the organic and conventional production system comparison (Mackay et al., 2007). Over time some differences in sheep live weight emerged, with ewe live weight lower under organic management. This reduced pasture intake, with an expected reduction in pasture growth and root turnover. The lower biomass production in the organic systems was reflected in lower abundance of plant feeding and plant associated nematodes in response to reduced root growth. Yeates (1980) found nematode abundance highly correlated with food availability. Further, herbivorous mesofauna also had a lower biomass in the less productive organic pastures. In contrast, total biomass of herbivorous fauna was higher in organic pastures (Fig. 3), where large porina (*W. cervinata*) and grass grub (*C. zealandica*) were more abundant, reflecting reduced grazing and treading pressures and more dead matter in pasture sward.

The reduced pasture intake under organic management resulted in approximately 10% less calculated dung to the soil surface, but approximately 15% higher calculated dry matter as litter to the soil surface (Table 1), with more herbage dead matter observed in the pasture sward. The abundance of bacterial feeding and fungal feeding nematodes was similar under both managements and did not suggest a difference in the food resources available in the respective systems. In Chapter 3 we also observed little effect of organic management on the NCR, however, Yeates et al. (1997) and Mulder et al. (2003) reported an increase in the relative contribution of fungal feeding nematodes under organic management. That the proportion of fungal feeding nematodes was not higher under organic management in this study (Table 7), suggests that a lower NCR is associated with less intensive management, rather than with organic management *per se*. For example, in the present study there was a larger difference in the NCR between the grazed and ungrazed pastures.

Increased dry matter input to the soil surface stimulated populations of litter (combined with soil) preferring *L. rubellus* (Doube et al., 1997), with its abundance nearly doubling under organic management. Here, soil carbon was somewhat higher in the topsoil. Total earthworm abundance was similar under both systems (Fig. 3), with soil preferring *A. caliginosa* less abundant in the organic system. Earthworm abundance did appear to respond to food availability on hill slopes, being lower on medium slopes, which were less fertile, less productive, and had lower dung and urine inputs (Lambert et al., 1983; Lopez et al., 2003).

There is some evidence in this study that mesofauna were positively influenced by organic management. This is despite sheep stocking rate, a management practice observed to affect mesofauna abundance (King and Hutchinson, 1976), being the same in both systems. The slightly higher treading pressures under conventional management (reflecting higher sheep live weight, Table 1) is not thought to influence the soil fauna, as the abundance of mesofauna, including Oribatida, was greater under grazed organic management compared with ungrazed management where there was no treading (Table 4). The use of ivermectin may have contributed to the decline of mesofauna in the surface soil of the conventional system. Ivermectin is used to control endoparasitic nematodes of sheep, but can also be effective on ectoparasitic mites, acting by inhibiting nerve function (Wolstenholme and Rogers, 2005). Ivermectin, entering the soil in dung and urine, can remain in the soil for long periods (Mougin et al., 2003). Ivermectin has been found to slow down the decomposition of dung in short term studies by influencing dung colonising organisms such as Diptera (Madsen et al., 1990; Sommer and Bibby, 2002; Svendsen et al., 2003; Yeates et al., 2007). On medium slopes, where the effects of ivermectin may be lower due to only 30% of dung being deposited there (Saggar et al., 1990), mesofauna abundance was similar between organic and conventional management. However, the correlation between dung (and ivermectin) deposition and Oribatida abundance was not high (Fig. 6). The total abundance of earthworms and nematodes was higher under conventional management, showing, as in several other studies, that ivermectin does not have detrimental effects on all soil fauna (Madsen et al., 1990; Yeates et al., 2002; Kaneda et al., 2006). The most plausible direct explanation of a decline in mesofaunal abundance under conventional management is that it was caused by higher earthworm activity (*A. caliginosa*). There is a negative correlation between earthworm abundance and Oribatida abundance (Fig. 6). Burrowing activities of earthworms disturb Oribatida (which make up a large proportion of the mesofauna) by competing for resources and altering habitats (Maraun et al., 2001; Schon et al., 2008). Earthworm activity results in significant alterations of the soil structure, forming pores and casts (Yeates and van der Meulen, 1995; Francis et al., 2001). Further, on medium slopes in this sheep grazed hill country where physical disturbances from earthworms and stock treading pressures were reduced, mesofauna abundance was higher.

Table 9. Mesofauna (1000's ind./m^2) differences between farmlets established in 1987 and 1996, in organic (O) and conventional (C) hill country pastures at low slopes, 0–7.5 cm soil depth, Manawatu, N.Z. (2007).

Farmlet (year established)	1987		1996		*P-value*
Management$^{\#}$	O	C	O	C	*Age*
MESOFAUNA					
Oribatida	111.2	24.2	23.9	14.3	***0.100***
Astigmata	0.4	0	0.3	0.1	*0.755*
Mesostigmata	32.1	15.8	7.5	21.8	***0.054***
Prostigmata	0.9	1.0	0.3	2.3	*0.791*
Scutacaridae	2.3	0.4	0	0.3	***0.066***
Total Acari	146.8	41.4	32.0	38.7	***0.045***
Entomobryomorpha	27.6	9.0	10.4	8.3	*0.876*
Poduromorpha	10.6	5.0	0.1	1.4	*0.251*
Sminthuridae	2.0	0.3	0.1	0.1	*0.233*
Neelipleona	0.1	0.1	0	0	***0.028***
Total Collembola	40.4	14.4	10.7	9.8	*0.734*
Protura	0.4	0.3	0.1	0.8	*0.790*
Lepidoptera	0	0	0.1	0	*0.792*
Coleoptera	1.7	10.1	0.1	0.6	*0.191*
Diptera	0	0.4	0.1	0.3	*0.884*
Hemiptera	0	0.4	0.1	0.3	*0.391*
Thysanoptera	4.1	4.3	1.7	5.5	*0.286*
Arachnida	0.1	0	0	0	*0.465*
Chilopoda	0.1	0.1	0	0.3	*0.352*
Pauropoda	0.1	0	0	0	*0.373*
Symphyla	0.4	0	0	0	*0.392*
Total mesofauna	194.0	62.4	44.9	56.1	*0.241*

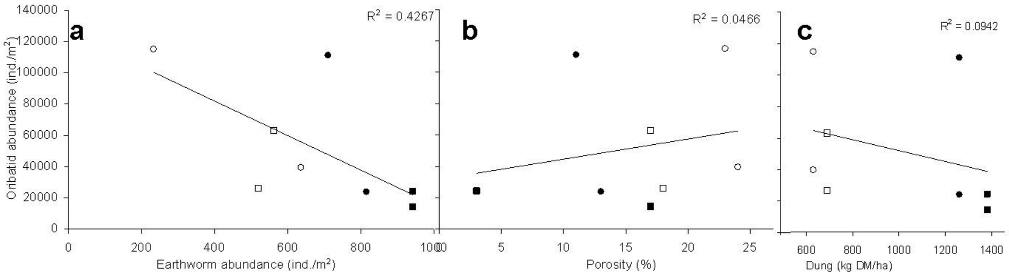

Fig. 6. Oribatida abundance plotted against (a) earthworm abundance, (b) soil porosity (%) as measured in resin embedded cores, and (c) calculated dung deposition on the soil surface. Circles: organic, squares: conventional, Solid symbols: low slope, hollow symbols: medium slope.

It is worth noting that mesofaunal abundance in the organic farmlet established in 1987 was 3–4 fold greater than that in the organic farmlet established in 1996 (Table 9, Fig. 5). The higher mesofauna abundance under the 1987 organic farmlet reflects high Acari (particularly, Oribatida) and Collembola abundance. Porosity at 2.5 cm depths (data not shown) was also higher in this farmlet, although there was little correlation between porosity and Oribatida abundance (Fig. 6). Earthworm and nematode abundance was very similar between the two replicates of the organic farm systems. It would be interesting to speculate on the reason for this difference, but it does point to the importance of allowing, when comparing biological systems, sufficient time from establishment for a new equilibrium to be reached, despite organic certification having been achieved.

Conclusion

The ungrazed pastures had different invertebrate communities than grazed pastures, with a lower NCR, more New Zealand endemic species, and larger Oribatida. The introduction of fertiliser and livestock grazing stimulated earthworm and nematode abundances. While stocking rates were the same in both production systems, sheep live weight was lower under organic management, resulting in reduced pasture intake, increased litter return to the soil and a higher abundance of *L. rubellus*. That the treading pressure under conventional management was not associated with decreased porosity reflects earthworm activity. In the less productive organic pastures the abundance of plant feeding nematodes was lower than under conventional management. The farmlet that had been under organic management for 20 years had more Oribatida than the farmlet under organic management for only 11 years. There was little evidence that organic management stimulated biological activity, and while it may have taken

Oribatida over 11 years to respond positively to organic management, it was likely to be result of reduced earthworm activity.

This organic/conventional comparison suggests that organic management *per se* is not necessarily beneficial to soil invertebrates, and it is management practices such as stocking rates and fertiliser regime which are more important in influencing invertebrate populations in this soil, though some would argue these are an integral part of an organic production system.

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Chapter Five:

Influence of irrigation and fertiliser on soil invertebrates in sheep grazed pastures

Chapter 1 to 4 have shown a response of different invertebrate groups to pastoral management practices that included at the systems level organic versus conventional management, and at another level the influence of such factors as fertiliser inputs, livestock type and stocking rate. This chapter explores the influence of irrigation (i.e., removal of water stress), fertiliser inputs and sheep grazing on the invertebrate community.

N.L. Schon, A.D. Mackay, M.A. Minor. Influence of irrigation and fertiliser on soil invertebrates in sheep grazed pastures.

Abstract

Water and soil fertility are both important to soil fauna, as they influence the quantity and quality of resources available and the soil physical and living environment. The influence of summer irrigation and phosphorus (P) fertiliser on soil fauna (macro-, meso- and microfauna) was examined in two long term trials. In an irrigation trial the ‘dryland’ treatment received no irrigation, while the other treatment was ‘irrigated’ when soil moisture fell to 20%; both treatments received 23 kg P/ha/yr as single super phosphate (SSP). In a fertiliser trial, one treatment received no fertiliser (‘unfertilised’), the other treatment was ‘fertilised’ with 23 kg P/ha/yr as SSP; since 1996 both treatments had been irrigated when soil moisture fell to 20%.

Irrigation and P fertiliser application stimulated pasture production, however invertebrate abundances were still very low in comparison with other New Zealand pastures. This could be due to the continued moisture stress that can occur despite irrigation, as the trigger used for irrigation (20% w/w) means all soil pores >3 µm diameter are drained between irrigation events. Invertebrates in the topsoil have few defence mechanisms against this level of moisture stress. It was nematodes, which can reproduce when pores >1 µm diameter are water filled, which were most responsive to increased pasture production in the fertiliser trial, with more plant feeding, plant associated and bacterial feeding nematodes. Frequent drought periods under dryland favoured short lived organisms such as CP2 nematodes and the short lived oribatid mite *Oppiella nova*. The effect of drought on the mesofauna was more pronounced deeper in the soil, with the proportion of Acari and Collembola at 7.5–15 cm depth lower in the dryland than in irrigated pasture (6 vs. 29 %, respectively). At sampling earthworm abundance was similar between the dryland and irrigated pastures (277 and 336 ind./m^2, respectively). However, a previous study showed that earthworms declined in the same dryland system with the onset of moisture deficit. Continued activity of earthworms in irrigated pastures is likely to sustain litter incorporation, fragmentation and decomposition. Continued moisture stress under irrigation at 20% soil moisture using the border strip method limited the invertebrate populations. As the area of land under irrigation is increasing nationally, to ensure optimum use of water, it is important to consider the irrigation schedule not only to optimise plant growth but also to optimise the invertebrate community and its activity and contributions to soil processes.

Introduction

Water availability is a key to sustained pasture production (Snaydon, 1987; Goh and Bruce, 2005). Drought decreases pasture production, reducing food resources to the soil food web and influencing the soil fauna (Coleman et al., 2004). Further, soil fauna are adapted to a high humidity interstitial environment (Lee, 1985), and regular dry periods may influence faunal life histories, with shorter lived, potentially opportunistic, *r*-strategists dominating drought affected areas (Lindberg and Bengtsson, 2005).

In drought prone areas, where pastoral growth is limited by available soil moisture, irrigation may be used to overcome this limitation. Irrigation to address low soil moisture moderates the abiotic environment of the soil fauna, reducing the risk of dehydration and anhydrobiosis, and would be expected to have a positive influence on the abundance of the soil faunal community as well as stimulating pasture productivity and food input into the soil food web. In Canterbury, New Zealand, on a Cambisol, Fraser and Piercy (1996) found that by eliminating moisture stress and ensuring sustained inputs of food into the soil food web, earthworms remained active throughout the year in contrast to the earthworms in a dryland environment, which aestivated for five months. However, in an Australian study, summer irrigation was found to have variable effects on earthworm species (decrease in *Aporrectodea caliginosa* and increase in *Lumbricus rubellus* population and activity) on three different soil types (Lobry de Bruyn and Kingston, 1997). Irrigation has been found to stimulate nematode populations in New Zealand pastures (Yeates, 1978).

Soil nutrient supply remains an important consideration in irrigated pastures after potential moisture stress is alleviated. Increasing soil fertility with phosphorus (P) applications further increases pasture production (Snaydon, 1987; Srinivasan and McDowell, 2009). This results in increased food resources available to the soil food web, which is expected to have a positive effect on earthworm and nematode abundances (particularly bacterial feeding, plant feeding and plant associated nematodes) (Yeates, 1980, 1984; Mulder et al., 2003; Curry et al., 2008). In more productive pastures stocking rates are typically higher, leading to a higher percent of dung returning to the soil food web, while also potentially increasing soil compaction and physical disturbance, both of which may decrease habitable pore space for soil fauna (Elliott et al., 1980).

This study investigated the impact of alleviating summer water deficit and increasing nutrient inputs and stocking rates on the soil fauna and soil food webs in two long term sheep grazed trials in Canterbury region, New Zealand. The irrigation trial included ‘dryland’ (no irrigation, fertilised) and ‘irrigated’ (irrigated, fertilised) pastures. The fertiliser trial included ‘unfertilised’ (irrigated, unfertilised) and ‘fertilised’ (irrigated, fertilised) pastures. It was expected that dryland would have low faunal abundances, and be dominated by drought tolerant and short lived organisms. Unfertilised pastures were expected to have low earthworm and nematode abundance. More productive pastures (irrigated and fertilised) were expected to have greater faunal abundance than dryland or unfertilised pastures, especially earthworms, bacterial feeding, plant feeding and plant associated nematodes. More intensive and productive pastures, grazed at higher stocking rates, were expected to show increased soil disturbance and compaction, and as a consequence decreased abundance of mesofauna (Acari) sensitive to soil disturbance.

Methods

Study sites

The study site was located at the AgResearch Winchmore Irrigation Research Station (43°47'S 171°48'E), 150 m a.s.l. on the Canterbury plains, New Zealand. The soils are classified as a Cambisol (FAO, 1988) (NZSC: Brown, Lismore stony silt loam) (Hewitt, 1993). Average annual air temperature is 11.1ºC and rainfall is 740 mm (with 640 mm rainfall the year preceding the sampling). Pastures are dominated by *Lolium perenne* (ryegrass) and *Trifolium repens* (white clover). DDT was applied to these pastures during the 1950’s and 1960’s to control grass grub, with the DDT residues currently present in lower concentrations under more productive irrigated and fertilised pastures (Boul et al., 1994). For further details of the study site see McDowell and Rowley (2008). Two long term trials were sampled and are summarised in Table 1.

The ‘irrigation’ trial, established in 1949, included two treatments: (1) no irrigation (dryland), and (2) irrigation: irrigated from September to May when topsoil (0–100 mm) fell to 20% w/w soil moisture. Irrigation used the border strip method. Both treatments received 23 kg P/ha/yr as single super phosphate (SSP) and had three replicated plots of 0.09 ha each. The plots were not grazed during winter, but rotationally grazed at 6 (dryland) or 18 (irrigated) stock units/ha, where a ‘stock unit’ (su) is defined as a ‘standard sheep’ consuming 550 kg dry matter per year (www.maf.govt.nz).

Table 1. Site properties and management inputs in sheep grazed pastures under different irrigation and fertiliser treatments, Canterbury, New Zealand (2007).

	Irrigation trial		Fertiliser trial	
Management	Dryland	Irrigated	Unfertilised	Fertilised
Stocking rate (stock unit/ha)*	6	18	6	17
Live weight (kg/ha)[1]	330	990	330	935
Irrigation	No	Yes	Yes	Yes
INPUTS				
Phosphorus (superphosphate) (kg P/ha/yr)	23	23	0	23
PASTURE PARAMETERS (kg DM/ha/yr)				
Pasture production [2]*	7.7	11.7	5.4	12.4
Pasture intake [3]	5.8	8.8	4.0	9.3
DM from litter [4]	8.2	22.2	8.0	21.7
DM from dung [5]	2.0	3.0	1.4	3.3
DM from roots [4]	3.0	7.0	2.0	7.0
Total DM	13.2	32.2	11.4	32.0
PASTURE COMPOSITION (%)				
Grass	52	65	64	65
Legumes	22	18	8	19
Other (including weeds)	11	9	16	7
Dead matter	15	8	12	8

[1] Standard sheep: 55 kg live weight. Treading pressure of grazing sheep: 65 kPa (Greenwood and McKenzie, 2001).

[2] Pasture data from 2002–2003. Irrigation trial: R. Moss and New Zealand Fertiliser Manufacturer's Research Association, pers. comm., DM: Dry matter.

*Rotationally grazed with no grazing in winter.

[3] 0.75x pasture production.

[4] Calculated from Parsons et al. (1983).

[5] 0.35x of animal intake (Takahashi et al., 2007).

The 'fertiliser' trial, established in 1952, included two treatments: (1) pastures receiving no fertiliser (unfertilised) and (2) pastures fertilised with 23 kg P/ha/yr as SSP (fertilised). Since 1996 both treatments were irrigated from September to May, when the topsoil fell to 20% w/w soil moisture using the border strip method. Before 1996 pastures had been irrigated when soil moisture fell below 15% w/w. The difference in these irrigation regimes was 50% and 25% available soil moisture, respectively (McDowell and Rowley, 2008). Each treatment was replicated four times in 0.09 ha plots. The plots were not grazed during winter, but otherwise were rotationally grazed at 6 (unfertilised) or 17 (fertilised) su/ha.

Soil sampling

Soil temperature (Checktemp, Hanna Instruments, UK) and moisture (TDR 300 Soil Moisture Probe, Spectrum Technologies Inc., USA) at 0–10 cm depth were recorded in the field at the time of sampling. After extracting the mesofauna, the soil cores were analysed for soil pH (1:2.25 soil:water), Olsen P (Olsen et al., 1954), total nitrogen and total carbon (dry combustion using LECO-2000, LECO Equipment Corp., St. Joseph, MI). Bulk density was determined by collecting three intact soil cores (10 cm ø, 7.5 cm deep) from each plot, drying (105ºC) and weighing.

Pore size distribution for pores <60 µm was determined using tension plates (see Chapter 1). Soil from each treatment was sieved (<2 mm) and saturated. Tensions of 10, 50, and 1500 kPa equated to pore sizes of 30, 6, and 0.2 µm ø, respectively.

Soil biological sampling

Soil fauna were sampled in October 2007 (Southern Hemisphere spring). Three macrofauna cores (15.5 cm ø, 15.5 cm deep), four cores for mesofauna (5 cm ø, 15 cm deep) and one composite sample for nematodes (5 cores, each 2.5 cm ø, 0–7.5 and 7.5–15 cm soil depths) were collected from each of 14 plots. Macrofauna cores were hand sorted (Wimbledon et al., 1996), mesofauna were extracted using a modified Berlese-Tullgren funnel, for details see Schon et al. (2008). Nematodes were extracted using a modified tray method as described by Yeates (1978). The Nematode Channel Ratio (NCR), Maturity Index (MI), Plant Parasitic Index (PPI) and ΣMaturity Index (ΣMI) were calculated (Bongers, 1990; Yeates, 1994, 2003). The Shannon-Wiener diversity index (H'), Margalef's richness (SR) and Pielou's evenness (J') were calculated to describe the diversity of soil fauna (Yeates, 1984; Ludwig and Reynolds, 1988).

Soil microbial biomass was measured using substrate induced respiration methods. One composite sample (20 cores, each 2.5 cm ø, and 0–7.5 cm soil deep) was collected from each plot. Samples were sieved to <2 mm and the amount of CO_2 respired in two hours was estimated by collecting 25 ml gas in a syringe and empting into a preevacuated Exetainer®, for methodology refer to Chapter 1.

Statistical analysis

The effects of irrigation and fertiliser application on soil and pasture properties, microbial respiration and the abundance of macrofauna, mesofauna, and nematodes were analysed using PROC MIXED in SAS v.9.1 (SAS Institute Inc., USA). Two depths (when available) were considered separately. The data were log (x+1) transformed prior to analysis. Treatment effects were analysed separately for each trial, due to differences in past management.

Analysing the effects of irrigation and fertiliser for combined data from both trials may have been more robust. However, underlying differences in the two trial areas in the soil C:N ratio, bulk density and porosity suggest that 11 years of irrigation on the fertiliser trial at the same rate as the irrigation trial (20% w/w) was not enough to remove the effects of 44 years of irrigation at 15% w/w, so the two trials were analysed separately.

The graphs and tables show untransformed arithmetic means. Error bars on figures show the standard errors of the means.

Results

Irrigation trial

The irrigation trial examined the influence of irrigation (dryland vs. irrigated) at high fertility. Agronomic and soil characteristics are given in Tables 1 and 2. Soil moisture was lower in dryland than in irrigated pastures (P=0.04), while soil pH (P=0.05) and total carbon (P=0.004) were higher under dryland. Dryland pastures had a lower proportion of grass than irrigated pastures.

The abundance and biomass of earthworms and other macrofauna were not significantly different under dryland and irrigated pastures (Table 3, Fig. 1).

The mesofauna were significantly more abundant in irrigated pastures than in dryland (0–7.5 cm, P=0.058), reflecting high Thysanoptera abundance (P=0.029, Table 4). Among mesofauna, Mesostigmata (P=0.041), Collembola (P=0.043) and Protura (P=0.029) were more abundant in irrigated pastures. Astigmata (P=0.006) and Oribatida were more abundant in dryland pastures, although the abundance of Oribatida was low (<1000 ind./m^2). In deeper soil (7.5–15 cm, Table 5) the mesofauna showed similar trends to 0–7.5 cm depth, with higher abundances of Mesostigmata (P=0.0002), Collembola (P=0.044), Protura (P=0.072) and Thysanoptera (P=0.051) under irrigation in comparison to dryland (Fig. 2).

At 0–7.5 cm depth nematode abundance was similar under dryland and irrigated pastures (0.36 x10^6 vs. 0.52 x10^6 ind./m^2, Table 6). The proportion of CP2 nematodes was higher under dryland (P=0.007), resulting in a lower MI and ΣMI, but higher PPI. The NCR was similar between dryland and irrigated pastures (0.87 vs. 0.81). Nematode assemblages were different in two treatments, with *Cephalenchus* more abundant under dryland pastures, and *Dorylaimus, Aporcelaimus* and *Dorylaimellus* more abundant under irrigated pasture. At 7.5–15 cm depth nematode abundance tended to be higher under irrigation than under dryland (Table 5). Similar to 0–7.5 cm depth, CP2 nematodes were more abundant under dryland than under irrigation (*P*=0.056, data not shown).

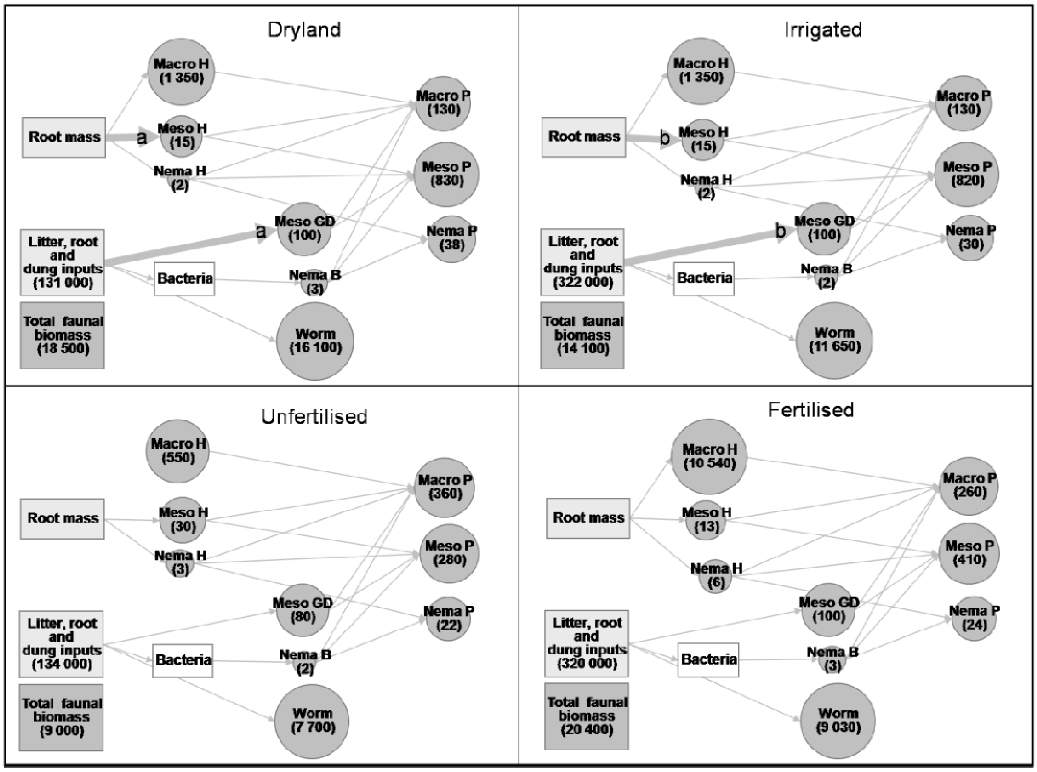

Fig. 1. Food webs of selected soil faunal groups in sheep grazed pastures under irrigation and fertiliser treatments, Canterbury, N.Z. Food webs and biomass calculation derived from Hunt (1987) and Mulder et al. (2005). Resource inputs are given in mg dry weight/m^2. Macrofauna (Macro), mesofauna (Meso) and nematode (Nema) herbivores (H) feed on plant material. Earthworms (Worm), mesofauna general detritivores (GD) and nematode bacterial feeders (B) feed on detrital inputs and associated microflora. The macrofauna, mesofauna and nematodes are in turn consumed by predators (P). Circle areas represent the log biomass of the fauna, actual biomass (dry weight mg/m^2) given in parenthesis. Biomass calculated as described in Chapter 1. Trophic groups with biomass <1.5 mg dry weight/m^2 were excluded. Wide arrow and $^{a,\,b}$ given in the arrow head indicate significant difference at α=0.05 within the functional group to which the arrows lead.

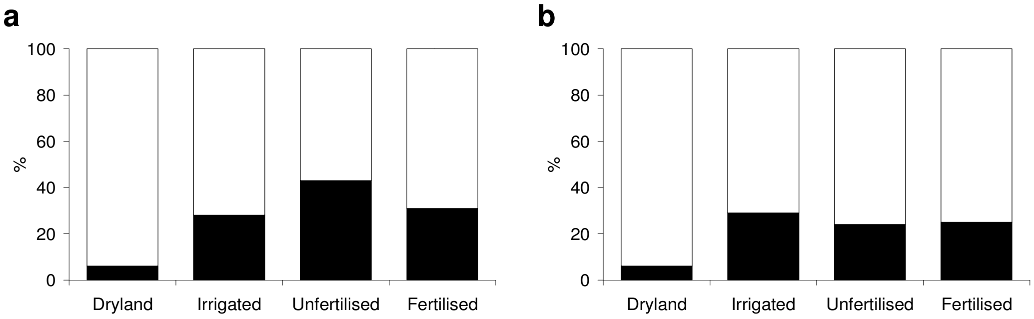

Fig. 2. Percent abundance of (a) Acari and (b) Collembola at 0–7.5 cm (white) and 7.5–15 cm soil depths (black) in sheep grazed pastures under different irrigation and fertiliser treatments, Canterbury, N.Z.

Table 2. Soil and herbage properties in sheep grazed pastures under different irrigation and fertiliser treatments, Canterbury, N.Z. (2007).

	Irrigation trial		Fertiliser trial	
Management	Dryland	Irrigated	Unfertilised	Fertilised
Soil moisture (%)[1]	**13.3**	**18.3**	22.3	20.0
Soil temperature (ºC)[1]	13.3	12.9	12.1	11.7
Bulk density (Mg/m^3)[2]	0.92	0.97	0.88	0.89
Porosity (% v/v of sieved soil)				
0.2–6 µm*	10	14	16	16
6–30 µm*	25	14	12	12
Microbial biomass (µg C/g soil)[2]	598	655	702	725
pH[2]	**5.4**	**5.3**	**5.6**	**5.4**
Olsen P (mg/L)[2]	52	24	14	22
Total N (%)[2]	0.4	0.4	**0.3**	**0.4**
Total C (%)[2]	**4.7**	**3.8**	4.3	4.4
C:N ratio[2]	11.7	9.1	**12.7**	**11.3**

[1] 0–10 cm depth.

[2] 0–7.5 cm depth.

Bold: *P*-value significant at α=0.1 between treatments within each trial.

*Pores 0.2–6 µm ø retain mostly plant unavailable water and exclude most microorganisms, with no predation on bacteria. Pores 6–30 µm ø retain mostly plant available water and accommodate most bacteria and their predators (Brewer, 1964).

Table 3. Earthworms and other macrofauna (0–15 cm soil depth) in sheep-grazed pastures under different irrigation and fertiliser treatments, Canterbury, N.Z. (2007).

	Irrigation trial		Fertiliser trial	
Management	Dryland	Irrigated	Unfertilised	Fertilised
EARTHWORMS (ind./m^2)				
Lumbricus rubellus (Hoffmeister, 1843)	35	53	26	40
Aporrectodea caliginosa (Savigny, 1826)	230	271	124	137
Aporrectodea rosea (Savigny, 1826)	6	0	0	0
Octolasion cyaneum (Savigny, 1826)	6	12	0	0
Total earthworms	277	336	150	177
Earthworm biomass (g wet wt/m^2)	107	78	51	60
SR	1.78	2.25	0.72	1.91
J'	0.23	0.23	**0.10**	**0.17**
H'	0.32	0.40	0.14	0.24
OTHER MACROFAUNA (ind./m^2)				
Costelytra zealandica (White 1846) larvae (Scarabaeidae, Coleoptera)	24	6	4	18
Elateridae larvae (Coleoptera)	0	0	26	18
Weevils (Circulionidae)		6		0
Coleoptera (other)	0	0	4	4
Diptera	12	59	0	4
Chilopoda (Myriapoda)	0	0	4	0
Total other macrofauna	35	71	40	44
Other macrofauna biomass (g wet wt/m^2)	4	9	3	30
SR	1.60	1.6	0.60	0.6
J'	0.09	0.04	0.03	0.03
H'	0.15	0.08	0.06	0.06

Bold: *P*-value significant at α=0.1 between treatments within each trial.

Table 4. Mesofauna (including Oribatida species) in sheep grazed pastures under different irrigation and fertiliser treatments, Canterbury, N.Z. (2007) at 0–7.5 cm soil depth.

	Irrigation trial		Fertiliser trial	
Management	Dryland	Irrigated	Unfertilised	Fertilised
MESOFAUNA (1000's ind./m^2)				
Platynothrus peltifer (Koch, 1839)	0	0.04	0.1	0
Tectocepheus sarekensis (Trägårdh, 1910)	0.1	0.04	0.3	0
Microppia minus (Paoli, 1908)	0	0	0.03	0.2
Oppiella nova (Oudemans, 1902)	0.2	0.04	0.1	0.03
Punctoribates punctum (Koch, 1839)	0	0	0.03	0.2
Liebstadia similis (Michael, 1888)	0.04	0.04	0	0.03
Oribatida nymphs	0.5	0.1	0.6	1.0
Oribatida (total)	0.8	0.3	1.2	1.5
Astigmata	**1.0**	**0.04**	0.03	0
Mesostigmata	**3.9**	**7.6**	4.6	4.4
Prostigmata	6.6	1.5	1.2	3.0
Scutacaridae	0.2	0.2	0.2	1.1
Total Acari	12.0	9.5	6.7	8.9
Entomobryomorpha	**6.0**	**12.8**	3.9	8.2
Poduromorpha	4.6	3.9	2.8	5.8
Sminthuridae	**0.2**	**0.4**	0.3	0.4
Neelipleona	0	0.1	0.1	0.1
Total Collembola	**10.8**	**17.2**	7.0	14.5
Protura	**0.1**	**0.7**	0.6	0.4
Coleoptera	0.1	0.1	0.3	0.2
Diptera	0.5	0.3	0.1	0.3
Hymenoptera	0	0.1	0	0.7
Psocoptera	0	0.04	0	0
Hemiptera	0.2	0.6	0.3	0
Thysanoptera	**0.2**	**17.1**	0.6	1.7
Arachnida	0.9	0	0	0
Chilopoda	0.04	0.04	0.1	0.03
Diplopoda		0		0
Pauropoda	0.04	0.1	**0.3**	**0.03**
Symphyla	0.1	0	0	0
Total mesofauna	**25.0**	**45.8**	16.0	26.7
SR	**7.06**	**4.9**	7.80	6.7
J'	0.33	0.37	0.41	0.36
H'	1.01	1.12	1.26	1.10

Bold: *P*-value significant at α=0.1 between treatments within each trial.

Table 5. Mesofauna and nematode abundance (1000's ind./m^2) in sheep grazed pasture under different irrigation and fertiliser treatments at 7.5–15 cm soil depth, Canterbury, N.Z. (2007).

	Irrigation trial		Fertiliser trial	
Management	Dryland	Irrigated	Unfertilised	Fertilised
Total mesofauna	**1.8**	**12.9**	8.0	9.5
Oribatida	0.1	0.3	2.3	0.4
Mesostigmata	**0.2**	**2.5**	1.8	2.7
Total Acari	**0.8**	**3.8**	5.0	3.9
Total Collembola	**0.6**	**7.1**	2.2	4.8
Thysanoptera	**0.04**	**0.7**	0.3	0.4
Total nematodes	96.9	117.6	171.0	195.9
Bacterial feeding	20.7	27.1	32.9	32.8
Fungal feeding	4.1	8.9	12.1	15.0
Plant associated	45.1	48.2	**87.9**	**103.9**
Predatory + omnivorous	27.0	33.4	38.1	44.2

Bold: *P*-value significant at α=0.1 between treatments within each trial.

Table 6. Nematode abundance in sheep grazed pastures (0–7.5 cm soil depth) under different irrigation and fertiliser treatments, Canterbury, N.Z. (2007).

	Irrigation trial		Fertiliser trial	
Management	Dryland	Irrigated	Unfertilised	Fertilised
NEMATODA (1000's ind./m^2)*				
Tylenchus	72.6	38.1	31.2	66.1
Cephalenchus	**13.2**	**0**	2.0	16.2
Ditylenchus	1.1	0	4.0	1.3
Heterodera	0	6.3	1.0	10.8
Heterodera/ Meloidogyne ♂	2.2	0	0	8.1
Tylenchorhynchus	39.6	1.6	0	0
Hoplolaimidae	5.5	12.7	70.5	85.0
Pratylenchus	1.1	0	1.0	1.3
Paratylenchus	6.6	4.8	0	0
Aphelenchus	12.1	14.3	11.1	9.4
Aphelenchoides	2.2	7.9	4.0	13.5
Seinura	1.1	1.6	0	0
Rhabditidae	7.7	20.6	10.1	10.8
Dauerlarvae	3.3	0	0	0
Panagrolaimus	11.0	25.4	15.1	59.3
Cephalobus	18.7	7.9	8.1	22.9
Heterocephalobus	9.9	11.1	**1.0**	**13.5**
Acrobeles	0	1.6	3.0	4.0
Plectus	19.8	23.8	17.1	13.5
Anaplectus	19.8	9.5	3.0	13.5
Prismatolaimus	0	0	2.0	4.0
Monhystera	1.1	1.6	3.0	1.0
Chromadoridae	1.1	0	5.0	2.7
Tripyla	0	3.2	**2.0**	**0**
Dorylaimus	**0**	**41.2**	**18.1**	**5.4**
Eudorylaimus	2.2	14.3	1.0	2.7
Labronema	0	3.2	4.0	1.3
Pungentus	**0**	**33.3**	16.1	66.1
Aporcelaimus	102.3	180.8	44.3	78.2
Dorylaimellus	**1.1**	**20.6**	16.1	29.7
Tylencholaimus	0	0	8.1	0
Doryllium	0	1.6	3.0	0
Nygolaimus	0	0	1.0	1.3
Clarkus	1.1	19.0	7.1	24.3
Mylonchulus	0	0	3.0	0
Alaimidae	4.4	6.3	**4.0**	**0**
Diphtherophora	0	3.2	1.0	0
Total nematodes	360.8	515.4	325.4	571.8
SR	6.15	5.8	**6.15**	**7.5**
J'	0.57	0.50	**0.69**	**0.54**
H'	2.12	1.88	2.57	2.03
NCR	0.87	0.81	0.73	0.86
Maturity groups (%)				
CP1	6	9	8	12
CP2	**49**	**24**	28	31
CP3	14	5	25	20
CP4	2	22	19	17
CP5	29	40	21	20
MI	2.05	2.28	2.08	1.21
PPI	0.93	0.40	1.08	0.96
Σ MI	2.98	2.68	3.17	2.17

Bold: *P*-value significant at α=0.1 between treatments within each trial.

**Mesodorylaimus, Meloidogyne,* Plectid, Belondirid, *Criconemoides,* were found at <3000 ind./m^2 at one treatment and are not included in the Table.

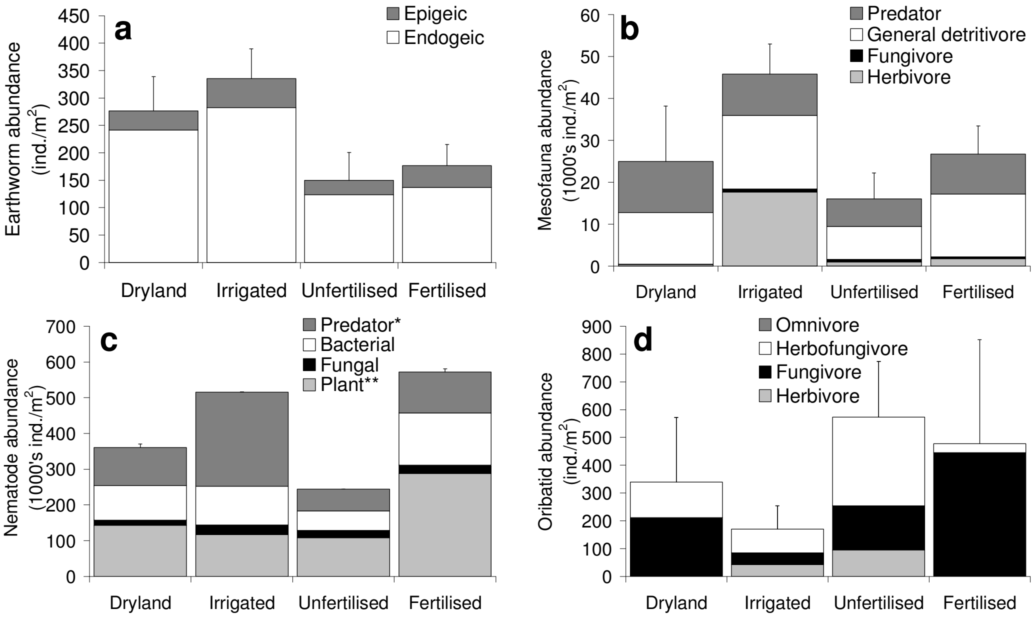

Fig. 3. Invertebrates in sheep grazed pastures under different irrigation and fertiliser treatments at 0–7.5 cm soil depths, Canterbury, N.Z. (a) Abundance of earthworm functional groups, b) abundance of mesofauna trophic groups, c) abundance of nematode trophic groups, and d) abundance of adult oribatid body widths.
*Predacious and omnivorous nematodes.
**Plant feeding and plant associated nematodes.

Fertiliser trial

The fertiliser trial examined the influence of phosphorus fertiliser (unfertilised vs. fertilised) under irrigation. The fertilised treatment had a lower pH (*P*=0.001) and soil C:N ratio (*P*=0.002) than the unfertilised plots (Table 2).

The abundance and biomass of earthworms and other macrofauna were similar under unfertilised and fertilised treatments (150 vs. 177 ind./m^2, Table 3). Earthworm J' was significantly higher under fertilised pastures (0.10 vs. 0.17, *P*=0.040).

Total mesofauna abundance was similar in both treatments and at both depths (Tables 4 and 5). At 0–7.5 cm depth Pauropoda were more abundant in unfertilised pastures.

There was no significant treatment effect on nematode abundance, although it was slightly higher in fertilised in comparison to unfertilised pastures (0.33 x10^6 vs. 0.57 x10^6 ind./m^2) (Fig. 3, Table 6). The bacterial feeding *Heterocephalobus* (*P*=0.032) was significantly more abundant under fertilised treatments. *Tripyla* (predacious, *P*=0.062), *Dorylaimus* (omnivorous, *P*=0.025) and Alaimidae (bacterial feeding, *P*=0.063) were significantly more abundant under unfertilised treatments.

Discussion

Application of both water and P fertiliser more than doubled pasture productivity, increasing calculated dry matter input to the soil food web (Table 1). Despite the large increase in the food resource and a reduction in moisture stress through irrigation, mesofauna and nematode abundances in this study were relatively low for New Zealand grazed pastures (McMillan, 1969; Adams, 1971; Yeates, 1984; Schon et al., 2008). Annual rainfall in the latter studies ranged from 850–1900 mm, compared with the 740 mm in this study, although with 385–580 mm of irrigation water added (McDowell and Rowley, 2008; Srinivasan and McDowell, 2009) annual inputs were in the same range as in this study. Earthworm abundance was also relatively low for New Zealand pastures (Springett, 1992; Schon et al., 2008), but was similar to that observed by Fraser and Piercy (1996) and Fraser et al. (1994) on soils in the seasonally dry Canterbury Plains.

Irrigating when topsoil (0–10 cm) falls to 20% w/w soil moisture leaves pores approximately >3 µm ø drained of water between irrigation events, exposing the invertebrate community to moisture stress. Historically (during 1980–1996), the average soil moisture at 20% w/w irrigation (irrigation trial) was 33% (R. Moss, pers. comm.) which was lower than the field capacity of 38% (McDowell and Rowley, 2008) and may have limited soil invertebrate populations. Despite raising the threshold for irrigation on the fertiliser trial in 1996 from 15 to 20% to stimulate pasture productivity (equivalent to four additional stock units in the irrigation trial (McDowell and Rowley, 2008)), the effects of past irrigation management appears to still be impacting on the invertebrate community. The slow apparent response to the change in the irrigation regime from a trigger of 15%, which is equivalent to permanent wilting point (Webb, 2009), to 20% moisture may be because even at the higher threshold invertebrates are still exposed to considerable moisture stress.

Acari and Collembola are likely to be the most affected by moisture stress, with their lifespan, dispersal and reproductive abilities providing limited defence against periodic drying (Lindberg and Bengtsson, 2005). Earthworms, which are mobile, have the capacity to survive by aestivating deeper in the soil, by entering diapause, or for epigeic species, by survival in the cocoon stage (Edwards and Bohlen, 1996). While only a few nematodes, such as *Paratylenchus*, have specific drought resistant stages, the nematodes live in water films and some bacterial feeding species are able to reproduce when pores as little as 1 µm ø contain water (Yeates, 1978, 1987; Yeates et al., 2002). The largest response to fertilisation and irrigation being observed for nematodes is consistent with this (Fig. 3). Increased plant growth directly stimulated plant feeding and plant associated nematodes at both depths (i.e., *Pungentus*), and through increased plant litter inputs stimulated bacterial feeding nematodes (i.e., *Panagrolaimus*).

Under dryland pastures there were annual drought stresses, with soil moisture in the district being reported to drop to as low as 6% during summer (Fraser and Piercy, 1996). Short lived species may be better adapted to drought disturbances, with the nematode assemblage in the dryland pasture having more CP2 nematodes than irrigated pastures (this resulted in a lower MI but not ΣMI). To continue activity during periods of low soil moisture, nematodes need to be able to access smaller pores where the water is held; the prevalent body widths in the nematode community are directly affected by the size distribution of water filled pores in which various taxa may live (Yeates et al., 2002). Under dryland, smaller *Tylenchus* and *Cephalenchus* (body width 25 and 22 µm, respectively) were more abundant, mirroring both reduced soil moisture and more 6–30 µm diameter pores (data from sieved soil) under dryland (Table 2). *Cephalenchus* also decreased under irrigation in the study reported by Yeates (1978). Plant feeding *Paratylenchus,* which has a drought resistant stage, was highest under dryland in this study even though plant growth was reduced. *Paratylenchus* was observed to be abundant in dry native tussock grasslands in New Zealand (Yeates, 1974), but not in dry pastures (Yeates, 1978).

Longer lived organisms, such as Oribatida, have also been suggested to be vulnerable to drought (Lindberg and Bengtsson, 2005); and in support of this we found them to be low in abundance under dryland. Of the oribatid species observed in this study most were short lived (<100 days) (Grishina, 1991) with body widths <350 µm (Fig. 3), with the exception of large *Platynothrus peltifer* (lifecycle of 130–332 days) which was not found under dryland (Table 4). Among adult Oribatida, short lived *O. nova* had a higher abundance in dryland in comparison to the irrigated treatments. Lindberg and Bengtsson (2005) found *Oppiella nova* to be one of the first Oribatida to recover after drought in a boreal spruce stand. The shorter lived Collembola also had a lower abundance under dryland in comparison to irrigated pastures. According to Lavelle and Spain (2001), Collembola are physiologically less drought resistant than Oribatida. This was also apparent in the current study.

Studying nematodes, Verschoor (2002) suggested that the effects of a soil moisture deficit would decrease with depth. In the present study the proportion of mesofauna residing deeper in the soil was lower under dryland where moisture was not replenished through irrigation (Fig. 2). Only 6% of Acari and Collembola were found in 7.5–15 cm soil depth under dryland in comparison to 27% under irrigated pastures. The latter values are similar to those observed at 7.5–15 cm depth in a typical sheep grazed pasture in New Zealand (Schon et al., 2008). This trend was not observed for nematodes.

Earthworm abundance and biomass were similar under dryland and irrigated pastures, although tending to be higher under dryland (Fig. 1). Fraser and Piercy (1996) observed similar earthworm abundances between dryland and irrigated pastures during the wetter months on the same irrigation trial. They also found that the activity of earthworms under irrigation (but not in dryland pastures) continued into the dry summer months. This equated to an annual average abundance of earthworms of approximately 370 ind./m^2 under dryland and 550 ind./m^2 under irrigation (Fraser and Piercy, 1996). Assuming that an individual *A. caliginosa* consumes about 20 g of dung per year (Edwards and Bohlen, 1996), this higher annual average abundance of earthworms would translate into a further 3700 kg DM/m^2 consumed. The increased biological activity under irrigation, along with the likelihood of higher decomposition rates over the warm summer months with regular wetting and drying cycles, are likely to result in higher CO_2 losses from the irrigated treatment. This might explain the lower soil C content of the irrigated pastures (Stewart and Metherell, 1999), despite higher pasture production, highlighting the likely role of earthworms and other macrofauna in litter fragmentation and decomposition throughout the year.

To an extent, the soil invertebrate community under irrigation may be more characteristic of a dryland soil due to continuing frequent moisture stress. This study suggests that the border strip method of irrigation limits the benefits of irrigation by limiting the contribution of invertebrates to soil development. With nearly a million ha of New Zealand under irrigation in 2006 (Aqualink Research Ltd., 2006), and with irrigated land area potentially increasing, it would be interesting to consider the benefits of an irrigation regime which would sustain soil moisture in the range that supported invertebrate activity and their provision of soil services, rather than just optimising plant growth.

Conclusion

Irrigation and P fertiliser application stimulated pasture productivity, however, invertebrate abundances were relatively low in comparison to other New Zealand pastures. Even using the higher irrigation threshold of 20% (rather than 15%), continued moisture stress at 20% irrigation limited invertebrate populations, with their limited defences against this stress. It was nematodes, which are able to reproduce when only smaller pores remain water filled, which were most responsive to increased pasture productivity in the fertiliser trial. Frequent drought periods under dryland favoured short lived organisms including CP2 nematodes and short lived oribatid species. The effects of drought on Acari and Collembola were more pronounced at 7.5–15 cm than at 0–7.5 cm depth. Earthworms tended to be more abundant under dryland at the time of sampling. However, their activity throughout the year was expected to be reduced under this treatment, reducing their effects on litter incorporation and aggregate formation.

Many studies have reported the importance of water availability for invertebrate activity. This study highlights the need to utilise this knowledge when considering irrigation regimes. The border strip method of irrigation employed in this study appears to limit invertebrate populations. To get the most out of irrigation, it is important the irrigation regime promotes invertebrate populations and their activities.

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Chapter Six:

Vulnerability of soil invertebrate communities to stock treading in three grassland soils

Earlier chapters have shown invertebrates to be sensitive to pastoral management, including stock treading. This chapter explores which invertebrates are most sensitive to stock treading pressure and whether they are able to recover once the stock treading pressure is removed.

N.L. Schon, A.D. MacKay. Vulnerability of soil invertebrate communities to stock treading in three grassland soils.

Abstract

Soil invertebrates are coming under increasing pressure as pastoral agriculture is intensified. The treading pressure of grazing livestock impacts on soil invertebrate populations through soil disturbance and destruction of habitable pore space. This study examined the sensitivity of soil invertebrates to stock treading pressure in three different soils by comparing their abundance and diversity in grazed paddocks with those under adjacent permanent fence lines. The resilience of the invertebrate communities within the same grazed paddocks was explored in mowing trials that had not been grazed for the previous three years, providing conditions for recovery of the invertebrate community.

Treading pressure reduced the abundance, biomass and diversity of the soil invertebrate community in all three soils. Invertebrates sensitive to stock treading included predatory and omnivorous nematodes, Oribatida and predatory macrofauna. Nematodes were more resilient than larger, longer lived invertebrates. Oribatid abundance showed little resilience, but several species which were not detected in the grazed paddock were found in the mown area. The removal of treading pressure in combination with irrigation appeared to be the major factor influencing invertebrate recovery. Different combinations of N and P fertilisers had few significant effects of soil invertebrates across soils, despite large differences in both the quality and quantity of plant litter available for invertebrates. Earthworms, with their ability to burrow, appeared resistant to treading pressure and exhibited the greatest resilience, doubling in abundance in the mowing trial. That the vulnerability of soil invertebrates to stock treading was consistent at all three sites would suggest that organism characteristics (i.e., life history and ability to move through the soil) and trophic interactions are important in structuring the biological community.

Introduction

Soils are coming under increasing pressure as pastoral agriculture is intensified. Soil communities are variable through time and respond to stresses and disturbances. Since the soil biology plays a central role in soil services, the vulnerability of communities to human induced disturbances needs to be understood. Vulnerability is a combination of sensitivity and/or resistance of a system to disturbance, properties that include the ability to respond to or withstand pressure, and resilience following disturbance, which includes the ability to recover (Pimm, 1984; Odum, 1985; Grimm et al., 1992; Wardle, 2002; Wall, 2004; Bardgett et al., 2005). Stock grazing and associated treading pressures are an example of a source of stress and disturbance.

Increased live weight loading by grazing animals on the soil impacts on soil structure, with a decline in macroporosity, not only reducing pasture growth, but also restricting air and water movement through the soil (Greenwood and McKenzie, 2001; Mackay, 2008). Soil compaction may also have a negative effect on invertebrate populations (Hassink et al., 1993; Clapperton et al., 2002; Yeates et al., 2002; Cole et al., 2008; Schon et al., 2008). The resistance of soil invertebrate communities to stock treading depends on a number of factors including livestock type and density, soil type and its susceptibility to compaction, as well as attributes of the community (Odum, 1985; Hewitt and Shepherd, 1997; Greenwood and McKenzie, 2001; Wardle, 2002). For example, earthworms are ecosystem engineers (Jones et al., 1994) with ability to restore their habitats. They may therefore be more resistant to stock treading than invertebrates, such as Oribatida, which are not ecosystem engineers and depend on existing habitable pores (Elliott et al., 1980).

Increased pasture production is associated with higher stocking rates in grazed pastures. Both phosphorus (P) fertiliser, which stimulates clover growth and biological nitrogen fixation, and nitrogen (N) fertiliser, which stimulates grass growth when clover vigour is low, increase soil fertility and pasture production. This can stimulate components of soil invertebrate communities by providing greater food resources (Yeates, 1976; Cole et al., 2005; Oliver et al., 2005; Curry et al., 2008). In pastures where food availability is not limiting, invertebrates may be more resilient following the removal of treading pressures (Wardle, 2002; Bardgett et al., 2005). The resilience of an invertebrate community is influenced by the dominant species and trophic interactions, with short lived species, typical of disturbed systems, being more resilient than longer lived organisms (Wardle, 2002).

This study examined the vulnerability of soil invertebrates to stock treading pressure on three different soils. The sensitivity of invertebrates to treading was examined in three grazed paddocks with reference to adjacent permanent fence lines where there was no stock treading. The resilience of the invertebrate community in the same grazed paddocks was examined in N and P plots in a field trial that had been mown rather than grazed for the previous three years. The mowing regime, with no stock treading and no moisture limitations, could provide optimal conditions for invertebrate recovery in a given soil.

Methods

Study sites

In 2004 N and P fertiliser trials were established in three separate regions throughout New Zealand. The sites spanned a distance of ~1000 km north to south. The northern most site was located in the Waikato region on an Andosol (FAO, 1988) or Allophanic soil (NZSC) (Hewitt, 1993). Further south in the Manawatu region another site was located on a Luvisol (FAO) or Pallic soil (NZSC). The southernmost site was located in Southland on a Cambisol (FAO) or Brown soil (NZSC). All sites were located on flat land and had mixed ryegrass (*Lolium perenne*) and clover (*Trifolium repens*) pastures. For further details of the sites see Table 1.

In the fertiliser trial treatments received P as superphosphate (SSP, to achieve target low or high Olsen P levels), and N as urea (0 or 400 kg N/ha). There were four replicates, each 0.17 ha, of each treatment. They were irrigated during summer months to prevent limitations due to moisture stress, mown 10–14 times throughout the year with a domestic rotary mower and received K fertiliser every three months and a basal fertiliser every six months (for more details refer to Mackay et al. unpublished).

Samples were collected in 2007 from the three sites. At each site a permanent fence line, grazed paddock and the fertiliser treatments (4 replicates) in the mown trial area were sampled (Fig. 1). The permanent fence line was a paddock boundary fence which was in place well before the trials were established in 2004. The fence lines were not affected by stock treading but received fertiliser through drift. Ruminants defoliated pasture under the permanent fence when grazing in the paddock (only in Andosol and Luvisols). In addition to no treading pressure, fence lines would have had no dung and urine return. The grazed paddock was uniformly grazed by ruminants utilising full herbage production. The grazed paddocks received maintenance fertiliser.

Table 1. The three sites sampled and their characteristics. At each site samples were collected from fence line, grazed paddock and mown areas.

Soil	Andosol	Luvisol	Cambisol
Soil series	Horotiu	Marton	Waikiwi
Texture	silt loam	silt loam	silt loam
Sand/Silt/Clay (%)	34/49/17	41/31/27	31/41/28
Plastic limit (%)[1]	59	39	44
Region	Waikato	Manawatu	Southland
Latitude	37°46'S	40°14'S	46°21'S
Longitude	175°18'E	175°40'E	168°32'E
Mean annual air temperature (ºC)	13.8	13.3	10.0
Annual rainfall (mm)	963	870	1146
Month sampled in 2007	August	July	September
Permanent fence line features	Grazed grass	Grazed grass	*Phormium* and *Eucalyptus*
Ruminants in grazed paddock	Various	Cows	Sheep
MOWN FERTILISER TRIAL PARAMETERS			
Nitrogen (urea) (kg N/ha/yr)	0/400	0/400	0/400
Phosphorus (SSP) to achieve Olsen P levels	22/75	10/65	10/65
Olsen P levels in 2007	23/80	26/68	14/48
Pasture production (kg DM/ha/yr with % clover in parenthesis)			
Low P low N	11 329 (29)	12 691 (14)	8 652 (32)
Low P high N	13 138 (6)	20 998 (2)	13 321 (2)
High P low N	13 690 (35)	14368 (22)	9 443 (26)
High P high N	15 738 (3)	23 061 (7)	15 001 (2)

[1]From New Zealand Soil Bureau (1968) and Singleton and Addison (1999).

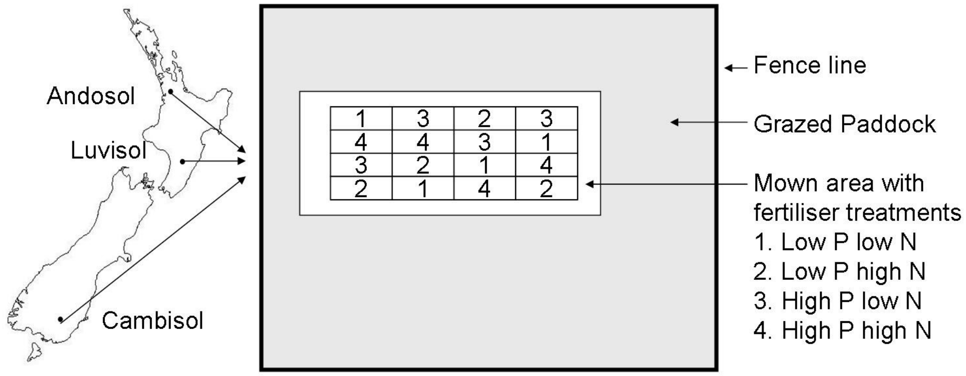

Fig. 1. Layout of the areas sampled at each site, from the northern Andosol to the southern Cambisol. Areas sampled include the permanent fence line, grazed paddock and the mown area with different nitrogen and phosphorus fertiliser combinations.

Soil biological sampling

Four cores for macrofauna (15.5 cm ø, 0–15.5 cm deep) were collected from the fence line and grazed paddock. Eight cores were collected from the mown area adjacent to two out of four of the fertiliser replicates. Macrofauna cores were hand sorted, and specimens identified in the laboratory (Wimbledon et al., 1996).

Four soil cores for mesofauna (5 cm ø, 0–7.5 cm deep) were collected from the fence line and grazed paddock and two cores were collected from each fertiliser replicate. Mesofauna were extracted using a modified Berlese-Tullgren apparatus, for details see Schon et al. (2008). Four composite soil samples for microfauna (nematodes) (each comprising 5 cores 2.5 cm ø, 0–7.5 cm deep) were collected from the fence line and grazed paddock and one composite sample was collected from each fertiliser replicate. Nematodes were extracted by the modified tray method described by Yeates (1978). The Nematode Channel Ratio (NCR), Maturity Index (MI), Plant Parasitic Index (PPI) and ΣMaturity Index (ΣMI) were calculated (Bongers, 1990; Yeates, 1994, 2003).

The Shannon-Wiener diversity index (H'), Margalef's richness (SR) and Pielou's evenness (J') were calculated to describe the diversity of soil fauna (Yeates, 1984; Ludwig and Reynolds, 1988).

Soil microbial biomass was measured using substrate induced respiration methods. Four composite samples (10 cores pooled, each core 2.5 cm ø, 0–7.5 cm deep) were collected from the fence line and grazed paddock. One composite sample was collected from each fertiliser replicate. Samples were sieved to <2 mm and the amount of CO_2 respired in two hours was estimated by collecting 25 ml gas in a syringe and empting into a preevacuated Exetainer®, for methodology refer to Chapter 1.

Soil and pasture sampling

Soil temperature (Checktemp, Hanna Instruments, England) and moisture (TDR 300 Soil Moisture Probe, Spectrum Technologies, Inc., USA) at 0–10 cm depth were recorded in the field at the time of sampling. After extraction the mesofauna cores were analysed for soil pH (1:2.5 soil:water), Olsen P (Olsen et al., 1954), total nitrogen and total carbon (dry combustion using LECO-2000, LECO Equipment Corp., St. Joseph, USA). Bulk density was determined by collecting three intact soil cores from the fence line, grazed paddock and mown area (10 cm ø, 0–7.5 cm depth), drying (105ºC) and weighing.

Pore size distribution for pores <60 μm ø was determined using tension plates (see Chapter 1). Tensions of 10, 50, and 1500 kPa equated to pore sizes of 30, 6, and 0.2 μm ø, respectively. Larger pores (>50 μm ø) were characterised in the Luvisol using fluorescent resin. Three 15 cm ø cores were collected from each area (fence line, grazed paddock and mown area) in 2009 when soil moisture was <40%. The cores were impregnated with a fluorescent resin, and images of horizontal soil sections at 2.5 and 5 cm depths were analysed using Solicon© analysis software (The University of Sydney, Cotton Research and Development Corporation) (Vervoort and Cattle, 2003).

Statistical analysis

The hypothesis that the macrofauna, mesofauna, and microfauna were not vulnerable to stock treading was tested for by determining whether there was a significant effect of treatments (fence line, grazed paddock and mown area) on their abundance, both within a site and across all three sites. Faunal abundances were log (x+1) transformed and analysed using PROC MIXED in SAS v.9.1 (SAS Institute Inc., USA), using Satterthwaite degrees of freedom. The effect of soil type/site was examined. The effect of the four fertiliser treatments in the mown area on the soil invertebrates were tested for both within a site and across all three sites. The graphs and tables show untransformed arithmetic means. The error bars in figures represent standard errors of the means.

Results

Site differences

Soil properties such as soil moisture, temperature and bulk density varied between sites (Table 2). Soil invertebrates were significantly influenced by soil type and/or site, including total earthworm abundance (P=0.018, Table 3), total mesofauna abundance (P=0.001, Tables 4, 5) and total nematode abundance (P=0.001, Table 6). Some of the differences in soil invertebrates between sites may have reflected their regional phenology and sampling date (McMillan, 1969; Yeates and Risk, 1976; Fraser and Piercy, 1996). Some invertebrates showed distinct geographical patterns. For example, the clover root weevil (*Sitona lepidus*) was most abundant in the northern site (159 ind./m^2 in grazed paddock), reflecting site of original establishment of this weevil in New Zealand (Gerard et al., 2007). The nematode, *Tylenchorhynchus* was most abundant in the southern site, a pattern observed previously by Yeates (1992). Among Oribatida, only small, cosmopolitan, *Microppia minus* was found at all locations (Table

5).The relative contribution of bacterial feeding over fungal feeding nematodes (i.e., NCR) was influenced by soil type/site, being lowest in the Luvisol. Other factors such as site history may also have been important (Fraser and Piercy 1996).

Table 2. Soil properties under the fence line (F), grazed paddock (G) and mown area (M, means of the four fertiliser treatments) at three sites, New Zealand (2007). For site characteristics refer to Table 1.

Soil	Andosol			Luvisol			Cambisol		
Management	F	G	M	F	G	M	F	G	M
Soil moisture (%)[1]	**46**^{a}	**29**^{b}	**42**^{a}	**51**^{a}	**50**^{a}	**46**^{b}	**30**^{a}	**61**^{b}	**62**^{b}
Soil temperature (°C)[1]	**10.1**^{a}	**9.9**^{a}	**9.7**^{b}	7.6	7.3	7.5	**7.3**^{a}	**7.5**^{b}	**7.8**^{b}
Bulk density (Mg/m^3)[2]	0.68	0.71	0.65	**0.73**^{a}	**1.10**^{b}	**0.76**^{a}	0.42	0.66	0.59
Porosity (% v/v sieved soil)									
0.2–6 μm*	7	15	7	**2**^{a}	**9**^{b}	**0**^{c}	**0**^{a}	**13**^{b}	**4**^{c}
6–30 μm*	**12**^{a}	**13**^{a}	**17**^{b}	**18**^{a}	**17**^{b}	**16**^{a}	**15**^{a}	**15**^{a}	**9**^{b}
Microbial biomass (μg C/g soil)[2]	634	803	991	1521	913	827	513	1343	1039
pH[2]	5.8	5.7	5.6	5.7	5.8	5.7	**5.0**^{a}	**6.0**^{b}	**5.7**^{c}
Olsen P (mg/L)[2]	36	24	52	39	41	47	57	35	37
Total N (%)[2]	0.68	0.72	0.71	**0.43**^{a}	**0.34**^{b}	**0.32**^{c}	**0.78**^{a}	**0.54**^{b}	**0.57**^{c}
Total C (%)[2]	7.7	7.1	7.1	**4.6**^{a}	**3.7**^{b}	**3.4**^{c}	**10.4**^{a}	**6.1**^{b}	**6.8**^{c}
C:N ratio[2]	11.3	9.9	10.0	**10.9**^{a}	**10.9**^{b}	**10.8**^{c}	**13.3**^{a}	**11.3**^{b}	**11.9**^{c}

[1] 0–10 cm depth.

[2] 0–7.5 cm depth.

[a,b] *P*-value significant at α=0.1 for treatment effects (for F, G and M using least squares means) in a given soil

Fence line

Under the fence lines, where no stock treading had occurred, soil bulk density was lower than in the grazed paddocks, the difference was significant in the Luvisol (Table 2). Under the fence lines earthworm abundance, including the dominant *Aporrectodea caliginosa*, was low but earthworm species richness was high (Table 3). Anecic *Aporrectodea longa* also followed this trend in the Luvisol, the only site at which it was detected. Under the fence line the highest abundances of Oribatida were detected (>20 000 ind./m^2, Table 4 and 5). Under the fence line total soil carbon and the soil C:N ratio were higher than in the grazed paddock as was the abundance of the fungal feeding nematode *Aphelenchoides.* The abundance of *Aphelenchoides* was similar under this treatment at all sites (~20 000 ind./m^2, Table 6). Under the fence line there were high abundances of herbivorous Thysanoptera, *Tylenchus, Paratylenchus*, Hoplolaimidae (Luvisol and Cambisols), and *Xiphinema* (Andosol). In the Cambisol, where trees were present along the fence line, Arachnida, Chilopoda and Diplopoda were more abundant there.

Grazed pasture

Bulk density and pores 0.2–30 µm ø were highest in the grazed paddocks, especially in the Luvisol (Table 2). In the Luvisol, where soil porosity (pores >50 µm ø) was examined more closely using resin impregnation, soil porosity was low in the grazed paddock (3%). While there was a decline in all pores, the decline in pores <2 mm in diameter was most apparent (Fig. 2). In these pastures the abundance of Oribatida was low (1 900 ind./m^2, Table 4). Macrofauna predators, represented by adult Coleoptera, were absent from grazed paddocks at all sites. No macrofauna predators were detected in the Cambisol (Fig. 3). Larger, predatory and omnivorous nematodes such as *Dorylaimus* and *Aporcelaimus* were less abundant in grazed paddocks.

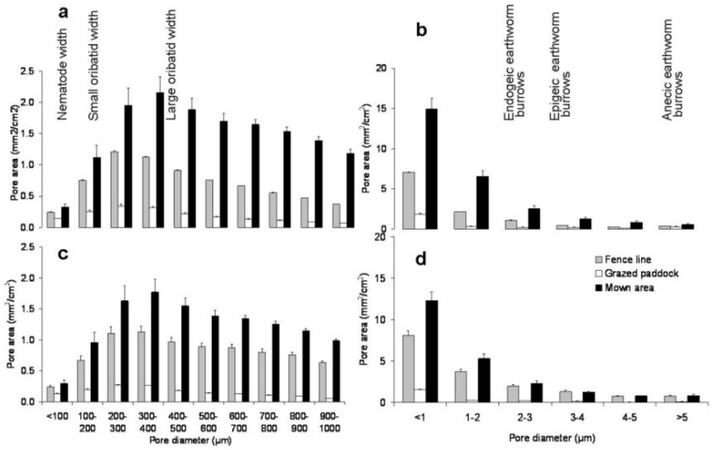

Fig. 2. Pore area (mm^2/cm^2) over range of pore sizes for the Luvisol as determined through resin impregnation. Total porosity is 11% for fence line, 3% for grazed paddock and 27% for mown area. (a) Pores <1 mm ø at 2.5 cm depth. (b) All pores (<1 to >5 mm ø) at 2.5 cm depth; the <1 mm bar is the sum of pores shown in (a). (c) Pores <1 mm ø at 5 cm depth. (d) All pores (<1 to >5 mm ø) at 5 cm depth; the <1 mm bar is the sum of pores shown in (c).

Table 3. Earthworm and macrofauna abundance under the fence line (F), grazed paddock (G) and mown area (M, means of the four fertiliser treatments) at three sites, N. Z. (2007). For site characteristics refer to Table 1.

Soil	Andosol			Luvisol			Cambisol			*P-value*		
Management	F	G	M	F	G	M	F	G	M	*Site*	*Tmt*	*Site*Tmt*
EARTHWORMS (ind./m^2)												
Lumbricus rubellus (Hoffmeister, 1843)	53	26	38	**0^{a}**	**13^{ab}**	**38^{b}**	**53^{a}**	**212^{b}**	**146^{b}**	***0.0002***	*0.117*	*0.476*
Aporrectodea caliginosa (Savigny, 1826)	**106^{a}**	**278^{b}**	**305^{b}**	**238^{a}**	**464^{b}**	**1020^{c}**	**66^{a}**	**914^{b}**	**1537^{b}**	***0.033***	***0.0001***	***0.012***
Aporrectodea rosea (Savigny, 1826)	**79^{a}**	**26^{b}**	**251^{c}**	**79^{a}**	**93^{a}**	**371^{b}**	0	265	33	***0.001***	***0.014***	***0.011***
Octolasion cyaneum (Savigny, 1826)	0	0	0	0	0	0	**0^{a}**	**0^{a}**	**66^{b}**	***0.002***	***0.0005***	***0.0001***
Aporrectodea longa (Ude, 1885)	0	0	0	40	93	132	0	0	0	***0.0001***	*0.603*	*0.727*
Total earthworms (ind./m^2)	**238^{a}**	**331^{a}**	**609^{b}**	**358^{a}**	**662^{b}**	**1563^{c}**	**119^{a}**	**1391^{b}**	**1781^{b}**	***0.0007***	***0.0001***	***0.0002***
Earthworm biomass (g wet wt/m^2)	124	168	197	**105^{a}**	**243^{b}**	**342^{b}**	**67^{a}**	**289^{b}**	**215^{b}**	*0.221*	***0.0002***	*0.744*
SR	**2.65^{a}**	**1.71^{b}**	**1.36^{c}**	**1.75^{a}**	**1.20^{b}**	**0.91^{c}**	2.71	0.93	0.92	***0.068***	***0.0001***	*0.816*
J'	0.43	0.29	0.42	0.52	0.58	0.61	**0.13^{a}**	**0.46^{b}**	**0.38^{b}**	***0.005***	*0.123*	*0.185*
H'	0.60	0.40	0.59	0.72	0.80	0.85	**0.17^{a}**	**0.63^{b}**	**0.52^{b}**	***0.005***	*0.1038*	*0.173*
MACROFAUNA												
Wiseana cervinata (Walker, 1865) larvae (Lepidoptera)	0	0	0	0	0	7	0	13	7	*0.411*	*0.618*	*0.745*
Costelytra zealandica (White, 1846) larvae (Coleoptera)	13	0	13	0	0	0	0	13	0	*0.284*	*1.0*	*0.319*
Click beetle larvae (Coleoptera)	40	13	34	0	0	0	13	0	0	***0.0005***	*0.356*	*0.404*
Weevils (Circulionidae, Coleoptera)	**53^{a}**	**159^{b}**	**192^{b}**	**0^{a}**	**146^{b}**	**40^{c}**	0	13	0	***0.0001***	***0.0002***	***0.020***
Coleoptera (adult)	26	0	0	66	0	7	0	0	0	***0.0001***	***0.056***	*0.232*
Diptera	**0^{a}**	**0^{a}**	**92^{b}**	0	0	20	0	0	0	***0.482***	***0.040***	***0.027***
Noctuidae (Lepidoptera)	0	0	0	0	13	0	0	0	0	***0.190***	*0.210*	*0.187*
Gastropoda	0	0	7	0	0	13	0	0	0	*0.829*	*0.406*	*0.917*
Total macrofauna (ind./m^2)	**132^{a}**	**172^{a}**	**338^{b}**	66	159	86	66	40	7	***0.0001***	*0.144*	***0.086***
Macrofauna biomass (g wet wt/m^2)	10	7	15	1	2	7	**11^{a}**	**14^{a}**	**0.2^{b}**	***0.004***	*0.812*	***0.034***
SR	4.0	2.9	5.4	0.0	1.8	1.4	0.0	0.0	0.0	***0.172***	***0.0002***	*0.229*
J'	**0.20^{ab}**	**0.08^{a}**	**0.37^{b}**	0.0	0.07	0.10	0.0	0.0	0.0	***0.0002***	***0.046***	***0.082***
H'	**0.45^{ab}**	**0.17^{a}**	**0.81^{b}**	0.0	0.16	0.22	0.0	0.0	0.0	***0.0001***	***0.044***	***0.075***

^{a,b}*P*-value significant at $\alpha=0.1$ for treatment effects (for F, G and M using least squares means) in a given soil. The *P*-values given are for the effects of site, treatments (F, G and M) and their interaction.

Table 4. Mesofauna abundance under the fence line (F), grazed paddock (G) and mown area (M, means of the four fertiliser treatments) at three sites, N. Z. (2007). For site characteristics refer to Table 1.

Soil	Andosol			Luvisol			Cambisol			P-value		
Management	F	G	M	F	G	M	F	G	M	*Site*	*Tmt*	_Site*Tmt_
MESOFAUNA (1000's ind./m^2)												
Oribatida	**23.7^{a}**	**0.6^{b}**	**10.5^{c}**	**22.4^{a}**	**1.9^{b}**	**2.0^{b}**	**20.5^{a}**	**0.3^{b}**	**1.1^{b}**	*0.367*	***0.0001***	*0.157*
Astigmata	0.5	0.8	3.4	**0.8^{ab}**	**2.2^{a}**	**0.2^{b}**	0	0.1	0.1	***0.0001***	***0.001***	***0.012***
Mesostigmata	11.2	50.5	15.2	**34.8^{a}**	**4.7^{b}**	**7.6^{b}**	**11.7^{a}**	**7.1^{ab}**	**1.9^{b}**	***0.268***	*0.217*	***0.037***
Prostigmata	4.9	0.3	2.0	1.8	0.4	2.5	**12.7^{a}**	**0.5^{b}**	**0.2^{b}**	*0.363*	***0.002***	***0.049***
Scutacaridae	0.3	0.3	0.4	0	0.3	1.1	1.3	0.9	0.1	*0.544*	*0.915*	***0.048***
Total Acari	35.3	7.0	28.8	**57.0^{a}**	**9.2^{b}**	**13.0^{b}**	**45.6^{a}**	**8.9^{ab}**	**2.8^{b}**	*0.362*	***0.003***	*0.141*
Entomobryomorpha	11.7	4.2	7.0	4.5	18.0	25.0	9.8	5.7	4.3	*0.392*	*0.887*	*0.566*
Poduromorpha	0.5	0	0.2	**2.3^{ab}**	**1.0^{a}**	**3.4^{b}**	**17.3^{a}**	**4.2^{a}**	**0.8^{b}**	***0.0001***	***0.078***	***0.0003***
Sminthuridae	0.6	0.6	0.4	0.1	0.1	0.6	**0^{a}**	**1.0^{b}**	**0.2^{a}**	*0.465*	*0.187*	*0.162*
Neelipleona	0.1	0	0.2	0	0	0.1	0	0.1	0.05	*0.734*	*0.552*	*0.627*
Total Collembola	12.9	4.8	70.9	**6.9^{a}**	**19.1^{a}**	**29.0^{b}**	**27.1^{a}**	**11.1^{ab}**	**5.4^{b}**	***0.104***	*0.692*	*0.247*
Coleoptera	0.9	1.0	0.5	**1.5^{a}**	**0.9^{a}**	**0.4^{b}**	1.0	0.1	1.0	*0.157*	*0.101*	*0.180*
Diptera	0.1	0.1	0.1	0	0	0.05	0	0.1	0.05	*0.221*	*0.750*	*0.902*
Hymenoptera	0.2	1.0	1.5	0	0	0	0	0	0	***0.0001***	*0.737*	*0.874*
Hemiptera	0.5	0	0.3	0.3	0	0.2	0	0	0	***0.099***	*0.109*	*0.686*
Thysanoptera	**1.6^{ab}**	**0.3^{a}**	**9.3^{b}**	**21.1^{a}**	**1.0^{b}**	**2.1^{b}**	**1.7^{a}**	**0^{b}**	**0.03^{b}**	***0.008***	***0.004***	***0.0003***
Isopoda	0.1^{a}	**0^{b}**	**0^{b}**	0	0	0	0	0	0	***0.028***	***0.032***	***0.006***
Amphipoda	0	0	0.02	0	0	0	0	0	0	*0.923*	*0.878*	*0.969*
Arachnida	0.1^{a}	**0^{b}**	**0^{b}**	0	0	0.02	**0.4^{a}**	**0^{b}**	**0^{b}**	***0.0001***	***0.0001***	***0.0001***
Chilopoda and Diplopoda	0	0.1	0.1	0.4	0.1	0.3	**0.3^{a}**	**0^{b}**	**0^{b}**	*0.172*	*0.325*	*0.142*
Diplopoda	0	0	0	0	0	0	**0.8^{a}**	**0^{b}**	**0^{b}**	***0.0001***	***0.0001***	***0.0001***
Pauropoda	0	0	16	0	0	0	0	0	0	*0.923*	*0.878*	*0.969*
Symphyla	**0.3**	0.1	0.1	0	0	0	0.4	0	0.7	***0.020***	*0.118*	*0.178*
Total mesofauna	52.2	14.5	48.6	**87.2^{a}**	**30.3^{b}**	**45.2^{b}**	**77.2^{a}**	**20.2^{ab}**	**10.0^{b}**	*0.385*	***0.019***	*0.282*
SR	4.39	6.44	4.45	3.97	5.44	5.39	4.12	5.70	7.52	*0.166*	*0.613*	*0.183*
J'	0.42	0.44	0.37	**0.42^{a}**	**0.42^{a}**	**0.32^{b}**	0.47	0.31	0.32	*0.694*	***0.032***	*0.627*
H'	1.28	1.35	1.13	1.27	1.29	0.96	1.43	0.95	0.97	*0.775*	***0.045***	*0.660*

^{a,b}*P*-value significant at α=0.1 for treatment effects (for F, G and M using least squares means) in a given soil. The *P*-values given are for the effects of site, treatments (F, G and M) and their interaction.

Table 5. Oribatid species abundance under the fence line (F), grazed paddock (G) and mown area (M, means of the four fertiliser treatments) at three sites, N. Z. (2007). For site characteristics refer to Table 1.

Soil	Andosol			Luvisol			Cambisol			*P-value*		
Management	F	G	M	F	G	M	F	G	M	*Site*	*Tmt*	*Site*Tmt*
ORIBATIDA (ind./m^2)												
Platynothrus peltifer (Koch, 1839)	0	0	0	0	0	0	260	0	320	***0.046***	*0.377*	*0.420*
Metabelba obtusus (Hammer, 1966)	**400^a**	**0^b**	**0^b**	0	0	0	0	0	0	***0.0001***	***0.0002***	***0.0001***
Tectocepheus velatus sarekensis (Michael, 1980)	**7 200^a**	**0^b**	**710^b**	0	0	0	0	0	0	***0.0001***	***0.0001***	***0.0001***
Lanceoppia sp.	0	0	0	0	0	0	**9 300^a**	**0^b**	**0^b**	***0.0001***	***0.0001***	***0.0001***
Microppia minus (Paoli, 1908)	0	0	33	**380^a**	**640^a**	**0^b**	0	0	30	***0.001***	*0.120*	***0.001***
Oppiella nova (Oudemans, 1902)	0	0	0	260	1 020	140	**1 020^a**	**0^b**	**190^b**	***0.010***	***0.055***	***0.048***
Oppiella sp.	0	0	0	0	0	0	**380^a**	**130^{ab}**	**20^b**	***0.0004***	***0.079***	***0.043***
Ramusella sp.	**200^a**	**0^b**	**0^b**	0	0	0	0	0	0	***0.028***	***0.032***	***0.006***
Achipteria sp.	**4 780^a**	**0^b**	**20^b**	0	0	0	**890^a**	**0^b**	**0^b**	***0.0001***	***0.0001***	***0.0001***
Punctoribates punctum (Koch, 1839)	**1 120^a**	**0^b**	**80^b**	0	0	0	0	0	0	***0.0001***	***0.006***	***0.0003***
Galumna rugosa (Hammer, 1968)	**1 430^a**	**0^b**	**20^b**	0	0	0	0	0	0	***0.0001***	***0.0001***	***0.0001***
Ceratozetes sp.	**610^a**	**0^b**	**20^b**	0	0	0	0	0	0	***0.0001***	***0.0001***	***0.0001***
Liebstadia similis (Michael, 1888)	0	0	0	5 090	0	1450	0	0	0	***0.003***	*0.169*	*0.140*
Scheloribates crassus (Hammer, 1967)	0	0	0	0	0	0	**8 020^a**	**130^b**	**0^c**	***0.0001***	***0.0001***	***0.0001***
Scheloribates sp.	0	0	0	**14 000^a**	**0^b**	**20^b**	0	0	0	***0.0001***	***0.0001***	***0.0001***
Setobates scheloribatoides (Ramsay, 1966)	1 430	130	5 680	0	0	16	0	0	0	***0.001***	*0.525*	*0.740*
Eupelops sp.	1 220	130	1 220	0	0	0	0	0	0	***0.0001***	*0.160*	*0.119*
Nymphs	**5 300^a**	**380^b**	**2 730^c**	2 670	260	334	640	0	590	***0.007***	***0.001***	***0.319***
Oribatida (adult)	**18 440^a**	**260^b**	**7 770^c**	**19 740^a**	**1 660^b**	**1 620^b**	**19 860^a**	**260^b**	**560^b**	***0.285***	***0.0001***	*0.147*
SR	**5.10^a**	**0^b**	**7.41^c**	3.2	1.8	0.88	**7.6^a**	**0^b**	**4.61^b**	***0.314***	***0.004***	*0.147*
J'	**0.43^a**	**0^b**	**0.13^{ab}**	0.07	0.05	0.02	**0.32^a**	**0^b**	**0.05^b**	***0.0001***	***0.001***	***0.001***
H'	**1.26^a**	**0^b**	**0.37^c**	0.19	0.16	0.05	**0.94^a**	**0^b**	**0.15^b**	***0.001***	***0.0001***	***0.002***

^{a,b}*P*-value significant at $\alpha=0.1$ for treatment effects (for F, G and M using least squares means) in a given soil. The *P*-values given are for the effects of site, treatments (F, G and M) and their interaction.

Table 6. Nematodes under the fence line (F), grazed paddock (G) and mown area (M, means of fertiliser treatments) at three sites, N.Z. (2007). For site characteristics refer to Table 1.

Soil	Andosol			Luvisol			Cambisol			*P-value*		
Management	F	G	M	F	G	M	F	G	M	*Site*	*Tmt*	*Site*Tmt*
NEMATODA (1000's ind./m^{2})												
Tylenchus	155.8	82.5	85.4	**111.9**^{a}	**53.9**^{b}	**69.6**^{ab}	106.7	159.8	165.9	***0.071***	*0.256*	*0.179*
Cephalenchus	9.6	4.3	9.6	4.9	3.0	5.8	0	3.4	5.2	*0.254*	*0.390*	***0.907***
Ditylenchus	0	0	0.6	17.0	3.0	7.5	0	0	0	***0.001***	*0.942*	*0.918*
Anguina	0	0	0	2.4	4.5	4.8	0	0	0	*0.870*	*0.818*	*0.933*
Heterodera juvenile	4.8	8.5	10.2	**7.3**^{ab}	**18.0**^{a}	**3.1**^{b}	0	6.8	8.1	*0.515*	*0.844*	*0.102*
Meloidogyne juvenile	0	0	0.6	**2.4**^{a}	**0**^{b}	**0**^{b}	0	0	0	*0.343*	*0.417*	*0.148*
Tylenchorhynchus	0	0	0	7.3	1.5	30.9	**2.7**^{a}	**163.2**^{b}	**136.2**^{b}	***0.0001***	***0.0002***	***0.002***
Hoplolaimidae	36.0	19.9	70.4	**265.1**^{a}	**44.9**^{b}	**56.2**^{b}	280.0	91.8	118.5	***0.028***	*0.145*	*0.809*
Pratylenchus	57.5	21.3	19.9	**31.6**^{a}	**190.1**^{b}	**95.0**^{b}	13.3	10.2	6.7	***0.024***	*0.458*	*0.163*
Paratylenchus	55.1	32.7	42.7	**323.5**^{a}	**1.5**^{b}	**3.8**^{b}	**64.0**^{a}	**6.8**^{ab}	**5.2**^{b}	***0.022***	***0.0001***	***0.094***
Aphelenchus	7.2	15.6	12.6	2.4	10.5	0.3	2.7	0	2.2	***0.0009***	*0.267*	*0.392*
Aphelenchoides	19.2	1.4	8.4	**19.5**^{ab}	**43.4**^{a}	**6.2**^{b}	18.7	3.4	8.9	*0.645*	*0.998*	***0.075***
Seinura	0	1.4	0.6	0	0	0	0	0	0	*0.152*	*0.541*	*0.632*
Diplogaster	**0**^{a}	**18.5**^{b}	**0**^{a}	0	0	0	0	0	0	***0.001***	***0.002***	***0.0001***
Rhabditidae	55.1	12.8	45.7	9.7	7.5	8.9	21.3	6.8	27.4	*0.381*	*0.190*	*0.477*
Dauerlarvae	2.4	4.3	15.6	4.9	0	0.3	16.0	37.4	54.8	***0.104***	*0.594*	*0.749*
Bunonema	0	0	1.8	0	0	0.3	0	0	0	*0.660*	*0.292*	*0.654*
Panagrolaimus	127.0	75.4	87.8	36.5	40.4	350.3	45.3	176.7	131.1	***0.060***	*0.733*	*0.775*
Cephalobus	112.6	75.4	126.9	31.6	59.9	22.6	136.0	23.8	39.2	***0.049***	*0.809*	*0.462*
Heterocephalobus	12.0	15.6	6.6	0	2.9	5.5	5.3	0	2.2	*0.376*	*0.519*	*0.496*
Euteratocephalus	0	18.5	0	0	0	0	0	0	0	***0.072***	***0.097***	***0.050***
Acrobeles	7.2	5.7	24.0	0	0	0.7	2.7	0	0	***0.001***	*0.405*	*0.432*
Acrobeloides	0	0	0	0	0	0	8.0	0	2.2	*0.168*	*0.632*	*0.779*
Cervidellus	**26.4**^{a}	**0**^{b}	**2.4**^{a}	0	0	0	0	0	0	***0.0001***	***0.013***	***0.002***
Teratocephalus	2.4	0	0	0	0	0	0	0	0	***0.072***	***0.080***	***0.044***
Plectus	31.2	8.5	16.8	0	0	1.4	189.3	132.6	122.2	***0.0001***	*0.909*	*0.936*
Anaplectus	0	0	1.8	24.3	3.0	23.3	2.7	0	2.2	***0.004***	*0.290*	*0.698*
Prismatolaimus	19.2	15.6	24.7	2.4	0	0.3	0	6.8	0.7	***0.0001***	*0.302*	*0.424*
Wilsonema	2.4	0	0	0	0	0	**32.0**^{a}	**0**^{b}	**0**^{b}	***0.0001***	***0.0001***	***0.0001***
Monhystera	16.8	12.8	18.6	9.7	0	2.4	10.7	0	6.7	***0.0004***	*0.306*	*0.492*

Management	F	G	M	F	G	M	F	G	M	*Site*	*Tmt*	*Site*Tmt*
Chromadoridae (Microbial)	0	0	1.8	0	0	0.3	0	0	1.5	*0.940*	*0.266*	*0.985*
Chromadoridae (Predatory)	2.4	0	0	0	0	0	0	0	0	***0.072***	***0.080***	***0.044***
Tripyla	28.8	4.3	10.8	0	1.5	1.7	21.3	51.0	37.0	***0.0002***	*0.214*	*0.747*
Tobrilus	14.4	0	2.4	**0^{a}**	**1.5^{b}**	**0^{a}**	8.0	3.4	19.3	***0.018***	*0.605.*	*0.170*
Dorylaimus	14.4	8.5	8.4	19.5	4.5	20.9	5.3	23.8	15.6	*0.673*	*0.156*	*0.248*
Mesodorylaimus	0	10.0	9.0	**12.2^{a}**	**3.0^{a}**	**17.1^{b}**	**2.7^{a}**	**34.0^{b}**	**45.2^{b}**	***0.047***	***0.0003***	***0.099***
Eudorylaimus	14.4	12.8	35.5	17.0	4.5	5.8	**10.7^{a}**	**34.0^{b}**	**67.4^{b}**	***0.001***	***0.087***	*0.544*
Labronema	0	0	0	0	1.5	1.7	0	0	0	***0.082***	*0.505*	*0.597*
Pungentus	31.2	55.5	58.4	**12.2^{a}**	**3.0^{a}**	**29.8^{b}**	**0^{a}**	**95.2^{b}**	**111.8^{b}**	***0.0001***	***0.0001***	***0.0001***
Aporcelaimus	76.7	28.4	81.2	**19.5^{a}**	**19.5^{a}**	**16.1^{b}**	96.0	54.4	82.9	***0.013***	*0.259*	*0.293*
Xiphinema	**14.4^{a}**	**0^{b}**	**5.4^{ab}**	0	0	0	0	0	0	***0.0001***	***0.071***	***0.032***
Axonchium	0	0	4.8	0	0	0	0	0	0	*0.810*	*0.735*	*0.871*
Doryllium	2.4	1.4	4.2	**0^{a}**	**0^{a}**	**15.8^{b}**	**0^{a}**	**23.8^{b}**	**23.0^{b}**	***0.211***	***0.0002***	***0.011***
Clarkus	26.4	5.7	37.9	0	0	0.3	**53.3^{a}**	**10.2^{b}**	**12.6^{b}**	***0.0001***	*0.602*	*0.203*
Mylonchulus	0	0	0.6	**36.5^{a}**	**0^{b}**	**1.4^{b}**	0	0	0.7	***0.005***	*0.106*	***0.024***
Cobbonchus	0	0	0	**4.9^{a}**	**0^{a}**	**20.9^{b}**	**13.3^{a}**	**6.8^{ab}**	**0.7^{b}**	***0.002***	*0.220*	***0.0004***
Alaimidae	9.6	1.4	7.2	19.5	0	5.5	**32.0^{a}**	**10.2^{ab}**	**6.7^{b}**	***0.026***	***0.039***	*0.138*
Trichodoridae	7.2	0	9.6	0	0	0	0	0	0	***0.007***	*0.329*	*0.330*
Diphtherophora	9.6	0	1.0	0	0	0	0	0	0	***0.099***	*0.565*	*0.669*
Total nematodes	1011.4	578.8	912.5	1053.1	522.4	517.4	1200.0	1176.0	1269.9	***0.003***	*0.290*	*0.403*
SR	6.05	6.54	5.19	**6.05^{a}**	**7.03^{b}**	**6.69^{b}**	5.96	4.43	6.01	***0.037***	*0.200*	*0.686*
J'	0.47	0.36	0.31	0.28	0.24	0.25	0.40	0.28	0.35	***0.0001***	***0.004***	*0.393*
H'	**1.81^{a}**	**1.40^{b}**	**1.20^{b}**	1.09	0.92	0.97	1.55	1.10	1.37	***0.0001***	***0.005***	*0.477*
NCR	0.92	0.93	0.94	**0.86^{a}**	**0.68^{b}**	**0.83^{a}**	0.96	0.94	0.92	***0.0001***	*0.112*	***0.062***
Maturity groups (%)												
CP1	18	19	17	5	9	9	**7^{a}**	**19^{b}**	**17^{b}**	***0.023***	*0.911*	*0.721*
CP2	45	44	39	**52^{a}**	**34^{b}**	**29^{b}**	**48^{a}**	**28^{b}**	**29^{b}**	***0.060***	***0.003***	*0.486*
CP3	17	15	16	**30^{a}**	**49^{b}**	**36^{a}**	27	28	26	***0.008***	*0.412*	*0.859*
CP4	10	15	18	**10^{a}**	**2^{a}**	**19^{b}**	**10^{a}**	**17^{b}**	**19^{b}**	***0.0001***	***0.002***	***0.0004***
CP5	9	7	11	3	5	7	8	8	10	***0.0001***	***0.004***	***0.007***
MI	1.75	1.78	1.91	**0.79^{a}**	**0.87^{a}**	**1.43^{b}**	1.61	1.26	1.74	***0.0001***	***0.001***	*0.141*
PPI	0.73	0.68	0.60	**1.75^{a}**	**1.69^{ab}**	**1.42^{b}**	1.01	0.74	0.85	***0.0001***	*0.118*	*0.860*
Σ MI	2.48	2.46	2.51	**2.54^{a}**	**2.56^{a}**	**2.85^{b}**	2.62	2.00	2.59	*0.196*	***0.008***	*0.849*

^{a,b}*P*-value significant at α=0.1 for treatment effects (for F, G and M using least squares means) in a given soil. The *P*-values given are for the effects of site, treatments (F, G and M) and their interaction.

Mown trial

In the mown areas, where no stock treading had occurred for the preceding three years, soil bulk density was lower than in the grazed paddock (Table 2). Earthworm abundance and total faunal biomass were high in the mown areas (Fig. 3). Earthworms and mesofauna tended to be more similar between the mown areas and grazed paddocks than the fence lines (Tables 3 and 4). Plant feeding and plant associated nematodes showed a similar response (Table 6). In contrast, larger nematodes (i.e., *Pungentus, Mesodorylaimus* and *Aporcelaimus*) were more similar between the mown areas and fence lines, tending to be more abundant under the mown areas.

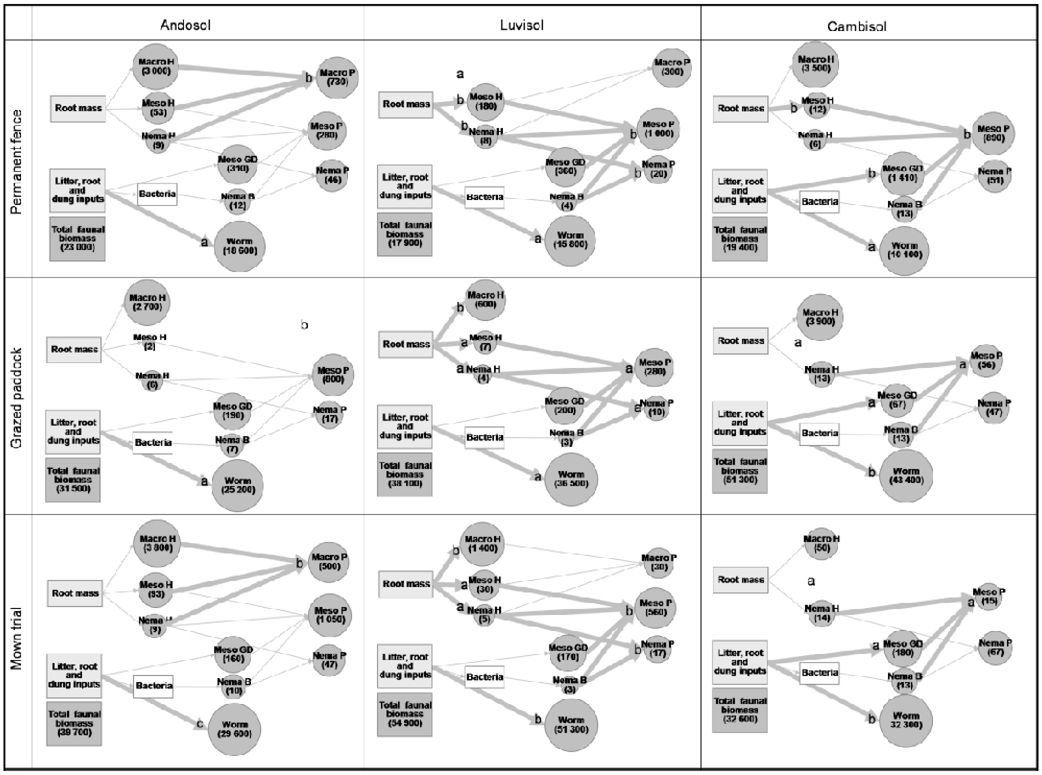

Fig. 3. Food webs of selected soil faunal groups under different pasture management regimes, New Zealand. Food web and calculations after Hunt (1987) and Mulder et al. (2005). Resource inputs are given in mg dry weight/m^2. Macrofauna (Macro), mesofauna (Meso) and nematode (Nema) herbivores (H) feed on plant material. Earthworms (Worm), mesofauna general detritivores (GD) and nematode bacterial feeders (B) feed on detrital inputs and associated microflora. The macrofauna, mesofauna and nematodes are in turn consumed by predators (P). Circle areas represent the log biomass of the fauna, actual biomass (dry weight mg/m^2) given in parenthesis. Biomass calculated as described in Chapter 1. Trophic groups with biomass <1.5 mg dry weight/m^2 were excluded. Results for the mown trial are means of the four fertiliser treatments. Wide arrow and $^{a,\ b}$ given in the arrow head indicate significant difference at α=0.05 within the functional group to which the arrows lead.

Table 7. Soil invertebrates in which there was a significant fertiliser effect in the mown area under different combinations of N and P fertiliser, N. Z. (2007). Low P, low N (LPLN); low P, high N (LPHN); high P, low N (HPLN); high P, high N (HPHN). For differences between the sites and details of amounts of fertiliser refer to Table 1.

Soil	Andosol				Luvisol				Cambisol				*P-value*	
Management$^{\#}$	LPLN	LPHN	HPLN	HPHN	LPLN	LPHN	HPLN	HPHN	LPLN	LPHN	HPLN	HPHN	*Fertiliser*	*Site* Fertiliser*
MACROFAUNA														
Octolasion cyaneum	53	0	0	0	0	0	0	0	**132**^{a}	**0**^{b}	**79**^{a}	**53**^{a}	***0.001***	***0.001***
Click beetle larvae	53	53	0	0	26	0	0	0	0	0	0	0	***0.001***	***0.004***
MESOFAUNA														
Hemiptera	146	0	828	255	64	255	64	64	0	0	0	0	*0.977*	***0.057***
Thysanoptera	**7930**^{b}	**255**^{a}	**14451**^{b}	**14260**^{b}	5539	955	891	955	64	64	0	0	***0.075***	***0.058***
Chilopoda	218	0	127	64	64	64	573	318	0	0	0	0	*0.160*	***0.094***
Oribatida														
Tectocepheus velatus sarekensis	**0**^{a}	**637**^{b}	**2101**^{c}	**0**^{a}	0	0	0	0	0	0	0	0	***0.004***	***0.001***
Nymphs	**509**^{a}	**1655**^{ab}	**6239**^{b}	**2228**^{b}	1210	0	64	64	446	1019	637	255	*0.950*	***0.097***
NEMATODA													*0.313*	***0.022***
Cephalenchus	8079	7663	3506	10067	1634	2768	10605	8561	**7046**^{a}	**0**^{b}	**0**^{b}	**10481**^{a}	***0.045***	*0.843*
Heterodera juveniles	18177	4790	10517	0	8168	0	6060	0	17614	2938	10166	4192	*0.114*	***0.081***
Aphelenchus	**14138**^{a}	**958**^{b}	**31551**^{c}	**13423**^{a}	0	0	0	1427	0	2938	6777	0	*0.730*	***0.087***
Bunonema	**0**^{a}	**957**^{a}	**7011**^{b}	**0**^{a}	1633	0	0	0	0	0	0	0	*0.171*	***0.001***
Plectus	20197	3832	31551	16779	**6535**^{a}	**0**^{b}	**0**^{b}	**0**^{b}	151482	132212	145714	71270	***0.006***	*0.172*
Prismatolaimus	**2020**^{a}	**19159**^{b}	**28045**^{b}	**40269**^{b}	1634	0	0	0	0	0	3389	0	*0.114*	***0.003***
Tripyla	14138	3832	24539	0	**6535**^{a}	**0**^{b}	**0**^{b}	**1427**^{b}	49320	38195	40664	23058	***0.038***	*0.277*
Dorylaimus	**14138**^{a}	**0**^{b}	**14023**^{a}	**10067**^{a}	14703	20301	34846	9988	31706	11752	16943	6289	*0.261*	***0.064***
Eudorylaimus	4039	6705	28045	6712	13069	3691	3030	0	56365	64637	44053	46116	*0.603*	***0.016***
Clarkus	14138	13411	28045	114096	0	923	0	0	**3523**^{a}	**26442**^{b}	**23721**^{b}	**0**^{a}	*0.289*	***0.008***
Diphtherophora	0^{a}	0^{a}	0^{a}	6712^{b}	0	0	0	0	0	0	0	0	***0.002***	***0.001***

^{a,b}*P*-value significant at α=0.1 for fertiliser effects (least squares means).

The *P*-values given are for the effects of fertiliser (different combinations of N and P) and their interaction.

The fertiliser treatments controlled some site properties, with Olsen P being higher under high P treatments (Table 2) and the percentage of clover being lower under high N treatments (Table 1) in all three soils. Pasture growth was at least 40–50% higher under the high fertility treatments in comparison to the low fertility treatments in the three soils.

There were some responses of soil invertebrate populations to fertiliser treatments. All invertebrates showing a significant fertiliser or fertiliser x site interaction are given in Table 7. Only the nematodes, *Heterodera, Plectus* and *Tripyla*, showed a consistent response to fertiliser independent of site. The clover cyst nematode, *Heterodera trifolii*, was more abundant under low N pastures where white clover (*Trifolium repens*) was more abundant (Table 7). Here bacterial feeding *Plectus* and predatory *Tripyla* were more abundant too.

Other invertebrates showed significant interactions between fertiliser treatments and site location (Table 7). Oribatid nymphs were low in abundance under low P, low N treatments in the Andosol. In the low P, high N treatment, *Octolasion cyaneum* in the Cambisol, and Thysanoptera and *Dorylaimus* in the Andosol were low in abundance.

Discussion

Several soil invertebrates were sensitive to stock treading and associated compaction. Of the three soils, the Luvisol is most susceptible to stock treading pressure and has a lower plastic limit (Table 1) (Hewitt and Shepherd, 1997), and the largest decline in bulk density. Closer examination of the Luvisol porosity using resin impregnation, found fewer pores of all sizes, particularly pores <2 mm diameter, in the grazed paddock compared to under the fence line (Fig. 2). This represents a loss of potential habitable pores for the soil mesofauna and microfauna, with body widths <2mm (Swift et al., 1979). Correspondingly, the biomass of mesofauna, predatory nematodes and macrofauna were low in the grazed paddocks (Fig. 3).

Dorylaimus and *Aporcelaimus,* with body widths ~70µm, were less abundant in grazed paddocks in this study in comparison to the fence line where nematode diversity was higher. Bouwman and Arts (2000) also observed that larger nematodes were sensitive to compaction. Reflecting their shorter life cycles, nematodes can respond faster to disturbances than larger invertebrates (Wardle, 2002) and hence were more resilient under mowing in comparison with other invertebrates sensitive to stock treading. Large, predatory and omnivorous nematodes increased in biomass from the grazed paddock to the mown area, reaching biomasses similar to those found under the fence line (Fig. 4), even though this was not directly comparable due to the different irrigation and fertiliser regimes. These large nematodes tend to be longer lived and underpin the maturity of the nematode assemblage. The maturity was lowest under grazing in the Cambisol (MI, ΣMI, Table 6) but not in the other soils. The maturity was higher under mown pastures in all soils. Plant feeding and plant associated nematodes which tend to respond positively to increased productivity (Yeates, 1980), were more abundant under the fence lines (high PPI, Table 5). Increased frequency of defoliation under the fence line in the Andosol and Luvisols (i.e., grazed each time the paddock on either side was grazed) may have stimulated root turnover (Barker et al., unpublished 1998), even though an increased frequency of defoliation was not found to increase root mass (McIvor and Smith, 1973; Matthew et al., 1991).

Oribatida, have been observed to be particularly sensitive to physical disturbances (Clapperton et al., 2002; Cole et al., 2008; Schon et al., 2008), and this is supported in this study with their low abundance in grazed paddocks and high abundance and diversity under fence lines. Oribatida, which are relatively long lived (Norton, 1994), showed little recovery. However, many oribatid species (particularly with body widths >175 μm) which were not found in the grazed paddock were detected in low abundances in the mown area (Table 5). This suggests that recovery of Oribatida populations can take longer than three years. Behan-Pelletier (1999) suspected it may take 4–7 years. Earthworm burrowing may also disturb the physical habitat for Oribatida and slow their population recovery (Maraun et al., 2001). This effect is consistent with Oribatida recovery in the mown area being highest in the Andosol where earthworm abundance was lowest.

In contrast to the impact of removing treading pressure and summer moisture stress, there was little effect of the different combinations of N and P fertiliser on soil invertebrates. Three nematode taxa showed consistent responses to N fertiliser application across the three sites, with the clover cyst nematode (*H. trifolii)* as well as predatory *Tripyla* and bacterial feeding *Plectus* less abundant under low N, where the proportion of clover was higher. The effect on earthworms may be due to the fact that samples were taken from the periphery of treatment areas. That few significant effects of fertiliser were observed in mesofauna and nematodes across the three sites was surprising as not only did pasture composition (i.e., legume content) differ between the low and high N treatments, but pasture productivity increased by at least 40% between the low and high N treatments. The poor response to increasing pasture production and associated litter suggests that even at the low P, low N treatment, there was sufficient food resources available to the soil invertebrates. It is calculated (as described in Appendix 1) from Parsons et al. (1983) that there is at least 15 000 kg DM/ha plant litter (not including litter returns from mowing) potentially entering the soil food web under the lowest fertiliser applications. Further, it may have been an increase in predatory and omnivorous nematodes, as more food became available, which caused the top down regulation of other nematodes, and inhibited a response to fertiliser (Wardle et al., 1998).

Earthworms, as ecosystem engineers, appeared resistant to stock treading in all three locations, with the quality and quantity of food resources presumably more important than negative effects of treading. Under the fence line, where earthworm abundance and biomass was low, but richness high (Fig. 4), food resources were of lower quality (higher soil C:N ratio) than the grazed paddock. Further, increased frequency of defoliation under the fence line may have suppressed litter potentially entering the soil food web as more herbage was removed by ruminant herbivores.

Reduced moisture stress in the mown and irrigated area may have extended earthworm activity (Fraser and Piercy, 1996; Edwards, 2004). Increased earthworm activity and root growth restored soil structure (Greenwood and McKenzie, 2001) to levels similar to under the fence line after three years. In another study on an Andosol (Chapter 1) the replacement of stock treading with mowing alone was observed to have little effect on the soil fauna, suggesting that irrigation was an important component in this study. The recovery of soil invertebrates appears to be driven by the removal of stock treading in combination with irrigation, rather than the influence of N and P fertiliser, and was consistent across the range of soil types and climatic regions.

Conclusion

Stock treading resulted in soil compaction in all three soils. Oribatida, large nematodes and macrofauna predators were sensitive to stock treading, while ecosystem engineering earthworms were resistant. Large predatory and omnivorous nematodes were resilient to stock treading and may have regulated the response of other nematodes to fertiliser. Oribatid recovery was slow, and their recovery may have been inhibited by earthworm burrowing. That only *Heterodera*, *Tripyla* and *Plectus* were significantly affected by combinations of N and P fertiliser suggests that food was not limiting soil fauna activity under any fertiliser combination.

The vulnerability of soil invertebrates to stock treading was consistent at all three sites. This suggests that organism characteristics (i.e., life history and ability to move through the soil) and trophic interactions may be more important than a soils susceptibility to compaction in structuring the biological community.

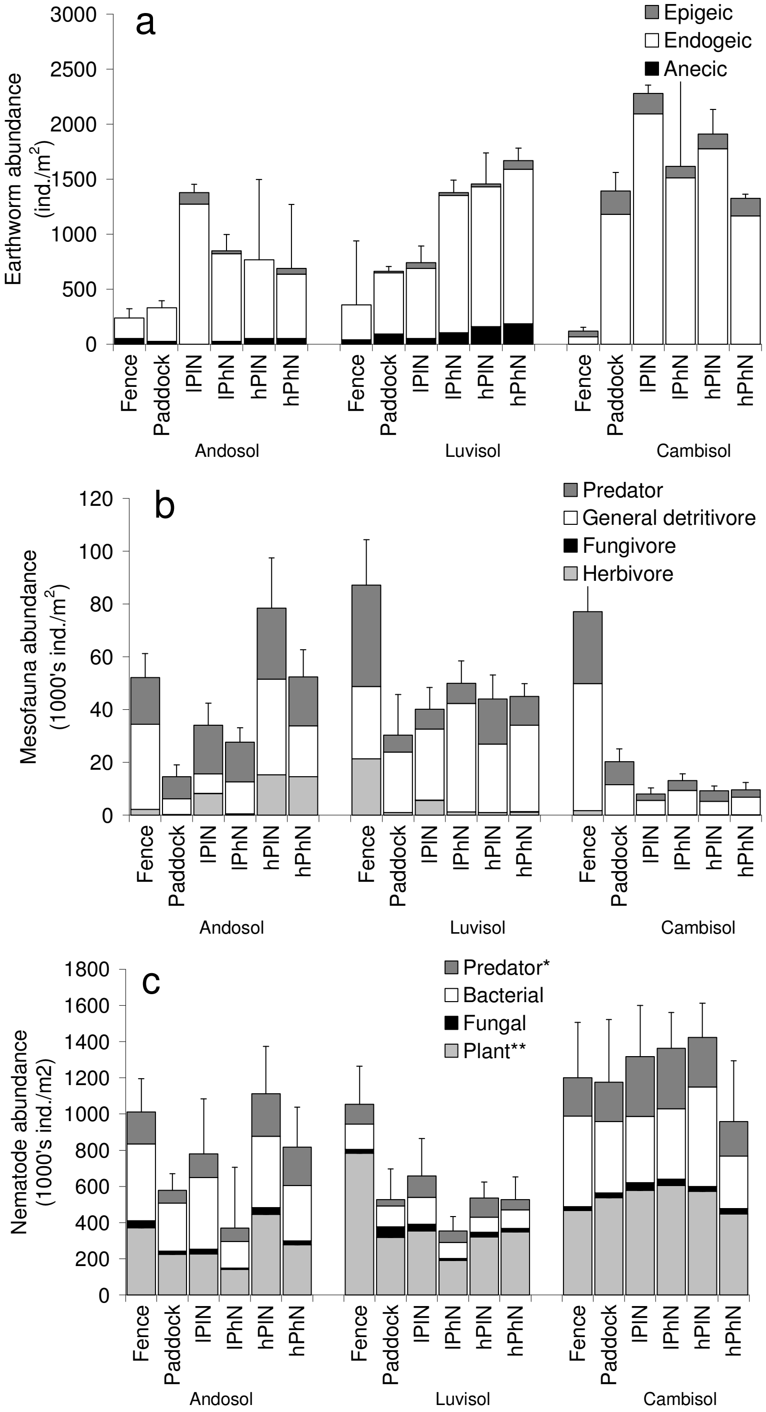

Fig. 4. Abundance of (a) earthworms, (b) mesofauna and (c) nematodes in functional groups in pastures under different management. Treatments include: permanent fence line (F), grazed paddock (P), and mown area fertiliser treatments low P low N (lPlN), low P high N (lPhN), high P low N (hPlN) and high P high N (hPhN).

*Predacious and omnivorous nematodes, ** Plant feeding and plant associated nematodes.

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Chapter Seven:

Influence of phosphorus inputs and sheep treading pressures on soil macrofauna and mesofauna in hill pastures on an Andosol and a Luvisol

This study tests the hypothesis that there would be some consistent responses by the soil fauna to pastoral management, by exploring the invertebrate responses to pastoral intensification in two different sheep grazed pastures.

N.L. Schon, A.D. Mackay, M.A. Minor. Influence of phosphorus inputs and sheep treading pressures on soil macrofauna and mesofauna in hill pastures on an Andosol and a Luvisol.

Abstract

Increases in pastoral productivity should not affect the long term sustainability of agricultural systems. Soil invertebrates (macrofauna and mesofauna) influence soil processes. On a Luvisol, with increasing inputs of phosphorus fertiliser and sheep stocking rates, earthworm abundance increased and Oribatid abundance decreased. To determine if these responses to intensification were consistent across contrasting soil types a comparison was conducted by collecting samples from two long term sheep grazed pastures on an Andosol. A low intensity pasture received 10 kg P/ha/yr and was stocked with sheep at 11.8 su/ha; a high intensity pasture received 50 kg P/ha/yr and was stocked with sheep at 17.0su/ha.

Epigeic and endogeic earthworm abundance increased (417 vs. 649 ind./m^2) with increased intensification of management in the Andosol. In contrast, Oribatida abundance declined (25.1 $x10^3$ vs. 17.1 $x10^3$ ind./m^2). Both these observations were consistent with those on the Luvisol (Cohen's *d* -0.661 for epigeic earthworms, -0.806 for endogeic earthworms and 0.695 for Oribatida). Oribatida decline was associated with a loss of habitable pores (pores <1 mm diameter). The two smallest oribatid species, *Microppia minus* and *Ramusella* sp., were more abundant under the high than low sheep stocking rate in the current study. Changes in other soil invertebrates, including Collembola and Mesostigmata, were not predictable between the two soils, possibly reflecting these organisms' different life histories and ability to respond quickly to short term changes in the environmental conditions. While these trends in invertebrate abundances may reflect site disturbance, they provide little insight into the long term effects on soil services. Higher earthworm abundances in the Andosol may explain the improved soil structure, with more pores of 1–3 mm diameter. This was not observed in the Luvisol. Potential litter incorporation rates would have been enhanced by the higher earthworm abundances, potentially ensuring sustained levels of soil carbon under the higher sheep stocking rates on the Andosol.

Invertebrates that show predictable responses to management practices, when linked to soil services, form the potential basis of a biological indicator for land managers. Even though the herbivorous macrofauna did not behave predictably across the two soils, their activity, which can have large consequences on plant growth and livestock carrying capacity, needs to be included in a biological indicator.

Introduction

New Zealand hill country pastures are more suitable for sheep farming than for intensive cattle grazing. Continued viability and profitability of sheep farming has only been maintained through ongoing increases in per hectare production, facilitated by a combination of increased stocking rates and animal performance. The increased demands for animal feed have largely been met through increased phosphorus (P) fertiliser inputs to stimulate pasture and legume growth. These trends are likely to continue into the foreseeable future, raising concerns about the ability of the pastoral soils to 'cope' with intensification and continue to provide important services.

Changes in the physical and chemical soil environment associated with increasing fertiliser applications and stocking rates influence soil fauna. As soil fertility and pasture productivity increase, the abundance of earthworms has the potential to increase as more food becomes available within the soil food web (Curry et al., 2008). As stock treading pressures increase, soils may become compacted (Greenwood and McKenzie, 2001), limiting habitable pore space for soil biota (Elliott et al., 1980). Soil inhabiting earthworms are capable of burrowing and increasing habitable pores (Lee and Foster, 1991). However, mesofauna with body widths 0.1–2 mm may be negatively influenced by compaction (Cole et al., 2008). Further, as physical disturbance and the rate of nutrient cycling increase, there is a tendency for shifts in organism life histories towards those with shorter generation times (Siepel, 1994; Ruf, 1998).

Schon et al. (2008) found higher earthworm abundance, lower mesofauna abundance, and a shift to smaller Oribatida with increasing sheep stocking rates and P fertiliser application in a Luvisol, typical of large areas of hill country in New Zealand. Volcanic soils also make up significant areas of New Zealand north island hill country. To test if the trends observed by Schon et al. (2008) were consistent in these volcanic soils as part of a larger study developing an invertebrate based biological indicator for pastoral soils, a long term sheep grazed trial on an Andosol was sampled. We explored the response of the macro- and mesofauna to intensification and expected that an increase in P fertiliser application and sheep stocking rate would result in increases in earthworm abundance but decreases in Oribatida.

Methods

Study sites

The present study was carried out at the AgResearch Hill Country Research Station (altitude 45–370 m), Whatawhata, Waikato region, New Zealand (37°48'S 175°05'E). The soil is classified as an Andosol (FAO, 1988) (NZSC: Allophanic, Dunmore silt loam) (Hewitt, 1993). The sheep grazed trial, which examined the influence of increasing single superphosphate fertiliser application, had been running since 1980. Two treatments were sampled, which are summarised in Table 1. The low intensity pasture had 10 kg P/ha applied annually, and was stocked with sheep at 11.8 su/ha; the high intensity pasture received 50 kg P/ha/yr and was stocked at 17.0 su/ha. No nitrogen fertiliser was applied. Treatments were operated as unreplicated, separate farmlets. Average annual rainfall was 1630 mm and average air temperature was 13ºC. Soil samples were collected from 0–12° slopes on north-west aspects in August 2007 (Southern Hemisphere winter).

Table 1. Treatment properties in sheep grazed hill country pasture on an Andosol, at Whatawhata, New Zealand (2008).

Management intensity	Low	High
Inputs		
Phosphorus as superphosphate (kg P/ha/yr)	10	50
Pasture parameters (1000's kg DM/ha/yr)		
Pasture intake[1]	6.5	9.4
Pasture production[2]	8.7	12.5
DM from litter [3]	5.8	10.8
DM from dung [4]	2.2	3.2
DM from roots [3]	2.0	4.0
Total DM	10.0	18.0
Livestock (sheep)		
Stocking rate (stock unit/ha)[5]	11.8	17.0
Live weight (kg/ha)[5]	650	935

[1] Pasture intake measured from cages from 2002–2003 (I. Power, pers. comm.).

[2] Calculated from: Pasture intake: 0.75x pasture production.

[3] Calculated from Parsons et al. (1983).

[4] 0.35x animal intake (Takahashi et al., 2007). Dung input on low slopes is higher than on medium and steep slopes (Saggar et al., 1990).

[5] Standard sheep consumes 550 kg DM/yr and has a live weight of 55 kg (www.maf.govt.nz) with associated treading pressure of 65 kPa (Greenwood and McKenzie, 2001).

The previously reported study (Schon et al., 2008) was located at AgResearch Hill Country Research Station (altitude 45–370 m), Ballantrae, Manawatu region, New Zealand (40°18'S 175°50'E). The soil is classified as a Luvisol soil, a sedimentary soil with some non allophanic Andosol. The two treatments sampled had either received no

P fertiliser or 45 kg P/ha/yr since 1981, were grazed by sheep at 9 and 16 su/ha, and had 4400 and 9200 kg DM/ha/yr pasture growth, respectively. Average annual rainfall was 1270 mm and average air temperature was 12ºC (Schon et al., 2008).

Soil biological sampling

Eight macrofauna cores (15.5 cm ø, 0–15.5 cm deep) and eight mesofauna cores (5 cm ø, 0–7.5 cm deep) were collected from two paddocks in each farmlet. Macrofauna were hand sorted (Wimbledon et al., 1996), mesofauna were extracted in a modified Berlese-Tullgren extractor as described by Schon et al. (2008). The Shannon-Wiener diversity index (H'), Margalef's richness (SR) and Pielou's evenness (J') were calculated to describe the diversity of soil fauna (Yeates, 1984; Ludwig and Reynolds, 1988).

Soil microbial biomass was measured by substrate induced respiration. Two composite samples (20 cores, each 2.5 cm ø, 0–7.5 cm deep) were collected from two paddocks in each farmlet. Samples were sieved to <2 mm and the amount of CO_2 respired in two hours was estimated by collecting 25 ml gas in a syringe and empting into a preevacuated Exetainer® (for methodology refer to Chapter 1).

Soil and pasture sampling

Soil temperature (Checktemp, Hanna Instruments, England) and moisture (TDR 300 Soil Moisture Probe, Spectrum Technologies, Inc., USA) at 0–10 cm depth were recorded in the field at the time of sampling.

After extraction the mesofauna cores were analysed for soil chemistry: pH (1:2.25 soil:water), Olsen P (Olsen et al., 1954), total nitrogen and total carbon (dry combustion using LECO-2000, LECO Equipment Corp., St. Joseph, MI). Bulk density was determined by collecting three intact soil cores (10 cm ø, 0–7.5 cm deep) from each farmlet, drying (105ºC) and weighing.

Pasture samples were collected using a 'trim' method (Piggot, 1989) and pasture species identified. Root biomass was determined by collecting two composite soil samples (20 cores each 2.5 cm ø, 7.5 cm deep) from two paddocks in each farmlet. Samples were crumbled and then washed until soil was removed in a hydropneumatic root washer. Samples were towel dried. Roots and tillers were separated, dried at 60ºC and weighed.

Pore size distribution for pores <60 µm ø was determined using tension plates (see Chapter 1). Soil from each treatment was sieved (<2 mm) and saturated. Tensions of 10, 50, and 1500 kPa equated to pore sizes of 30, 6, and 0.2 µm ø, respectively. Larger pores were characterised using cores impregnated with a fluorescent resin. Two 15 cm ø cores were collected from each paddock in each farmlet in 2009 when soil moisture was <40%. The cores were impregnated with a fluorescent resin, and images of horizontal soil sections at 2.5 and 5 cm depths were analysed using Solicon© analysis software (The University of Sydney, Cotton Research and Development Corporation) (Vervoort and Cattle, 2003).

Statistical analysis

To test the hypothesis that there was no significant effect of management intensity on the abundance of macrofauna and mesofauna the data were log (x+1) transformed and analysed using PROC MIXED in SAS v.9.1 (SAS Institute Inc., USA), using Satterthwaite degrees of freedom. The graphs and tables show untransformed arithmetic means. Error bars on figures show the standard errors of the means.

Even though the treatments on the Andosol are not replicated, we believe that the differences between treatments can be with confidence attributed to the differences in management, since the trial was set up over 25 years previously on similar soils and slopes. Large scale experiments such as this one can be difficult to replicate, but with caution statistics can still be used (Oksanen, 2001). Due to low replication a significance level of α=0.1 was chosen.

A comparison (meta analysis) was conducted in SAS v.9.1 using the present study and the data published by Schon et al. (2008). Effect size was calculated using Cohen's *d,* which is the difference between means divided by the standard deviation (Cohen, 1988). Earthworm and mesofauna data were examined for a consistent trend with increased fertiliser application and sheep stocking rates.

Results

Soil and pasture properties

While there was a tendency for a higher Olsen P, soil total N and total C under higher phosphorus applications on the Andosol, these differences were not significant

(Table 2). Pasture production (and calculated dry matter entering the soil as litter) was higher under high P applications. The low and high intensity pastures on the Andosol contained different proportions of *Lolium perenne* (ryegrass, 20% vs. 40%, respectively) and *Agrostis capillaris* (browntop, 17% vs. 10%, respectively). Both pastures contained <2% *Trifolium repens* (white clover).

In the sieved Andosol soil, both treatments had the same percentage of pores 0.2–30 µm ø, but pores 6–30 µm ø were reduced under the higher stocking rate (Table 2). Intact cores of Andosol soil embedded with resin showed little difference in porosity between the two treatments at both 2.5 and 5 cm depths (Fig. 1). Most pores <1 mm ø were in the range of 200–400µm.

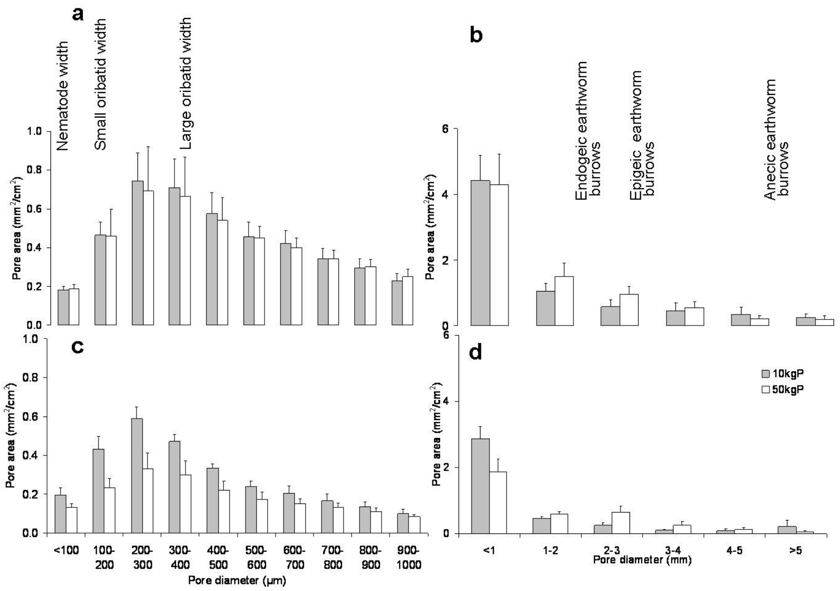

Fig. 1. Pore areas (mm^2/cm^2) over a range of pore sizes in an Andosol under two sheep grazed pastures with differing management intensities at Whatawhata, N.Z., estimated from undisturbed resin embedded cores. (a) Pores <1 mm ø at 2.5 cm depth. (b) All pores (<1 to >5 mm ø) at 2.5 cm depth; the <1 mm bar is the sum of pores shown in (a). (c) Pores <1 mm at 5 cm depth. (d) All pores (<1 to >5 mm ø) at 5 cm depth; the <1 mm bar is the sum of pores shown in (c).

Soil fauna

The total earthworm abundance in the Andosol tended to increase with intensification (417 vs. 649 ind./m^2, Table 3, Fig. 3, P=0.132). Only two earthworm species, *Aporrectodea caliginosa* and *Lumbricus rubellus,* were observed. No anecic species were detected. Among other macrofauna, the root feeding *Costelytra zealandica* larvae (grass grub) were not detected under low P applications but had a high abundance and biomass under high P applications (106 ind./m^2 and 10.5 g/m^2, P=0.061). Grass grub was the only non earthworm macrofauna detected under the higher stocking rate, resulting in low macrofauna richness there.

Total mesofauna abundance in the Andosol was lower under the high stocking rate (63 x10^3 vs. 30 x10^3 ind./m^2, Table 4, P=0.012), where Acari (particularly Oribatida and Mesostigmata), Collembola (particularly Poduromorpha) and herbivorous Thysanoptera (P=0.016) were less abundant (Table 4 and Fig. 3). Only eight oribatid species were observed in the Andosol. Due to the high abundance of New Zealand endemic *Setobates scheloribatoides*, only ~10% of Oribatida were cosmopolitan, a much lower percentage than what was reported for the Luvisol by Schon et al.(2008), where nearly all Oribatida were cosmopolitan. The abundance of the herbifungivores oribatid *S. Scheloribatoides* was reduced by 40% under the high stocking rate (Table 4, Fig. 3). Only 13% of Oribatida fell in the smallest body width class (<175 μm) at the low stocking rate. This percentage was nearly twice as high under the high stocking rate (25%).

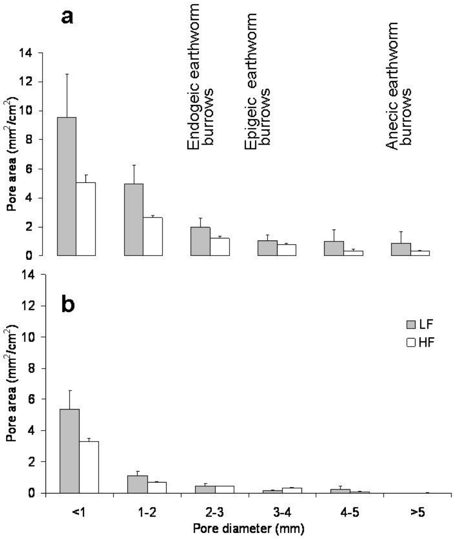

Fig. 2. Pore areas (mm^2/cm^2) over a range of pore sizes in an Luvisol under two sheep grazed pastures with differing management intensities at Ballantrae, N.Z., estimated from undisturbed resin embedded cores. (a) Pores <1 to >5 mm ø at 2.5 cm depth. (b) Pores <1 to >5 mm ø at 5 cm depth. Note that the scales on the y-axes differ from those in Fig. 1.

Andosol vs. Luvisol

Comparison of the current data from an Andosol with the earlier study by Schon et al. (2008) on a Luvisol shows some large effect sizes, as measured by Cohen's *d* (Table 5). Consistent responses in earthworms and Oribatida to intensification were seen. Earthworms, including both endogeic and epigeic earthworms, increased with higher P inputs and higher sheep stocking rates in both soils. In contrast, Oribatida abundance decreased with intensification in both soils, with the proportion of fungivorous and small (body widths <175 μm) oribatids increasing as pore size decreased (Fig. 1 and 2). Collembola and Mesostigmata showed no consistent trend with intensification in the two soils. We should point out that the two soils were located in different regions in the North Island of New Zealand, with the northern Andosol under a higher rainfall and warmer temperature regime than the Luvisol.

Table 2. Soil and herbage properties in two sheep grazed hill country pastures in New Zealand. At Whatawhata (Andosol soils with silt loam texture) low intensity pasture received 10 kg P/ha/yr and high intensity pasture received 50 kg P/ha/yr. At Ballantrae (Luvisols with silt loam texture) low intensity pasture received no fertiliser and high intensity pastures received 45 kg P/ha/yr. *P*-values are for the differences between low and high intensity at Whatawhata.

Soil type	Andosol			Luvisol	
	Whatawhata (2007)			Ballantrae (2006)[1]	
Management intensity	Low	High	*P*-value	Low	High
Soil moisture (%)[2]	50	52	*0.574*	44	44
Soil temperature (ºC)[2]	10.7	10.6	*0.293*	13.9	13.6
Bulk density (Mg/m^3)[3]	0.76	0.71	*0.746*	0.79	0.89
Porosity (% v/v of sieved soil) (0–7.5 cm)					
0.2–6 μm*	10	14	*0.200*	30	18
6–30 μm*	17	13	***0.019***	**46**	**25**
Porosity (intact cores from 2.5 cm depth)					
Porosity (%)	7	8	*0.819*	19	10
Mean pore area (mm^2)	3.3	2.8	*0.648*	3.6	3.3
Pores that fit <175 μm16-sided polygon (%)	17	16	*0.823*	12	14
Pores that fit >350 μm16-sided polygon (%)	54	58	*0.750*	65	63
Porosity (intact cores from 5 cm depth)					
Porosity (%)	4	4	*0.796*	7	5
Mean pore area (mm^2)	3.3	2.8	*0.829*	1.4	1.8
Pores that fit <175 μm16-sided polygon (%)	24	17	*0.160*	22	23
Pores that fit >350 μm16-sided polygon (%)	43	58	*0.117*	45	46
Microbial biomass (μg C/g soil)[2]	1027	1046	*0.885*	–	–
pH[3]	5.1	5.3	*0.568*	5.3	5.4
Olsen P (mg/L)[3]	26	87	*0.210*	8	82
Total N (%)[3]	0.77	1.04	*0.266*	0.49	0.52
Total C (%)[3]	8.6	11.5	*0.239*	6.1	5.9
C:N ratio[3]	11.1	11.1	*0.805*	12.6	11.3
HERBAGE COMPOSITION (%)					
Grass	74	60	*0.658*	67	77
Legume	2	1	*0.912*	3	4
Other (including weeds)	0	1	***0.001***	**1**	**4**
Dead matter	24	38	*0.658*	29	15
Root mass (g dry wt/m^2)[2]	193	148	*0.86*	–	–

[1] From Schon et al. (2008), Parfitt et al. (2009) and unpublished data.

[2] 0–10 cm depth.

[3] 0–7.5 cm depth.

*Pores 0.2–6 μm ø retain mostly plant unavailable water and exclude most microorganisms, with no predation on bacteria. Pores 6–30 μm ø retain mostly plant available water and accommodate most bacteria and their predators (Brewer, 1964).

Table 3. Mean populations of earthworms and other macrofauna at 0–15 cm soil depth in low and high intensity sheep grazed hill country pastures on an Andosol, Whatawhata, N.Z. (2007). Diversity and percentage in functional groups included.

Management intensity	Low	High	*P-value*
EARTHWORMS (ind./m^2)			
Lumbricus rubellus (Hoffmeister, 1843)	73	132	*0.754*
Aporrectodea caliginosa (Savigny, 1826)	344	517	*0.145*
Total earthworms	417	649	*0.132*
Earthworm biomass (g wet wt/m^2)	161	189	*0.702*
SR	0.63	0.45	*1.0*
J'	0.59	0.57	*0.950*
H'	0.41	0.40	*0.955*
OTHER MACROFAUNA (ind./m^2)			
Costelytra zealandica (White, 1846) larvae (Scarabaeidae, Coleoptera)	0	106	***0.061***
Click beetle larvae (Elateridae, Coleoptera)	26	0	*1.0*
Weevils (Circulionidae, Coleoptera)	33	0	*0.406*
Coleoptera (adult)	13	0	*0.149*
Diptera larvae	20	0	*0.364*
Total macrofauna	93	106	*0.109*
Macrofauna biomass (g wet wt/m^2)	11	10	*0.206*
SR	1.44	0	*0.410*
J'	0.18	0	*0.270*
H'	0.29	0	*0.270*

Table 4. Mean populations of Oribatida and other mesofauna (0–7.5 cm soil depth) in low and high intensity sheep grazed hill country pastures on an Andosol, Whatawhata, N.Z. (2007).

Management intensity	Low	High	*P-value*
MESOFAUNA (1000's ind./m^2)			
Platynothrus peltifer (Koch, 1839)	1.5	0.4	*0.821*
Metabelba obtusus (Hammer, 1966)	0.6	0.2	*0.865*
Microppia minus (Paoli, 1908)	0	0.1	*0.334*
Ramusella sp.	2.4	2.7	*0.221*
Minunthozetes semirufus (Koch, 1841)	0.1	0	*0.334*
Galumna rugosa (Hammer, 1968)	0.9	0.8	*0.985*
Setobates scheloribatoides (Ramsay, 1966)	11.3	4.5	*0.423*
Eupelops sp.	2.8	2.4	*0.952*
Nymphs	5.7	6.0	*0.229*
Oribatida (adult)	19.5	11.1	*0.215*
Total Oribatida	25.1	17.1	*0.346*
Mesostigmata	15.8	8.7	*0.491*
Prostigmata	0.4	0.3	*0.169*
Scutacaridae	0.1	0.4	*0.252*
Total Acari	35.8	20.8	*0.247*
Entomobryomorpha	3.2	4.5	*0.213*
Poduromorpha	4.3	0.7	*0.299*
Sminthuridae	0.8	0.6	*0.676*
Neelipleona	0.2	0.3	*0.974*
Total Collembola	8.5	6.0	*0.481*
Diplura	0.1	0.2	*0.911*
Protura	0	0.1	*0.334*
Coleoptera	0.4	0.2	*0.582*
Diptera	0.4	0.8	*0.343*
Thysanoptera	17.9	1.7	***0.016***
Isopoda	0	0.1	*0.334*
Symphyla	0	0.4	***0.020***
Total mesofauna	63.0	30.2	***0.012***
SR	3.43	4.20	*0.293*
J'	0.37	0.45	***0.084***
H'	1.04	1.28	***0.075***

Table 5. Comparison between Andosol and Luvisol at Whatawhata (this study) and Ballantrae (Schon et al., 2008), using Cohen's *d* as a measure of mean effect size. The analysis compares the response of macro- and mesofauna to two levels of management intensities at these two sites. Strong positive effects (**bold**) indicate consistent trends between the two sites. Medium effect sizes (*italics*) indicate similar trends observed between the two sites.

	Mean effect size (Cohen's *d*)	Standard deviation
Total earthworms	**-0.864**	-0.055
Epigeic	*-0.661*	0.089
Endogeic	**-0.806**	0.034
Anecic	-0.137	0.091
Total mesofauna	*0.660*	0.121
Oribatida	*0.695*	0.200
Trophic groups (%)		
Fungivore	*-0.522*	0.097
Herbivore	**1.138**	0.553
Herbifungivore	0.375	0.107
Omnivore	*0.568*	0.161
Body widths (%)		
<175 µm	*-0.643*	0.142
175–350 µm	0.330	0.153
>350 µm	*0.589*	0.444
Mesostigmata	0.035	0.403
Total Acari	*0.527*	0.021
Total Collembola	0.021	0.201
Thysanoptera	0.483	0.582

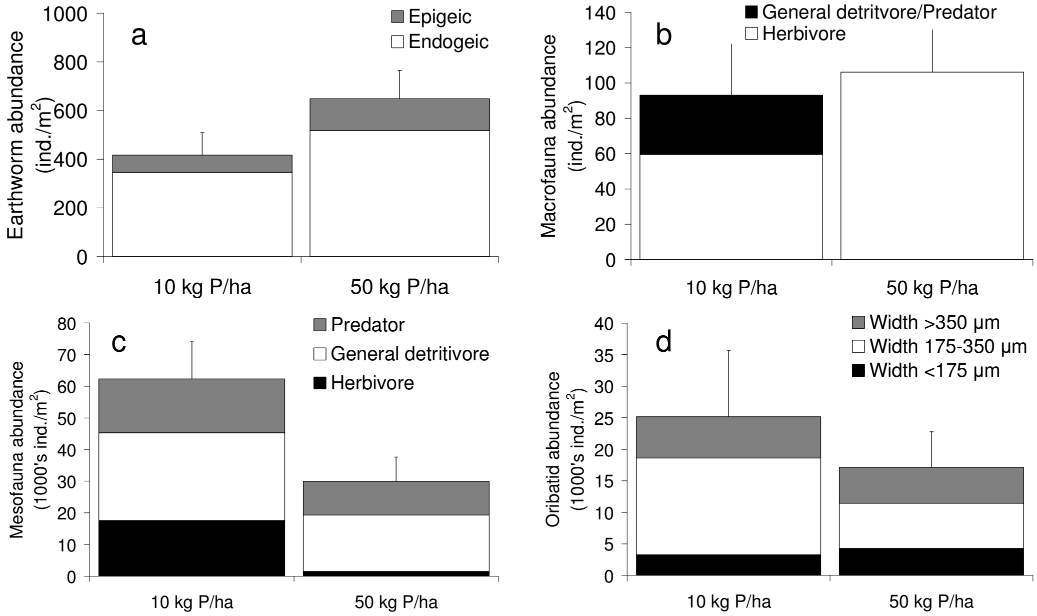

Fig. 3. Abundance of (a) earthworms, (b) other macrofauna (c) mesofauna and (d) adult Oribatida in various functional groups in an Andosol under two sheep grazed pastures with differing management intensities at Whatawhata, N.Z.

Discussion

The long term effects (25 years) of a five-fold increase in P fertiliser application and associated higher sheep stocking rates on an Andosol were reflected in higher soil fertility, pasture production and plant litter contribution to the soil (Tables 1 and 2). Similar responses were observed under similar treatments in a Luvisol (Schon et al., 2008). Pasture production was most similar between the high P treatment in the current study (Andosol) and the high P treatment in the study reported by Schon et al. (2008) on a Luvisol. Although Olsen P was similar in both soils, the difference in climate (1630 mm annual rainfall in Andosol and 1270 in Luvisol) probably controlled pasture production.

Earthworms, which typically respond positively to increased food availability (Curry et al., 2008), were found to increase in abundance (1.6x) and biomass (1.2x) in the high intensity Andosol, broadly in line with increases in pasture production (1.5x) and calculated dry matter input to the soil (1.8x). The increase in earthworm abundance included both epigeic and endogeic earthworms. A consistent effect of management on earthworm abundance (high Cohen's *d*, Table 5) was observed between the Andosol (this study) and the Luvisol (Schon et al., (2008), and was expected to reflect increased food availability (Fig. 4). The low earthworm diversity (two species) detected in this study is not uncommon in New Zealand farms (Springett, 1992). Six species were found in the sheep grazed pastures on Luvisol (Schon et al., 2008), which also had higher earthworm abundances.

Other soil macrofauna did not respond in a consistent manner to management across the two soils. In the Andosol, the abundance and biomass of herbivorous macrofauna doubled under high intensity, while they were more abundant under low intensity in the Luvisol. Grass grub (*C. zealandica*) which are more abundant in pastures with legumes and high fertility grasses (East et al., 1981), were found only under high P inputs in the current study, but were less abundant in this treatment in the Luvisol. In both soils, a common feature of pastures with higher grass grub abundance was a greater proportion of dead matter in the pasture sward, reflecting reduced sheep grazing intensity (East and Willoughby, 1980). At grass grub densities similar to those found in this study, pasture growth has been found to be negatively affected (Fenemore, 1966; van Toor and Dodds, 1994), with decreases in growth of up to 50% in the Waikato region (East et al., 1982). In our study high grass grub root feeding intensity may have caused a decline in root mass and legume contribution to the pasture (Table 2) while increasing competition with other above- and belowground herbivorous fauna. Contrary to the report by Gillingham et al. (2008), the proportion of clover did not increase with increased phosphate application in the Andosol; grass grub infestation may have affected clover populations and associated sward composition.

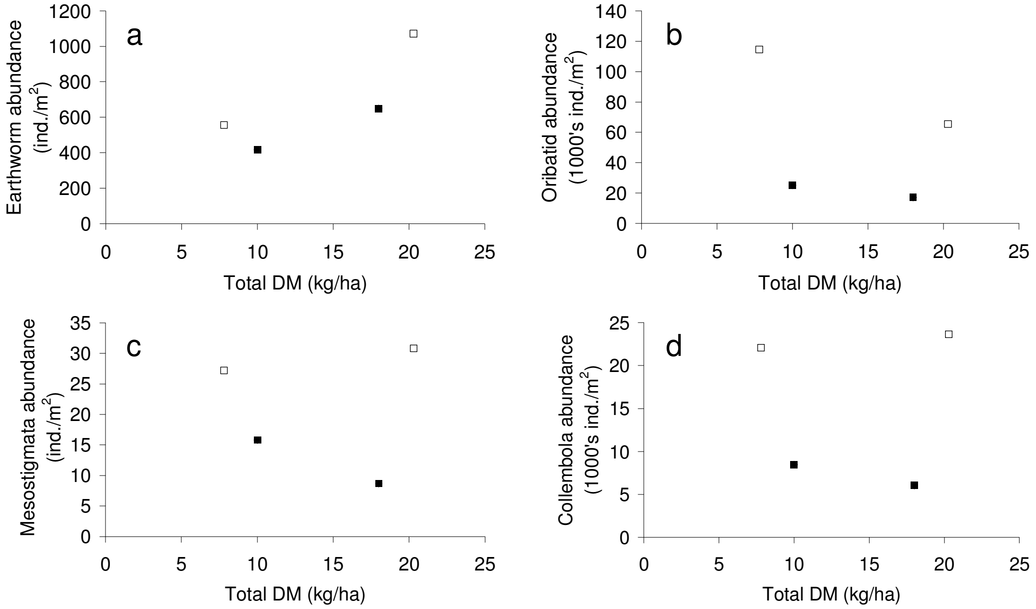

Fig. 4. Response of soil invertebrates to calculated dry matter (DM) input to the soil food web in an Andosol (solid squares) and a Luvisol (hollow squares) sheep grazed pastures, each at two differing management intensities. (a) Earthworm, (b) adult Oribatida, (c) Mesostigmata and (d) Collembola abundance.

The decline in soil mesofauna with intensification is consistent with other studies (King and Hutchinson, 1980; Clapperton et al., 2003; Schon et al., 2008) (Fig. 3, Table 5). As observed by Cole et al. (2008), it is Oribatida which are particularly sensitive to treading disturbances. In contrast, Mesostigmata and Collembola had inconsistent responses to management intensification. In the Andosol, both groups declined in abundance with intensification (15.8 $x10^3$ to 8.7 $x10^3$ ind./m^2 for Mesostigmata, 8.5 $x10^3$ to 6.0 $x10^3$ ind./m^2 for Collembola). In contrast, both groups increased with intensification in the study by Schon et al. (2008) on a Luvisol (27.2 $x10^3$ to 30.9 $x10^3$ ind./m^2 for Mesostigmata, 22.1 $x10^3$ to 23.6 $x10^3$ ind./m^2 for Collembola). Mesostigmata and Collembola have previously been found to increase with food availability (Bardgett et al., 1993; Cole et al., 2008), but to decrease with compaction (Koehler, 1999; Larsen et al., 2004; Cole et al., 2008). The varying response of Mesostigmata and Collembola to increased stocking rates and P fertiliser applications may reflect differences in soil properties (and their effect on food availability and compaction), or it may reflect the life histories of species. Mesostigmata and Collembola are considered to have attributes of *r*-selected organisms (coloniser), in contrast to Oribatida which are more K-selected (persister) (Norton, 1994). Short lived, *r*-selected organisms will respond faster to changes in environmental conditions and while this may give an indication of site disturbance, it is not useful in understanding their long term effects on soil services.

Across the two soils both earthworms and Oribatida showed consistent but differing responses to intensification. Oribatida have been observed to be negatively influenced by both physical disturbance and earthworm burrowing (Maraun et al., 2001; Cole et al., 2008) and it may be a combination of both increased stock treading and earthworm burrowing that results in the negative effects on Oribatida with pastoral intensification found in this study. However, it appears that soil pore size distribution, which is an inherent property of soil type and affected by stock treading and earthworm burrowing, is more important. Across both soils there was a relationship between oribatid abundance and the volume of pores <1 mm diameter (Fig. 5). In the Luvisol, the large difference in oribatid abundance was reflective of a large difference in soil porosity between low and high intensities (in comparison to the Andosol). Further, in both soils there were more small oribatid mites (i.e., *M. minus* and *Ramusella* sp. in the Andosol) and fewer large oribatid species, which tend to have longer life cycles (Grishina, 1991), at higher intensities.

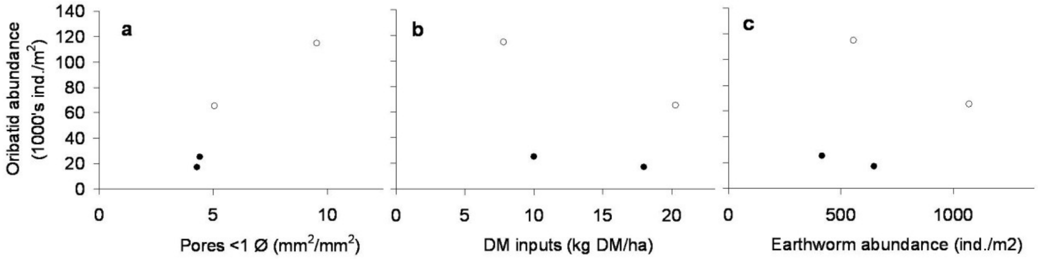

Fig. 5. Total oribatid abundance under two sheep grazed pastures on an Andosol and a Luvisol each at two management intensities, plotted in relation to (a) area of soil pores <1 mm in ø at 2.5 cm depth as measured in resin embedded cores, (b) calculated total dry matter input (litter, dung and roots) to the soil, and (c) total earthworm abundance. Andosol: solid squares; Luvisol: hollow squares.

In both soils earthworm abundance increased as pastures became more productive, and associated food availability increased. While cattle treading has been found to have detrimental impacts on earthworm populations (Lambert, 1986), the lower individual treading pressures of sheep (Greenwood and McKenzie, 2001) does not compromise their activity to the same degree. Increased activity of earthworms may have beneficial effects on both litter incorporation and maintenance of soil structure (Lee, 1985). Earthworm burrowing by the dominant *A. caliginosa,* with burrow diameters of ~2.5 mm (Springett, 1983), may have led to more 1–3 mm diameter pores in the Andosol. This was not observed in the Luvisol (Fig. 1 and 2), possibly reflecting the higher vulnerability of this Luvisol to sheep treading. The higher dry matter inputs and activity of litter incorporating epigeic earthworms contribute to the soil carbon in the topsoil (0–7.5 cm) being sustained. Using the method employed by De Ruiter et al. (1993) we calculated that in the Luvisol earthworms were turning over 120 and 140 kg C/ha/yr at low and high intensity, respectively. Schipper et al. (2009) found no long term change in soil total carbon at 0–7.5 cm with increased sheep stocking rates in the Andosol with higher P fertiliser inputs. This may in part be due to the absence of peregrine anecic earthworms, which have limited distribution in New Zealand (Springett, 1992), but incorporate plant litter to much greater depths.

Conclusion

This study on an Andosol found that earthworm abundance responded positively to increasing food availability, but Oribatid abundance was lower due to increased physical disturbance from the combined effect of sheep treading and increased earthworm activity. These invertebrate responses to intensification mirrored those previously reported on the Luvisol, and as such may be useful as biological indicators that link invertebrate populations to soil processes underpinning soil services. Despite the inconsistent response of non earthworm macrofauna to intensification, they remain an important component of the soil biological community, having large effects on plant growth, and need to be included in a biological indicator.

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Chapter Eight:

Influence of soil faunal communities on nitrogen dynamics in legume based mesocosms

Earlier chapters have shown that invertebrate communities change in response to pastoral management. This chapter explores the potential links between different functional invertebrate groups and nutrient availability in combinations of compacted/uncompacted and nitrogen fertilised/unfertilised soils.

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Abstract

Soil invertebrates play an important part in nutrient cycling and supply. It has been suggested that invertebrates have the greatest influence on nitrogen (N) availability in soils of low N fertility, and therefore low invertebrate abundance in intensive pastoral systems with high N inputs is less important. In constructed soil ryegrass/clover mesocosms, the influence of invertebrates on N cycling and the fate of ^{15}N labelled plant litter in a low or high N environment (no urea vs. urea applied monthly at a rate equivalent to 20 kg N/ha) and in a soil with low or high bulk density (0.8 vs. 1.1 Mg/m^3) was explored by the introduction of different elements of the invertebrate community. This included microbes only (M), M + earthworms (M+W), M + mesofauna and nematodes (M+I), and all fauna (M+W+I).

The results from this mesocosm study highlight that in a compacted and high N fertility environment, typical of intensive pastures, invertebrates do play an important role in nitrogen supply. Invertebrates potentially increase the availability of N to plants through excretion of excess N, production of nutrient rich faecal pellets, earthworm casts and burrows. At high bulk density and low N, N made available by invertebrates resulted in higher plant growth (6.4 vs. 7.4 g) without higher N losses to the environment. At high N, where pasture growth was not limited by N, the N made available by invertebrates increased both herbage N% (2.62 vs. 3.22%) and the amount of N lost in leachate. In compacted soils the populations of Collembola and nematodes were higher in the presence of earthworms, while they were not at low bulk density. At low bulk density other factors appear to have reduced plant growth, and invertebrates had limited effects on plant growth. Forty four days after the application of ^{15}N labelled litter, more of the litter was decomposed and incorporated into the soil in high N than low N mesocosms, and invertebrates increased the plant uptake of surface applied ^{15}N plant litter. The influence of invertebrates was dependent on bulk density, suggesting that in this study, invertebrates in compacted soils improved soil structure, N availability and root growth.

Introduction

Soil fauna contribute to the soil services of water and nutrient supply through their participation in the processes of litter fragmentation and incorporation, nutrient cycling, aggregate building and pore construction. Earthworms have been found to increase litter decomposition and incorporation (Bradford et al., 2002), plant growth (Scheu et al., 1999), N_2O emissions (Rizhiya et al., 2007) and improve soil structure and water and air movement (Bastardie et al., 2003). Macrofauna have large influences on soil properties (Cole et al., 2006). Mesofauna and nematodes also play an important role in decomposition and nutrient supply, stimulating decomposition, nutrient uptake by plants, and pasture growth (Anderson et al., 1981; Siepel and Maaskamp, 1994; Bardgett and Chan, 1999; Bardgett et al., 1999; Ke et al., 2005; Chamberlain et al., 2006; Pieper and Weigmann, 2008). In the presence of bacterial feeding nematodes Anderson et al. (1981) and Ingham et al. (1985) observed an increase in nitrogen (N) mineralisation, while Bardgett and Chan (1999) found a similar response in the presence of fungal feeding Collembola in a fungal dominated soil in a montane grassland.

Pastoral management practices can directly influence soil fauna through changes in the physical habitat (i.e., soil compaction) and food supply (i.e., fertiliser applications), producing both positive and negative effects on the soil fauna and the soil services to which they contribute. Several mesocosm studies have observed negative effects of soil compaction on soil biota (Murphy et al., 1995; Bouwman and Arts, 2000; Buck et al., 2000; Larsen et al., 2004), akin to the impact of increasing stocking rates, which have been observed to decrease oribatid populations (Zyromska-Rudzka, 1977; Clapperton et al., 2002; Cole et al., 2008; Schon et al., 2008).

Fertiliser applications stimulate pasture production and the abundance of both earthworms and nematodes (Yeates, 1976; Curry et al., 2008; Schon et al., 2008). In turn, invertebrates stimulate nutrient cycling and plant growth. It has been suggested that the contributions made by invertebrates to nutrient supply and plant growth decline as N availability increases (Ingham et al., 1985). However, Laakso et al. (2000) reported the opposite effect in mesocosms containing mesofauna and nematodes, with their populations increasing N uptake by plants as N availability increases. Further, Laossi et al. (2010) observed increased plant growth in the presence of anecic earthworms in nutrient rich soil, but observed little added effect of earthworms with the application of fertiliser. We are not aware of any studies which have examined the influence of soil invertebrates on N supply and their interactions with N fertiliser inputs and soil compaction.

The aim of this mesocosm study was to examine the influence of soil invertebrate composition on the rate of cycling of litter into plant available N in legume based pastures on two soils of differing levels of N availability, and bulk density. The hypothesis was that the presence of soil fauna will have a positive effect, accelerating N cycling and plant growth, particularly in mesocosms where no N was applied.

Methods

The mesocosms included 16 treatments with 7 replicates of each. The treatments included two levels of compaction, two levels of nitrogen and four levels of fauna. This included microbes only (M), M + earthworms (M+W), M + mesofauna and nematodes (M+I), and all fauna (M+W+I). More details about the treatments are given in Table 1.

Table 1. The design of the mesocosm experiment. There were two levels of compaction (bulk density, BD), two levels of nitrogen and four invertebrate communities, 16 treatments total. The treatments were located in blocks which were rotated weekly.

Compaction*	0.8 (low BD)		1.1 (high BD)	
N status**	0 (low N)	20 (high N)	0 (low N)	20 (high N)
Invertebrate community***	M	M	M	M
	M+W	M+W	M+W	M+W
	M+I	M+I	M+I	M+I
	M+W+I	M+W+I	M+W+I	M+W+I

*Low BD: 0.8 Mg/m^3, High BD: 1.1Mg/m^3.

**Low N: 0 kg N/ha, High N: 20 kg N/ha monthly

***M: Microbes only, M+W: Microbes + earthworms, M+I: Microbes + mesofauna and nematodes, M+W+I: Microbes + earthworms + mesofauna and nematodes.

Establishing mesocosms

The soil used in the mesocosms was a Pallic soil (NZSC, Marton silt loam) (Hewitt, 1993) (FAO, 1988: Luvisol) collected from an area (40°14'S 175°40'E) within a pasture growth trial (0–15 cm soil depth), that had been under a cut and carry regime for the previous five years. This soil had a Olsen P of 61, pH of 6.4, and total carbon of 3.4%, total nitrogen of 0.32%, and field bulk density (BD) of 0.73 (Chapter 6). The soil was air dried and sieved (<5 mm). The soil was defaunated by freezing at -20ºC for 48 hours, thawing and repeating the freezing for 48 hours, and then heating to 65ºC for a further 48 hours (Bardgett et al., 1998). The soil moisture content was adjusted to 34% w/w, equivalent to 80% field capacity, and was left for a week. The soil was then packed into 15 cm ø PVC pipe (13 cm height) at two bulk densities (BD, 0.8 and 1.1 Mg/m^3) at day -55 (55 days before invertebrate communities were introduced into the mesocosms). A BD of 1.1 Mg/m^3 was equivalent to that found in a neighbouring grazed paddock (Chapter 6). After the mesocosms were watered to 80% field capacity the low BD soil self-compacted, increasing BD from 0.8 to 0.9 Mg/m^3, while the high BD soil swelled, decreasing BD from 1.1 to 1.0 Mg/m^3. The mesocosms were kept at 18ºC, with a 14 hour light and 10 hour dark cycle. Throughout the experiment the soil moisture was maintained at 80% field capacity through watering several times a week and weighing weekly. Urea was applied to the high N treatment monthly at 20 kg N/ha equivalent. The timing of treatment manipulations are given in Table 2, more details are given below.

Table 2. Timing of treatments and manipulations during the mesocosm study. The manipulations of invertebrates and urea were to the appropriate treatments.

Day	
-55	Soil was packed into mesocosms at two bulk densities.
-50	Soil extract added (microbial inoculation)
-35	Clover plants and ryegrass seed added.
-14	Earthworms added
0	Mesofauna and microfauna added and urea applied.
17	Mesocosms moved from temperature controlled room to glasshouse
28	Urea applied.
42	Grass harvested.
49	Half of previous grass harvest returned to mesocosms.
55	Gas samples collected
56	Leachate collected and grass harvested.
57	Urea applied.
63	Half of previous grass harvest returned to mesocosms and ^{15}N labelled ryegrass added.
85	Gas samples collected
86	Leachate collected and grass harvested.
91	Urea applied.
92	Half of previous grass harvest returned to mesocosms.
106	Gas samples collected
107	Leachate collected and grass and clover harvested.
108	Soil sampled.

At day -50, the mesocosms were inoculated with a soil extract. The soil extract was prepared by mixing 20 kg of unsieved moist soil with 40 L of distilled water. The soil extract was prepared using methods similar to those used by Bardgett et al. (1998) to reinoculate the soil with microflora. After soaking for six days the soil extract was collected by centrifuging 1L aliquots at 1000 rpm (146 g) for 5 minutes and then filtering through Whatman filter paper #1 (11 µm pores). This process was found to eliminate nematodes.

At day -35, two ‘Tribute’ white clover (*Trifolium repens*) plants and 18 ‘Impact AR1’ perennial ryegrass (*Lolium perenne*) seeds were sown in each mesocosm. The clover plants were grown from stolons planted in sterilized sand three weeks previously, with Nodulaid (to stimulate *Rhizobium* nodules) added to the sand in the later stages of growth.

At day -14, earthworms (*Aporrectodea caliginosa*), which had been weighed the previous day and stored in water, allowing emptying of intestinal contents, were added to the earthworm treatments. Two juvenile earthworms with a combined average wet weight of 0.47 g were added to each of the M+W and M+W+I mesocosms.

Addition of mesofauna and nematodes at day 0

At day 0, mesofauna and microfauna were added to the appropriate treatments. The mesofauna were extracted live from soil cores (5 cm ø, 0–7.5cm depth) through modified Tulgren-Berelese funnels (mesh size <2 mm) into vials containing defaunated, wet cow dung (0.5 g dry weight). The dung and mesofauna from a single soil core (~50 individuals) were then transferred into each M+I and M+W+I mesocosm. The microfauna were extracted from soil cores (5 cm ø, 0–7.5cm depth) through the modified tray method described by Yeates (1978). All microfauna were combined in distilled water, and a 10 ml subsample containing ~3600 nematodes was added to each M+I and M+W+I mesocosm. In the M and M+W treatments dung and distilled water were added. Also at day 0, 10 ml urea solution (a rate equivalent to 20 kg N/ha) was added to the high N treatment, with 10 ml distilled water being added to the low N treatment. Clear barriers ~15 cm high were placed around each mesocosm to prevent invertebrates escaping or cross contaminating mesocosms (e.g., Collembola).

At 17 days the growth of pasture was poor, which was attributed to insufficient light (20 µmol/m/s), with the intensity of Growlux lights not strong enough. At this stage the mesocosms were moved to a glass house (340 µmol/m/s) with a daily average of 16ºC (daily averages: 12ºC minimum, 25ºC maximum), the daylight period was extended to 14 hours using artificial light. Sticky traps were used to deter aphids.

^{15}N enrichment

At day 63, 1 g of ^{15}N labelled perennial ryegrass was chopped to <1 cm in size and was added to each mesocosm. The ryegrass was labelled by growing ryegrass seed in sand with the addition of urea enriched with ^{15}N at 5.2 atom % (‰). The ryegrass litter which was applied contained 4.73% total N at 4.9 ‰ ^{15}N. A total of 2.32 mg ^{15}N was added to each mesocosm.

At days 55, 85 and 106 (i.e., -8, 23 and 44 days after the addition of labelled litter) gas was collected. Gas samples were collected by placing each mesocosm into a sealed bucket. A 25 ml gas sample was collected in a 12 ml preevacuated Exetainer® at 0 minutes and 60 minutes. Samples were analysed for N_2 and N_2O and their ^{15}N content using automated isotope ratio mass spectrometry (PDZ-Europa Ltd 20-20). The day after gas was collected, leachate was collected and the grass harvested. Leachate samples were collected by applying water (70 ml) every hour until saturation was reached. The volume of leachate was recorded, and leachate was analysed for nitrate (NO_3^-) and ammonium (NH_4^+) colorimetrically in an autoanalyser, these samples were not analysed for ^{15}N. Ryegrass was harvested at a height of about 10 cm. White clover was low growing and not trimmed at intermediate harvests. After each harvest the ryegrass was dried, and half returned back to the same mesocosm. Samples from the last two harvests at high BD were analysed for ^{15}N using automated isotope ratio mass spectrometry (PDZ-Europa Ltd 20-20), and from the last harvest at low BD for total herbage N% by combustion (Elementar Vario-Max), with a linear conversion of 0.933 between the two methods.

Final soil analysis

The mesocosms were destructively sampled at day 108. Four 5 cm ø cores were collected from each mesocosm from 0–7.5 and >7.5 cm depths. The cores were analysed for mesofauna, microfauna, soil structure (collected in 5 cm ø PVC pipe; see below) and soil chemistry (Olsen P, pH, ^{15}N; see below). Earthworms were recovered by hand sorting all soil, except for that used in the resin technique. Mesofauna were extracted using a modified Berlese-Tullgren apparatus. Nematodes were extracted by the modified tray method. Due to similarities in the nematode community in all treatments (dominated by bacterial feeders), only nematodes from three replicates were indentified to genus and are reported. Soil collected in the PVC pipe was impregnated with fluorescent resin, and images of horizontal soil sections at 2.5 and 5 cm depth analysed using Solicon© analysis software (The University of Sydney, Cotton Research and Development Corporation) (Vervoort and Cattle, 2003). Other soil analyses carried out on sieved soil (for three replicates only) included soil pH (1:2.5 soil:water) and plant available soil phosphorus status (Olsen et al., 1954) for 0–7.5 cm depths. Soil was also analysed for ^{15}N automated isotope ratio using mass spectrometry (PDZ-Europa Ltd 20-20) at 0–2.5, 2.5–7.5 and 7.5 cm depths (only M and M+W+I at high BD, and both low and high N were analysed).

Fate of ^{15}N

The 1 g mass of applied litter at N: 4.73%, and ^{15}N: 4.9 ‰ ($^{15}N_{L‰}$) contained 47.3 mg N (N_L). Because the labelled litter was not the only source of N to the soil, with N also from nitrogen fixation (clover) and urea fertiliser, some assumptions were made to calculate the fraction of the total labelled ^{15}N litter that was taken up by the plants growing in the mesocosm. The main assumptions were:

During the period 57 to 107 days, a fraction (*F*) of soil total soil N (N_{TS}) was mineralised and entered the soil available pool (N_{AS}) for plant uptake. N_{TS} was calculated using the soil N% and the weight of soil in each mesocosm (1.9 kg), and could be used to calculate the total soil ^{15}N from the soil ^{15}N ‰ ($^{15}N_{TS‰}$). At a soil N content of 0.35%, there is approximately 6500 mg N/mesocosm in the N_{TS}.

1. A fraction (*D*) of litter N_L was mineralised and entered the N_{AS} for plant uptake.
2. Fertiliser N (*U*) was applied as urea to the high N mesocosms at day 0, 28, 57 and 91. The 70 mg N/mesocosm applied at and after day 57 was assumed to be available to pass through the N_{AS} and be taken up by plants. The natural abundance of ^{15}N ‰ of urea was assumed to be 0.37 (Bronson et al., 2000).
3. Nitrogen fixation by clover was assumed to be negligible.
4. The total flux through the N_{AS} can be calculated using Eqn. 1.

Eqn. 1 $$N_{AS}\,(\text{mg/mesocosm}) = (F.\ N_{TS} + D.N_L + U)$$

5. A fraction (*P*) of the N_{AS} was taken up by plants. *P* was estimated from the apparent recovery of U calculated as the difference in plant N uptake (N_H, Eqn. 2) between the low and high N treatments divided by U. This gave a value of 0.64 which is within the range (0.5–0.9) observed by Elgersma et al. (2000). This value was also assumed to be the fraction of mineralised soil N taken up. Using a value of 0.64 for *P* was consistent with a value of 0.01 for *F* for the fraction of the soil N pool (N_{TS}) mineralising and entering the N_{AS} in the period day 57 to 100. Calculations of plant N uptake (N_H, Eqn. 3) and ^{15}N uptake ($^{15}N_H$, Eqn. 4) used these *P* and *F* values.

Eqn. 2 $P = (\mathrm{N}_{\mathrm{H}\,(\text{high N})} - \mathrm{N}_{\mathrm{H}\,(\text{low N})})/U$

Eqn. 3 $\mathrm{N}_{\mathrm{H}}\,(\text{mg/mesocosm}) = P.\,(F.\mathrm{N}_{\mathrm{TS}} + D.\mathrm{N}_{\mathrm{L}} + U)$

Eqn. 4 ${}^{15}\mathrm{N}_{\mathrm{H}}\,(\text{mg/mesocosm}) = P.(F.\mathrm{N}_{\mathrm{TS}}.\,{}^{15}\mathrm{N}_{\mathrm{TS}\text{‰}} + U.{}^{15}\mathrm{N}_{\mathrm{U}\text{‰}} + D.\mathrm{N}_{\mathrm{L}}.{}^{15}\mathrm{N}_{\mathrm{L}\text{‰}})/100$

If the plant ${}^{15}\mathrm{N}_{\mathrm{H}}$ uptake is measured, then assuming values for P and F, the fraction of ${}^{15}\mathrm{N}$ labelled litter decomposed (D) and cycled through the N_{AS} can be estimated (Eqn. 5). While increasing F to 0.02 can increase D by about 10% (the relative differences between treatments remain the same), we are confident that 0.01 is a more appropriate F value to use, because in soils receiving no N additions the amount of N taken up by the plant (N_{H}) divided by P (0.64) is 65 mg N/mesocosm, which is equivalent to about 0.01 of the N_{TS} (Eqn. 6).

Eqn. 5 $D = (100.{}^{15}\mathrm{N}_{\mathrm{H}}/P - F.\mathrm{N}_{\mathrm{TS}}.{}^{15}\mathrm{N}_{\mathrm{TS}\text{‰}} - U.{}^{15}\mathrm{N}_{\mathrm{U}\text{‰}})/\mathrm{N}_{\mathrm{L}}.{}^{15}\mathrm{N}_{\mathrm{L}\text{‰}})$

Eqn. 6 $F = (\mathrm{N}_{\mathrm{H}\,(\text{low N})}/P)/\mathrm{N}_{\mathrm{TS}}$

${}^{15}\mathrm{N}$ recovery from soil and pasture was calculated relative to a natural abundance of 0.37‰ as this was the measured abundance of ${}^{15}\mathrm{N}_{\mathrm{TS}\text{‰}}$ 44 days after the addition of ${}^{15}\mathrm{N}$labelled litter (>2.5cm depths), and that observed for legume based pastures for ${}^{15}\mathrm{N}_{\mathrm{H}\text{‰}}$ (Ledgard et al., 1985).

Statistical analysis

To investigate the effect of N and BD on soil invertebrates, and the effect of N, BD and combinations of soil invertebrates on soil and pasture properties the data were analysed using PROC MIXED in SAS v.9.1 (SAS Institute Inc., USA), using Satterthwaite degrees of freedom. Invertebrate data were log (x+1) transformed prior to analysis.

Results

Over the course of the experiment soil pH declined (6.4 to 5.7), but Olsen P (61 to 59 mg/L) remained largely unchanged (Table 3). Average earthworm wet weight nearly doubled (0.47 to 0.84 g). Over the same period mesofauna, dominated by Collembola, increased from 50 to 2600 ind./mesocosm in treatments to which they were added (Table 4), and reached 870 ind./mesocosm in the treatments where mesofauna were not intentionally added. Nematode abundance increased from 3600 to 12 500 ind./mesocosm in treatments to which they were added, with over 79% being CP1 bacterial feeding nematodes (Table 5). In treatments where nematodes were not intentionality added they reached 4800 ind./mesocosm with 87% being CP1 bacterial feeding nematodes. In a mesocosm study using methods similar to this, Bardgett (1998) also observed a dominance of short lived bacterial feeding nematodes, due to insufficient time for longer lived plant feeding and predatory nematodes to establish (Mikola et al., 2005).

Table 3. Herbage, leachate, gas and soil characteristics of the mesocosms at low and high N, and low and high bulk density (BD) at 23 days, 44 days or cumulative after the addition of ^{15}N labelled litter.

	N		BD		*P-value*	
	Low	High	Low	High	N	BD
HERBAGE						
Pasture growth (g, at 23 days)	3.7	4.5	3.9	4.3	***0.0001***	*0.172*
Herbage N (%, at 23 days) [1]	3.4	4.2	-	3.9	***0.0032***	-
Pasture growth (g, at 44 days)	2.6	4.0	3.1	3.5	***0.0001***	***0.038***
Herbage N (%, at 44 days)[1]	1.9	2.6	2.1	2.5	***0.0001***	***0.007***
Clover growth (g)[2]	0.4	0.3	0.3	0.4	*0.488*	*0.601*
LEACHATE (cumulative)						
Volume (ml)	148	130	157	123	***0.036***	***0.0002***
NO$_3^-$ (µg)	98	145	132	111	***0.082***	*0.340*
NH$_4^+$ (µg)	48	68	65	51	***0.040***	*0.162*
Mineral N (µg)	146	213	197	162	***0.035***	*0.225*
GAS (23 days after)[3]						
N$_2$ (%)	78.6	78.3	78.4	78.5	*0.365*	*0.338*
^{15}N$_2$ (‰)	0.366	0.366	0.366	0.366	*0.235*	*0.105*
N$_2$O (ppm)	0.33	0.49	0.36	0.46	*0.699*	*0.220*
^{15}N$_2$O (‰)	0.350	0.365	0.364	0.352	*0.794*	*0.218*
SOIL[2]						
Olsen P (mg/L)[4]	59	58	58	59	*0.394*	*0.732*
pH[3]	5.74	5.67	5.67	5.76	***0.004***	***0.009***
Porosity (% at 2.5 cm depths)	40	48	47	40	***0.007***	***0.011***

[1] Herbage N values only for M and M+W+I treatments.
[2] Only assessed at 44 days after the addition of labelled litter.
[3] Gaseous emissions (collected in one hour) were higher 23 than 44 days after labelled litter addition.
[4] Initial values were 61 Olsen P and 6.4 pH.

The abundance of mesofauna and nematodes in mesocosms to which they were not added (M and M+W) was significantly lower than where they were added (M+I and

M+W+I). All possible steps were taken to avoid contamination. Likely sources of contamination include: clover stolons which were grown in sterilised sand and transplanted into the mesocosm pots, microbial inocula, insufficient freezing of soil, transport through earthworm intestines even after being in water for 24 hours, and through the air (e.g., Collembola even though the mesocosms had plastic barriers). Taxa which were not significantly higher in treatments with invertebrates added included organisms which were naturally low in abundance in the inoculation sample or were longer lived (i.e., Astigmata, Oribatida, Poduromorpha and Sminthuridae, among Collembola, Coleoptera, Diptera, Thysanoptera and Tardigrada with abundances <180 ind./mesocosm). In mesocosms which had nematodes added, plant feeding and plant associated nematodes were relatively more abundant.

Influence of nitrogen and bulk density

Plant growth was influenced by both N and BD (Table 3). Plant growth was higher under high N treatments, and high N in combination with high BD. The percent of N in the herbage was higher in high N mesocosms at 23 days and 44 days after the addition of ^{15}N labelled litter.

Nitrate (NO_3^-) was the dominant form of N in the leachate, typical of aerobic, warm and moist soils. NO_3^- tended to increase with N addition. The cumulative amount of ammonium (NH_4^+) lost through leachate was higher at high N than at low N (Table 3). Total mineral N lost was 146 μg from low N and 213 μg from high N mesocosms (P=0.0035). Gaseous emissions were not significantly influenced by N or BD treatments and ^{15}N values were similar to natural abundance.

In resin embedded cores, soil porosity was higher at 2.5 cm depth under low BD (0.47 vs. 0.40% at high BD, P=0.011, Table 3), with similar trends observed at 5 cm depth. Pores <1 mm ø were more abundant under high BD. High N also increased soil porosity (P=0.007).

Table 4. Mesofauna in each treatment (ind./mesocosm) at 108 days. Statistical analysis was carried out on all treatments to determine the influence of N, Bulk density (BD) and their interaction, this was indicated only when significant (α=0.1).

Bulk density	Low								High								*Significant P-value*
Nitrogen	Low				High				Low				High				
Invertebrates*	M	M+W	M+I	M+W+I	M	M+W	M+I	M+W+I	M	M+W	M+I	M+W+I	M	M+W	M+I	M+W+I	
MESOFAUNA																	
Oribatida**	21	30	69	30	36	30	105	36	35	23	85	36	91	100	31	51	
Astigmata	161	159	577	307	221	148	296	251	177	251	413	463	249	221	235	261	
Mesostigmata	23	19	77	44	27	18	32	49	23	17	39	56	28	35	36	25	
Prostigmata	0	0	9	0	0	0	32	6	0	0	1	12	0	0	1	0	
Scutacaridae	18	15	18	12	18	0	45	0	9	14	24	0	18	9	27	9	
Acari	228	244	837	426	326	221	591	384	265	321	683	611	473	453	348	387	
Entomobryomorpha	264	37	1522	216	790	2190	2667	2114	584	293	3167	2658	193	408	563	2845	*N*
Poduromorpha	225	0	14	9	0	18	9	81	18	0	15	0	9	9	0	9	
Sminthuridae	126	0	32	75	27	0	257	27	18	45	27	59	9	0	60	522	
Collembola	307	37	1535	249	663	1880	2754	2129	505	264	3177	2295	141	351	508	2921	*N*
Coleoptera	9	14	14	0	21	9	0	9	9	18	9	0	15	9	18	14	
Diptera	9	12	14	12	14	21	36	9	9	41	9	132	45	21	18	9	
Hemiptera	31	5	40	58	53	8	308	141	23	57	58	17	36	26	19	68	*BD*N*
Thysanoptera	0	0	9	9	0	9	0	0	0	0	9	9	0	9	9	9	
Total mesofauna	536	296	2427	739	1056	2120	3659	2661	800	675	3921	2980	663	854	890	3388	

*M: microbes, W: earthworms, I: mesofauna + nematodes

**Oribatid species include *Microppia minus, Oppiella nova*, *Ramusella* sp., *Liebstadia similis* and *Zygoribatula novazealandica*. *L. similis* was affected by N application (higher under low N).

Table 5. Microfauna in each treatment (ind./mesocosm) at 108 days. Statistical analysis was carried out on all treatments to determine the influence of N, Bulk density (BD) and their interaction, this was indicated only when significant (α=0.1).

Bulk density	Low								High								*Significant*
Nitrogen	Low				High				Low				High				*P-value*
Invertebrates*	M	M+W	M+I	M+W+I	M	M+W	M+I	M+W+I	M	M+W	M+I	M+W+I	M	M+W	M+I	M+W+I	
MICROFAUNA**																	
Tylenchus	0	45	321	0	0	0	0	23	0	0	101	225	0	0	72	32	
Hoplolaimidae	0	0	458	631	0	0	91	231	0	0	201	2142	0	0	1267	476	
Pratylenchus	0	0	92	45	0	0	0	370	0	0	151	676	0	0	362	63	
Paratylenchus	0	0	687	586	0	215	0	23	0	127	101	1748	0	0	290	190	
Aphelenchoides	91	564	458	135	637	43	183	670	0	506	955	451	502	0	145	634	
Diplogaster	272	451	1282	226	2368	43	183	254	130	25	1458	1578	370	70	1375	190	*BD*N*
Rhabditidae	1610	1894	4441	1894	0	3689	10332	2820	1994	1164	2514	7385	476	1509	3040	3997	*BD*N*
Dauerlarvae	159	0	641	271	0	0	274	139	0	76	2011	958	26	35	109	0	*N*
Panagrolaimus	91	451	504	135	3005	343	914	462	0	76	201	338	53	737	796	349	*N*
Cephalobus	45	0	4029	90	182	815	1829	1433	0	101	1106	2988	0	35	1303	1269	
Heterocephalobus	0	0	92	0	0	0	0	116	0	0	0	0	0	0	253	32	*N*
Plectus	0	23	0	0	0	0	0	23	0	25	352	56	0	0	36	32	
Monhystera	0	45	92	0	0	0	0	0	0	0	0	0	0	35	0	0	
Total nematodes	2268	3540	13416	4014	6192	5148	13806	6564	2124	2100	9252	18660	7461	3204	10197	14562	*BD*N*
NCR	0.97	0.85	1.00	0.95	0.90	0.98	0.98	0.89	1.00	0.77	0.88	0.96	0.65	1.00	0.97	0.89	
MI	1.07	1.20	1.33	0.74	1.13	1.16	1.13	1.24	1.00	1.30	1.30	1.14	1.35	1.03	0.94	1.35	
PPI	0	0.02	0.35	0.80	0	0.19	0.01	0.30	0	0	0.09	0.48	0	0	0.58	0.10	
ΣMI	1.07	1.22	1.68	1.54	1.13	1.34	1.15	1.54	1.00	1.30	1.39	1.62	1.35	1.03	1.52	1.46	
Tardigrada	54	0	144	126	36	90	18	96	36	276	666	192	72	132	516	144	*BD*
Enchytraeidae	621	240	180	882	0	180	342	84	1224	180	1008	468	1404	195	1098	72	*BD*

*M: microbes, W: earthworms, I: mesofauna + nematodes.

***Cephalenchus, Ditylenchus, Pungentus, Doryllium, Acrobeloides, Tripyla* and *Dorylaimus* were low in abundance and were detected in less than two treatments.

Table 6. Herbage, leachate and gas characteristics of the mesocosms at low and high N, and low and high bulk density (BD), with and without invertebrate communities at 23 days, 44 days or cumulative after the addition of ^{15}N labelled litter.

	Low N		High N		*P-value*	
Invertebrates*	M	M+W+I	M	M+W+I	*Fauna low N*	*Fauna high N*
LOW BD						
HERBAGE						
Pasture growth (g, at 23 days)	3.2	3.3	4.6	4.3	*0.605*	*0.291*
Pasture growth (g, at 44 days)	2.4	2.2	4.1	3.6	*0.428*	*0.121*
Herbage N (mg, at 44 days)	40	40	100	90	*0.286*	*0.404*
LEACHATE (cumulative)						
Volume (ml)	182	186	146	112	*0.861*	***0.076***
NO$_3^-$ (µg)	153	90	77	233	*0.473*	*0.194*
NH$_4^+$ (µg)	60	83	56	63	*0.624*	*0.267*
Total mineral N (µg)	213	173	134	295	*0.700*	*0.200*
GAS (23 days after)[1]						
N$_2$ (%)	78.1	78.3	78.0	77.8	*0.643*	*0.278*
N$_2$O (ppm)	0.35	0.30	0.34	0.38	*0.848*	*0.105*
HIGH BD						
HERBAGE						
Pasture growth (g, at 23 days)	4.1	4.5	4.8	4.9	***0.079***	*0.937*
Herbage N (mg, at 23 days)	141	163	203	222	***0.0003***	*0.119*
Pasture growth (g, at 44 days)	2.4	2.9	4.3	4.4	*0.167*	*0.191*
Herbage N (mg, at 44 days)	50	60	120	150	*0.356*	***0.027***
LEACHATE (cumulative)						
Volume (ml)	178	115	108	93	***0.048***	*0.183*
NO$_3^-$ (µg)	112	60	97	164	***0.091***	*0.786*
NH$_4^+$ (µg)	28	38	89	48	*0.891*	*0.424*
Total mineral N (µg)	140	98	186	212	*0.144*	*0.883*
GAS (23 days after)[1]						
N$_2$ (%)	79.5	78.5	78.0	78.5	*0.760*	*0.506*
N$_2$O (ppm)	0.48	0.35	0.36	0.36	*0.839*	*0.257*

*M: microbes, W: earthworms, I: mesofauna + nematodes

[1] Gas collected in one hour.

Influence of fauna

Total mesofauna and nematode abundance were on average higher at high N than at low N (Table 4 and 5). For example, nematodes *Panagrolaimus* and *Heterocephalobus* were more abundant at high N, while dauerlarvae were more abundant at low N. Mesofauna and nematode abundance were also affected by BD, with Hemiptera, and the nematodes *Diplogaster* and Rhabditidae more abundant at the low BD, high N combination. There was no evidence of a negative effect of BD on Oribatida, in fact they were slightly more abundant (not significant) at high BD. Total mesofauna and nematode abundance tended to be lower in the presence of earthworms at low BD, but showed little response to earthworms at high BD (Fig. 1). Tardigrada and Enchytraeidae were more abundant at high BD.

At high BD pasture growth was higher at low N (Table 6) in the presence of invertebrates (M+W+I), while herbage N was stimulated in their presence at high N.

The combined presence of all invertebrates (M+W+I) stimulated N uptake by plants, whereas M+W and M+I alone did not affect plant uptake of N at high BD (data not shown). In all treatments soil invertebrates tended to reduce the volume of leachate lost, significantly decreasing the amount of NO_3^- lost at high BD, low N (*P*=0.091). Gaseous emissions were not significantly influenced by invertebrates, contrary to observations by van Groenigen (2010).

Earthworms had a greater effect on soil porosity at low BD than at high BD, increasing the area of 1–3 mm ø pores (Fig. 2). In the presence of earthworms 0.2–0.8 mm ø pores were more abundant under at high BD.

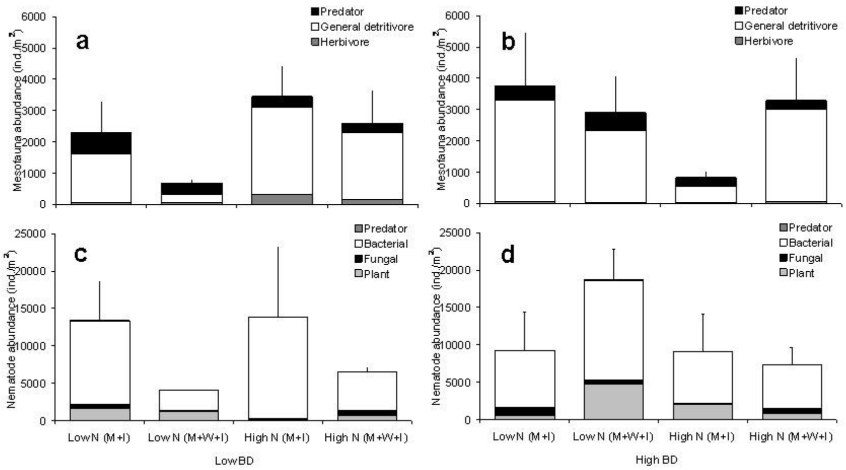

Fig. 1. Invertebrate trophic groups in mesocosms at day 44 at low and high BD, low and high N, with microbe + mesofauna and nematodes (M+I), and microbe + earthworm + mesofauna and nematodes (M+W+I). (a) Total mesofauna abundance at low bulk density (BD) and (b) high BD. (c) Total nematode abundance at low BD and (d) high BD.

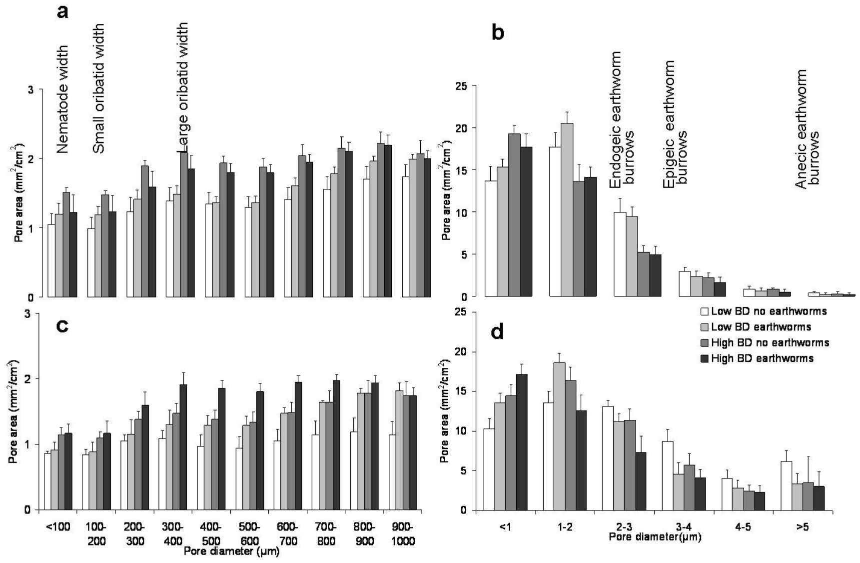

Fig. 2. Pore areas (mm^2/cm^2) over ranges of pore sizes for treatments with and without earthworms at low and high bulk density (BD) as measured through resin embed cores at 108 days. (a) Pores <1 mm ø at 2.5 cm depth. (b) All pores (<1–>5 mm ø) at 2.5 cm depth; the <1 mm bar is the sum of pores shown in (a). (c) All pores (<1–>5 mm ø) at 5 cm depth. (d) Pores >1 mm ø at 5 cm depth; the <1 mm bar is the sum of pores shown in (c).

Fate of ^{15}N

Of the added ^{15}N labelled litter, 13–25% of the total ^{15}N was recovered in the herbage and soil samples (Table 7). Twenty three days after the addition of labelled litter there was no difference in the percent abundance of ^{15}N in herbage between treatments. Forty four days after the addition of labelled litter the abundance of ^{15}N found in the ryegrass was higher in low N than high N (0.45 vs. 0.41 ‰). Soil invertebrates increased the mass of ^{15}N in the herbage and decreased the ^{15}N‰ in the soil, even though they did not significantly increase the total recovery of ^{15}N from soil and herbage.

Table 7. Influence of invertebrate communities on the recovery of total N (^{15}N plus ^{14}N) and ^{15}N 44 days after the addition of ^{15}N labelled litter at low and high N in mesocosms at high bulk density.

	Low N		High N		*P-value*	
Invertebrates*	M	M+W+I	M	M+W+I	*N*	*Fauna*
Herbage ^{15}N (mg, after 44 days)	0.58	0.76	1.30	1.31	***0.0001***	***0.073***
Soil Total N (%)	0.35	0.34	0.35	0.33	*0.536*	*0.177*
Soil ^{15}N‰[1]	0.42	0.39	0.39	0.38	***0.067***	***0.059***
Recovery of ^{15}N from soil and herbage (mg)	0.57	0.38	0.40	0.30	*0.193*	*0.771*
Decomposition of litter (%)[2]	29	41	66	67		

*M: microbes, W: earthworms, I: mesofauna + nematodes

[1] Soil ^{15}N‰ at 0–2.5 cm depths, at >2.5cm depths soil ^{15}N‰ was 0.37 across all treatments.

[2] See Eqn. 1–6

Lower rates of litter decomposition in the microbe only treatment (M) resulted in more ^{15}N being recovered from 0–2.5 cm soil depth at low N than at high N in these treatments. It was estimated that approximately 20% of labelled litter was still present on the soil surface in the low N, M treatments, i.e., ~0.5 mg more ^{15}N was present at 0–2.5 cm depth at the end of the experiment in comparison to the other treatments, out of the total of 2.32 mg ^{15}N applied. It was calculated that the decomposition of the ^{15}N labelled litter was lowest in the low N, microbe only treatment and highest in the high N mesocosm (Table 7).

Discussion

The present mesocosm study highlights that in a compacted and high N fertility environment, typical of intensive pastures, invertebrates play an important role in nutrient supply. Soil invertebrates increased plant growth at low N, and stimulated N uptake by plants at high N in the present study in the soil compacted to a BD of 1.1 Mg/m^3. The finding that N uptake was influenced by the invertebrate community at high N fertility was somewhat surprising, given that the available N was not limiting plant growth. In two other mesocosm experiments, which examined the influence of invertebrates on plant growth and N uptake at low and high N inputs, similar results were obtained (Laakso et al., 2000; Laossi et al., 2010). These authors found that N fertiliser stimulated plant growth even though N inputs were lower (~50 kg N/ha vs. ~80 kg N/ha in this study) and soil N contents higher (0.47–0.86% vs. 0.32% in this study). Laossi et al. (2010) observed anecic earthworms (but not endogeic earthworms) stimulating plant growth at low N. That they did not observe this in soils where the N content was 0.12% suggests that at this low N content, mineralisation by invertebrates was low and not available to plants. At high N, Laakso et al. (2000) observed an increase in N uptake by plants as invertebrate communities became more complex (microbivorous nematodes vs. microbivorous nematodes + detritivorous and predatory mesofauna).

Invertebrates increased plant uptake of N by 20–25% (Fig. 3) through their impact on the soil physical environment. Invertebrates rework organic matter in the soil profile to excrete excess N, form nutrient rich faecal pellets and earthworm casts, and earthworms burrow and create pores to improve aeration and root penetration (Ingham et al., 1985; Lee and Foster, 1991; Yeates and Pattison, 2006). In this study, earthworm burrowing did not increase the volume of leachate collected despite influencing soil pore size distribution. Earthworm burrowing increased the amount of pores 1–3 mm ø at low BD, which are equivalent to burrow diameters of *A. caliginosa* (2.5 mm ±0.22) as reported by Springett (1983), but had little effect on pores >1 mm ø at high BD (Fig. 2). Buck et al. (2000) also reported reduced rates of earthworm burrowing at bulk densities >1.0 Mg/m^3 common in New Zealand. In the compacted soils in this study there were more pores <1 mm ø and some evidence of more pores 0.2–0.8 mm ø at 5 cm depth in the presence of earthworms. In high N mesocosms, where N was in excess of plant demand for maximal plant growth, the stimulating effect of invertebrates on porosity and implicitly on soil aeration was reflected in higher herbage N% and more NO_3^- in leachate (Fig. 3). Increased production of NO_3^- in the presence of endogeic earthworms has also been observed by Sheehan et al. (2006). In low N mesocosms plant uptake of the additional N made available by invertebrate activity was insufficient to lead to an accumulation of N in soil solution and leachate. This reflects the beneficial effects of invertebrate mediated mineralisation in soils where N is limiting plant growth, allowing for greater uptake of N by plants without losses to the environment.

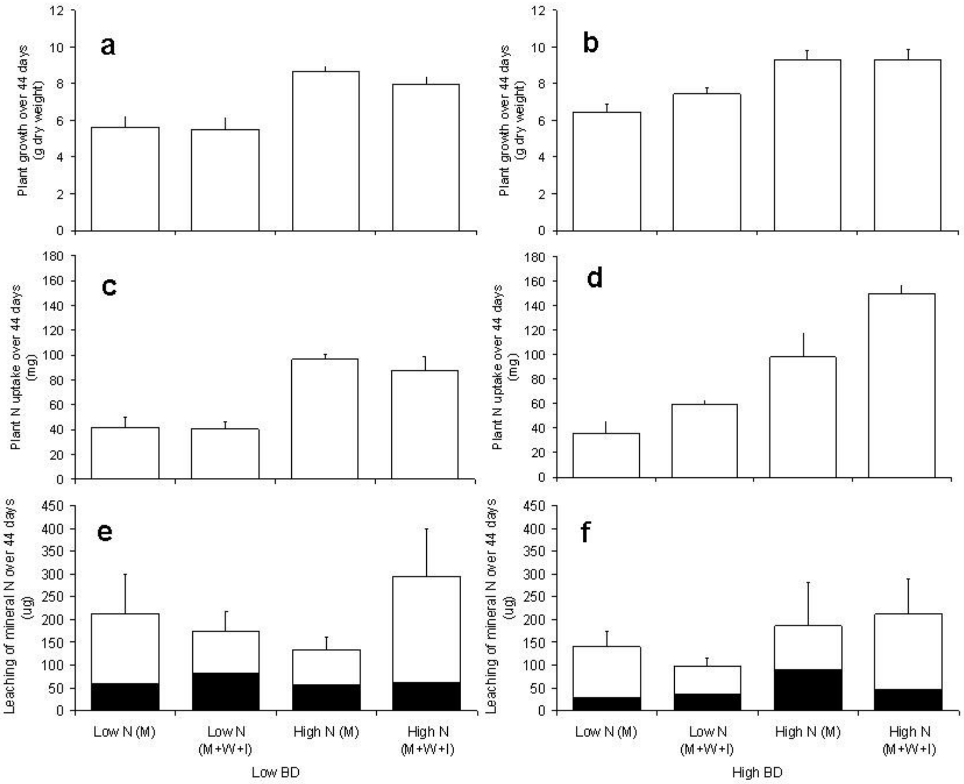

Fig. 3. Effect of invertebrates on mesocosms at low and high bulk density (BD), low and high N, with microbe + mesofauna and nematodes (M+I), and microbe + earthworm + mesofauna and nematodes (M+W+I). Plant growth over 44 days at (a) low BD and (b) high BD. Plant N uptake over 44 days at (c) low BD and (d) high BD. Mineral N lost as NO_3^- (□) and NH_4^+ (■) at (e) low BD and (f) high BD.

Pasture growth was lower at low than high BD, despite increased soil porosity, suggesting that another factor was limiting plant growth at this level of compaction. Further, at low BD the invertebrate community did not stimulate plant growth, which may reflect sufficient porosity in the short term for plant and microbial processes. The studies by Laossi et al. (2010) simulating a pastoral system and by Laakso et al. (2000) simulating a forest system, both appeared to have lower bulk densities than the low BD treatment in this study but still showed a positive influence of the soil fauna. In this study, the presence of invertebrates improved N availability at low BD, increasing plant uptake of N and the amount of mineral N lost in the leachate, particularly at high N (Fig. 3).

Gaseous emissions were higher under high N than low N and at 23 days after the addition of labelled litter than at 44 days after. Under field conditions Saggar et al. (1996) reported that litter left on the soil surface was quickly oxidised and lost. Though large amounts of litter N may have been lost as gaseous emissions, litter (both ^{15}N labelled and harvest returns) was the dominant food resource for soil fauna, as indicated by the dominance of bacterial feeding nematodes (i.e., *Panagrolaimus* and *Heterocephalobus*) and detritivorous Collembola. At high N, where pasture growth and litter returns were higher, abundances of mesofauna and nematodes were on average higher, while earthworm biomass was not. Their increased activity at high N is supported by the increased decomposition of ^{15}N labelled litter (Table 7), because there was less ^{15}N was recovered from the soil, there was increased flux of ^{15}N available for plant uptake. In the absence of soil fauna (M), the decomposition of ^{15}N litter was reduced at low N, with the high recovery of ^{15}N at 0–2.5 cm soil depth. The rates of litter decomposition and incorporation in this study were higher than those reported by Seeber et al. (2006) for endogeic earthworms. These authors observed greater rates of incorporation by litter feeding epigeic and anecic earthworms.

A number of interactions were found between invertebrate groups, in addition to the interaction between the presence or absence of invertebrates and soil attributes. At low BD, where earthworms had a larger effect on soil structure, earthworm burrowing appeared to have had a negative influence on other soil invertebrates: abundance of nematodes, Oribatida and Collembola tended to be lower in the presence of earthworms (Fig. 1). Similar observations have been reported in other studies (Yeates, 1981; Maraun et al., 2001; Lopez et al., 2003; Salmon, 2004). In these low BD mesocosms pasture growth was not stimulated by invertebrates. In contrast, at high BD, where earthworms had a lesser effect on soil structure, nematodes and Collembola were more abundant. In these compacted soils herbage N uptake was stimulated by invertebrates. While soil compaction has been found to have a negative influence on mesofauna and nematode populations (Murphy et al., 1995; Larsen et al., 2004), some earthworm activity may have been beneficial to the meso- and micro-fauna by restoring pores (Yeates, 1981; Maraun et al., 2001; Lopez et al., 2003; Salmon, 2004).

In pastoral systems N is required in large quantities for plant uptake, and hence can often limit plant growth (McLaren and Cameron, 1990). The efficient cycling of N is critical as land managers strive for production gains, whilst limiting the environmental impact of farm systems. In this study, invertebrates were measured to have a positive influence in N availability to rye grass. Invertebrates living in our pastoral soils are under greater pressure as pastures intensify. To remain efficient into the future, invertebrate populations need to be encouraged.

Conclusion

While many studies have explored the role of invertebrates on nutrient availability, this study highlights the importance of invertebrates in nutrient cycling in compacted (high BD) and high N fertility (high N) mesocosms. In the high BD mesocosms, soil invertebrates stimulated the mineralisation of organic N and the uptake of N by plants at both low and high N fertility. Even though invertebrates stimulated N uptake by plants at high N, their contribution to mineralisation was also more likely to be lost via leachate and gaseous emissions. Invertebrates improved N availability and ^{15}N uptake by plants. At high BD earthworms appeared to have a lesser effect on soil porosity, however, populations of Collembola and nematodes were higher in the presence of earthworms, which was associated with increased uptake of N by herbage. At low BD invertebrates had no impact on plant growth and other factors may have been limiting plant growth.

The results of this study, while needing to be tested under field conditions, demonstrate to land managers the importance of the soil invertebrate community even under managed (and fertilised) systems.

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Chapter Nine:

Relationship between potential food resources, soil physical conditions and invertebrate abundance and biomass in twelve pastoral soils

Chapters 1 to 7 explored the responses of invertebrates to a wide range of practices in a diversity of pasture ecosystems. This chapter collated the data collected from each of these 7 chapters and explores which factors (food resources or soil physical condition) are having the largest influence on the abundance and diversity of the soil invertebrate community.

N.L. Schon, A.D. Mackay, M.A. Minor. Relationship between potential food resources, soil physical condition and invertebrate abundance and biomass in twelve soils.

Abstract

Pastoral agriculture influences potential food resources available for the soil food web as well as soil physical conditions. This study explored the relationship between food resources, soil physical condition and soil invertebrates in 42 treatments across 12 soil series under New Zealand pastures.

The response of invertebrates to food resources and porosity was associated not only with the size class of invertebrate (i.e., earthworm vs. nematode) but also with the functional group (i.e., bacterial feeding vs. plant feeding). Soil porosity, a surrogate for habitable pores, showed larger and more consistent trends across the soils than potential food resources, as calculated from pasture production data. This may be because in productive pastures, food resources may not always be limiting invertebrate populations. However, some fauna members such as anecic earthworms, Collembola and bacterial feeding nematodes were associated with the increased organic matter inputs, and the nematode Plant Parasitic Index was positively associated with root mass. Invertebrates associated with soil porosity included endogeic earthworms, Oribatida and larger (plant feeding and predatory) nematodes. Overall it seems that management practices which improve soil porosity will be beneficial not only for plant growth, but also for sustaining biological communities, and indirectly, for the ecosystem services these communities support.

Introduction

Soils provide important ecosystem services including water and nutrient supply. Soil invertebrates are intimately involved in processes which regulate these services (Brussaard, 1998; Coleman et al., 2004; Wall, 2004; Lavelle et al., 2006). As land managers increase fertiliser inputs and stocking rates to maintain profits, this puts increasing stress on the physical and nutrient loadings of the soil, affecting invertebrates. In order for the soil services to continue to be provided, soils need to be managed to sustain the biological communities.

Fertiliser application can stimulate invertebrate abundance and activity through increased pasture production, which flows through as more food resources to the soil food web (Yeates, 1976; Zyromska-Rudzka, 1977; Cole et al., 2005; Oliver et al., 2005; Sjursen et al., 2005; Cole et al., 2006; Yeates and Pattison, 2006; Curry et al., 2008). Increasing stocking rates to utilise increased pasture production may inhibit invertebrate abundance and activity as stock treading can cause soil compaction and a loss of habitable pore space (King and Hutchinson, 1976; Elliott et al., 1980; King and Hutchinson, 1980; Lambert, 1986; Clapperton et al., 2002; Drewry, 2006; Nielsen et al., 2008). Increased fertiliser application is typically associated with increased stocking rates, and whether invertebrate abundance is stimulated or inhibited may depend on the type of invertebrate but also other local factors such as soil type and weather, and their influence on pasture production and compaction (Yeates, 1984).

This study explored the relationship between potential food resource inputs to the soil, and soil physical condition, as affected by pastoral management, across twelve soils under grazed pasture throughout New Zealand. The aim was to gain a better understanding of the relationship between invertebrates, food resources and soil physical condition.

Methods

Sites and treatments

Data were collected at 14 field sites under 42 treatments. These included nine different managements in sheep grazed pastures, 17 different managements in dairy grazed pastures and 15 in ungrazed pastures (Table 1).

Table 1. Sites, their soils, treatments and number of replicates ('Reps') sampled for soil fauna. Potential dry matter (DM) (kg DM/ha/yr) entering the soil food web, average annual stock live weight (LW) loading (kg/ha) and the standing biomass (kg dry weight/ha) of the macrofauna, mesofauna and nematodes for each treatment are also given. The symbol (S) used in the Figures is also given.

Site* (n=14)	Soil Order**	Soil series	Treatment (n=42)	Reps	DM	LW	Biomass Macro	Meso	Nema	S
TYPICAL SHEEPGRAZED PASTURES										
Whatawhata[1]	Allophanic	Dunmore	Low fertility	1	10.0	650	283	3.8	0.8	●
			High fertility	1	18.0	935	322	2.6	0.7	●
Ballantrae[2]	Brown, Pallic	Mangamahu,	Low fertility	1	7.8	495	369	18.6	–	●
	(non Allophanic)	Ngamoka	High fertility	1	20.3	880	641	13.7	–	●
Ballantrae[3]	Brown	Ngamoka	Organic	2	18.5	660	388	8.1	0.4	●
	(non Allophanic)		Conventional	2	17.1	720	438	8.2	0.5	●
TYPICAL DAIRYGRAZED PASTURES										
Whareroa[4]	Allophanic	Egmont	3 cows/ha	5	34.1	1 350	166	4.1	0.9	■
			4 cows/ha	5	38.4	1 800	290	2.0	0.8	■
			5 cows/ha	5	41.7	2 250	399	2.6	1.3	■
Newstead[5]	Allophanic	Horotiu	2.3 cows/ha	1	21.2	1 150	499	10.2	0.2	■
			3 cows/ha	1	38.2	1 500	312	1.5	0.4	■
			3.8 cows/ha	1	43.5	1 900	495	2.2	0.4	■
Manawatu[6]	Allophanic	Kiwitea	Organic	1	16.3	970	283	1.8	0.7	■
			Conventional	1	26.5	1 450	544	5.1	0.5	■
Newstead[5]	Gley	Te Kowhai	2.3 cows/ha	1	21.2	1 150	414	7.3	0.3	■
	(non Allophanic)		3 cows/ha	1	38.2	1 500	324	5.8	0.3	■
			3.8 cows/ha	1	43.5	1 900	337	2.0	0.2	■
Manawatu[6]	Pallic	Tokomaru	Organic	1	17.5	1 050	612	7.4	0.3	■
	(non Allophanic)		Conventional	1	20.5	1 150	592	5.1	0.5	■
Manawatu[6]	Recent	Manawatu	Organic	1	10.4	580	822	8.8	0.3	■
	(non Allophanic)		Conventional	1	31.2	1 650	475	7.5	0.4	■
UNGRAZED PASTURES										
Whareroa[4]	Allophanic	Egmont	Fallow	5	38.0	0	322	7.2	0.5	×
			Cut and carry	5	24.4	0				×
Ballantrae[3]	Brown	Ngamoka	Ungrazed	2	17.0	0	222	2.5	0.7	×
	(non Allophanic)									
Waikato[7]	Allophanic[#]	Horotiu	Low P, low N	4	-	0	466	8.9	0.7	×
			Low P, high N	4	-	0	1334	14.1	0.8	
			High P, low	4	-	0	1192	19.6	0.5	
			High P, high N	4	-	0	1436	5.9	0.3	
Manawatu[7]	Pallic[#]	Marton	Low P, low N	4	-	0	876	3.4	0.4	×
	(non Allophanic)		Low P, high N	4	-	0	577	3.3	0.2	
			High P, low	4	-	0	830	13.4	0.3	
			High P, high N	4	-	0	1736	7.8	0.2	
Southland[7]	Brown[#]	Waikiwi	Low P, low N	4	-	0	481	1.3	0.7	×
	(non Allophanic)		Low P, high N	4	-	0	223	2.5	0.9	
			High P, low	4	-	0	387	2.0	0.9	
			High P, high N	4	-	0	269	1.4	1.2	
PASTURES DISTURBED BY WEATHER EXTREMES										
Winchmore[8]	Brown[##]	Lismore	Dryland	3	16.0	330	169	4.2	0.6	Δ
	(non Allophanic)		Irrigated	3	10.2	990	131	9.3	0.3	Δ
			Unfertilised	4	9.4	330	101	3.6	0.2	Δ
			Fertilised	4	16.0	935	198	5.2	0.3	Δ
Manawatu[6]	Recent[###]	Manawatu	Organic	1	13.8	800	1095	0.7	0.5	Δ
	(non Allophanic)		Conventional	1	29.4	1 650	441	1.1	0.4	Δ

*The study is described in: [1]Chapter 7, [2]Schon et al. (2008), [3]Chapter 4, [4]Chapter 1, [5]Chapter 2, [6]Chapter 3, [7]Chapter 6, [8]Chapter 5.

**Soil order according to New Zealand Soil Classification (Hewitt, 1993). Allophanic soils had a P retention of >60%, and non Allophanic soils had a P retention of <60%.

[#] At this site an adjacent permanent fence line and grazed paddock were also sampled.

[##] Sheep grazed, annual drought.

[###] Dairy grazed, alluvial deposition during flooding in 2004.

Soils spanned five soil orders (and 12 soil series) and were predominantly silt loams. Sites were located on experimental research farms and commercial farms in temperate New Zealand climates, from Waikato in the north to Southland in the south. At each location the invertebrate community (macrofauna, mesofauna and nematodes) was described and the influence of management practices on potential food resources, and soil physical condition was assessed. The findings of each field investigation have been reported in seven Chapters and a previous publication (Table 1).

Quantifying the invertebrate community

Separate, replicated soil cores were collected for macrofauna, mesofauna and nematodes in winter. Macrofauna cores were hand sorted in the laboratory and mesofauna were extracted using a modified Berlese-Tullgren apparatus, as used by Schon et al. (2008). Nematodes were extracted by the modified tray method described by Yeates (1978). Invertebrates were counted, identified and allocated to trophic groups according to Petersen and Luxton (1982), Symstad et al. (2000), Dindal (1990) and Yeates et al. (1993). The Nematode Channel Ratio (NCR), Maturity Index (MI), Plant Parasitic Index (PPI) and ΣMaturity Index (ΣMI) were calculated (Bongers, 1990; Yeates, 1994, 2003). Food webs (Fig. 1) were derived following Hunt (1987) and Mulder et al. (2005) as described in Chapter One. Microbial biomass was measured by Substrate Induced Respiration (results are not included here).

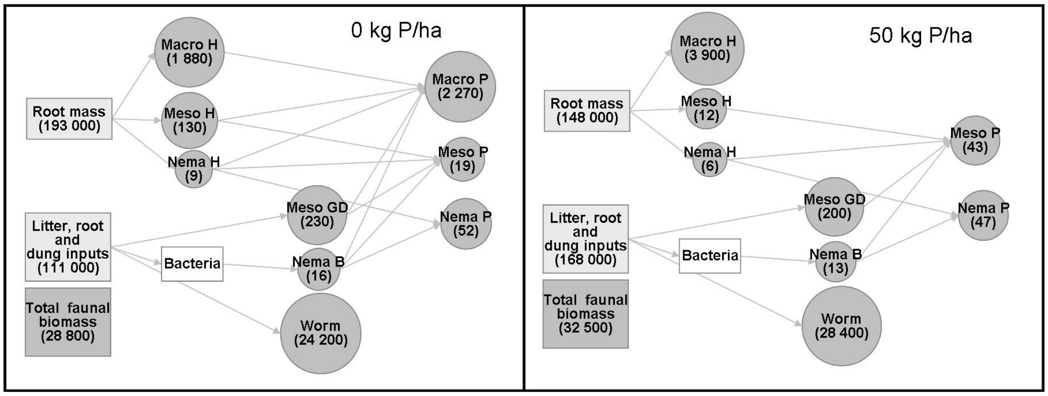

Fig. 1. Food webs of selected soil faunal groups under contrasting pasture management regimes with 0 and 50 kg P/ha/yr, Whatawhata, New Zealand in 2007. Resource inputs are given in mg dry weight/m^2. Macrofauna (Macro), mesofauna (Meso) and nematode (Nema) herbivores (H) feed on plant material. Earthworms (Worm), mesofauna general detritivores (GD) and nematode bacterial feeders (B) feed on detrital inputs and associated microflora. The macrofauna, mesofauna and nematodes are in turn consumed by predators (P). Circle areas represent the log biomass of the fauna, actual biomass (dry weight mg/m^2) given in parenthesis. Biomass calculated as described in Chapter 1. Trophic groups with biomass <1.5 mg dry weight/m^2 were excluded.

Quantifying potential food resources

Potential food resources available to the soil food web include plant litter (both aboveground and belowground), dung inputs from grazing animals and living plant roots. These inputs tend to be correlated with pasture production, with more productive pastures potentially having more food available to the soil food web. Imported feed (such as pasture silage, maize, lucerne, as well as organic fertilisers), are also potential food sources in pastoral systems. Pasture production was assessed using the ‘trim’ technique or by using a ‘pasture plate meter’ (Piggot, 1989). When information on pasture production was not available from the trial, pasture intake (with a utilisation factor) was estimated assuming that a standard sheep consumes 550 kg DM/ha/yr and a standard dairy cow consumes 4500 DM/ha/yr (www.maf.govt.nz). Dry matter from plant litter was calculated using Parsons et al. (1983) (see also Chapter 1). In more fertile dairy grazed pastures increased pasture intake (lowest line on graph, Fig. 2) results in increased total dry matter returned to the soil. Dry matter from dung was calculated as 35% of pasture intake (Takahashi et al., 2007). Standing root biomass was estimated by washing soil samples through a hydropneumatic root washer and drying the roots.

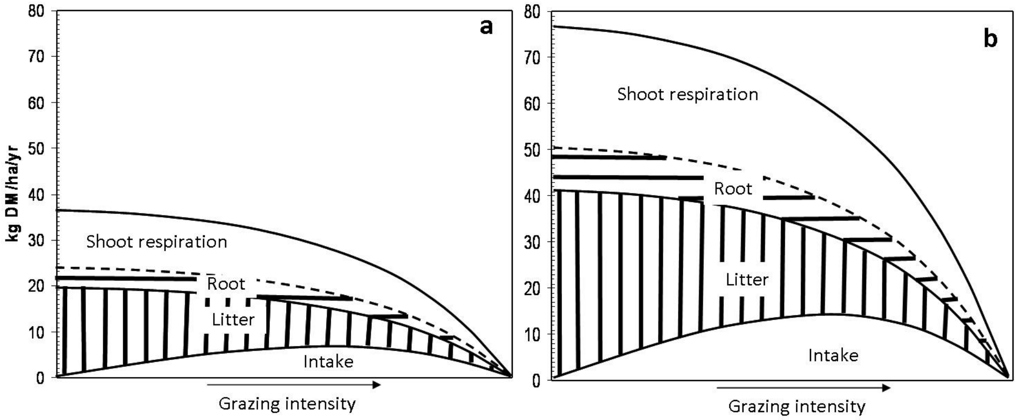

Fig. 2. Dry matter inputs potentially available to the soil food web in a (a) sheep grazed and (b) dairy grazed pasture, modified from Parsons et al. (1983). The unhatched “intake” area represents pasture intake by stock, the area with vertical lines represents litter return from pastures, and area with horizontal lines represents litter return from roots.

Quantifying soil physical condition

Soil physical condition analysis included a description of the habitable pore space as well as the physical loadings of livestock. Pore size distribution for water filled pores <60 µm ø was determined using tension plates. Soil from each treatment was sieved (<2 mm) and saturated. Tensions of 10, 50, and 1500 kPa equated to water filled pore diameters of 30, 6, and 0.2 µm ø, respectively. Pores>50 µm ø were characterised using a fluorescent resin technique. The cores were impregnated with a fluorescent resin, and images of horizontal soil sections at 2.5 and 5 cm depths were analysed using Solicon© analysis software (Cattle et al., 2000; Vervoort and Cattle, 2003). For more details on methodology, see Chapter 1. Stock physical loading was calculated assuming that a standard sheep weighs 55 kg and a standard cow weighs 450 kg. The treading pressure of a cow is about double that of a sheep (Greenwood and McKenzie, 2001), with some soils being more susceptible to compaction than others (Hewitt and Shepherd, 1997).

Influence of treatment

To observe whether trends for soil invertebrates with food availability and physical condition were consistent across all sites, regression analysis was carried out using PROC REG in SAS v.9.1. It is well established that soil type is important in regulating soil fauna (Yeates, 1984) and the influence of management practices differs between soil type. For this reason, Allophanic soils which are more resilient to degradation (Lowe and Palmer, 2005) were examined separately from the non Allophanic soils.

To gain a better understanding of the relationship between invertebrates, food resources and soil porosity, the results for functional groups of earthworms, dominant mesofauna groups, and nematode trophic groups with respect to potential food resources and soil pore size distribution were analysed separately at each site using canonical correspondence analysis (CCA) with PCord v.4 (MJM Software, USA). An analysis was also conducted between invertebrate groups, total dry matter to the soil, and soil porosity. This analysis was to determine whether either food resources or habitable pore space had a larger influence on the invertebrates. In CCA settings, the data were biplot scaled, the rows and columns were compromised, and the null hypothesis of no significant effect of food resources and soil porosity on invertebrates tested using a Monte Carlo Test.

Results and discussion

Pastoral management influences both food resources available to the soil food web and physical condition of the soil. In the typical sheep grazed and dairy grazed pastures in this study the calculated amount of dry matter potentially entering the soil food web was 7.8–43.5 1000's kg DM/ha/yr, with standing faunal biomass 171–831 kg DM/ha and mean annual stock live weight loading 495–2250 kg/ha (Table 1).

Potential food resources

Increasing fertiliser application increases pasture growth which positively influences root growth and turnover, reinforcing aboveground production and litter return. Increasing stocking rates increases dung deposition on the soil surface. Since potential dry matter to the soil food web was calculated from pasture production information (Fig. 2), there was a strong positive correlation with stock live weight (Fig. 3).

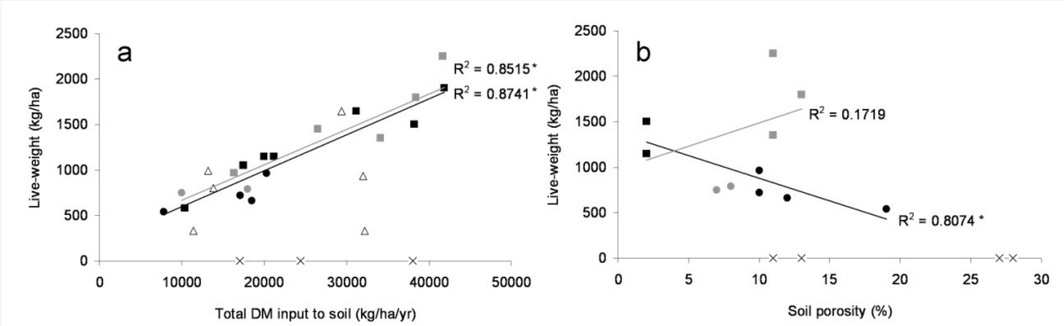

Fig. 3. Relationship between mean annual live weight of grazing stock and (a) dry matter (DM) potentially entering the soil system and (b) soil porosity as measured by resin impregnation. Trend line for Allophanic soils is grey, and non Allophanic soils is black. See Table 1 for symbols used. Note: there are fewer points on the porosity chart as porosity was only examined on the typical sheep grazed and dairy grazed pastures as shown in Table 1, and Ballantrae and Manawatu ungrazed plots (fence line, and N and P trial area). Significant regressions (α=0.1) are indicated by * after the R^2 value.

Across all sites total earthworm and nematode abundance did not respond positively to total dry matter to the soil (Fig. 4), although there were particular functional groups, such as microbial feeding nematodes, which did. The CCA analysis showed that anecic earthworms, Collembola and microbial feeding nematodes – all feeding on microbes and organic matter – have the closest association with dry matter inputs (Fig. 5). Other groups, such as Oribatida, responded negatively to the potential increases in dry matter to the soil, highlighting the important interaction between an increase in food resources and associated increase in stock live weight loading with increased pasture production.

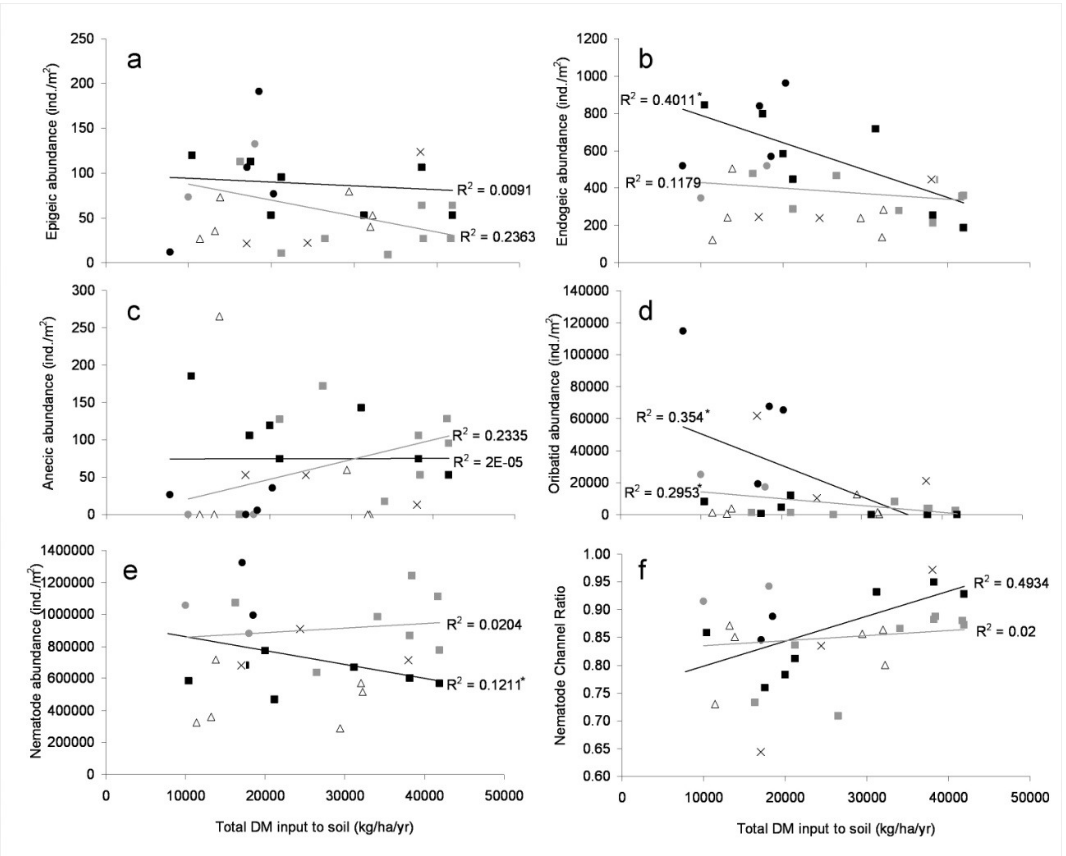

Fig. 4. Relationship between dry matter (DM) potentially entering the soil system and invertebrates. (a) epigeic earthworm abundance, (b) endogeic earthworm abundance, (c) anecic earthworm abundance, (d) oribatid mite abundance (e) nematode abundance, and (f) the Nematode Channel Ratio. Trend line for Allophanic soils is grey, and non Allophanic soils is black. See Table 1 for symbols used. Significant regressions ($\alpha=0.1$) are indicated by * after the R^2 value.

Plant feeding nematodes are the dominant group of nematodes found in grasslands (Yeates and Bongers, 1999). Their abundance, as well as the PPI, responded positively to the increased pasture growth/root mass, particularly in non Allophanic soils (Fig. 6) (Chapter 2, Chapter 4). The PPI was not higher in sheep grazed pastures with dense swards where root mass was higher (Hume and Brock, 1997; Nie et al., 1997), which suggests lower quality roots under longer grazing rotations and lower soil fertility. The CCA showed some correlation between root mass and herbivorous Thysanoptera (Fig. 5). There was also some correlation between root mass and endogeic earthworms and predatory nematodes; this association is more likely to reflect more porous soils where root mass is higher, as was observed by Gradwell (1960). Macrofauna herbivores were present at all sites but did not reflect root mass as they have very sporadic distributions (see Chapter 7). The clover cyst nematode (*Heterodera trifolii*) and clover root weevil (*Sitona lepidus*) were more abundant in pastures where clover was more abundant (Chapter 3).

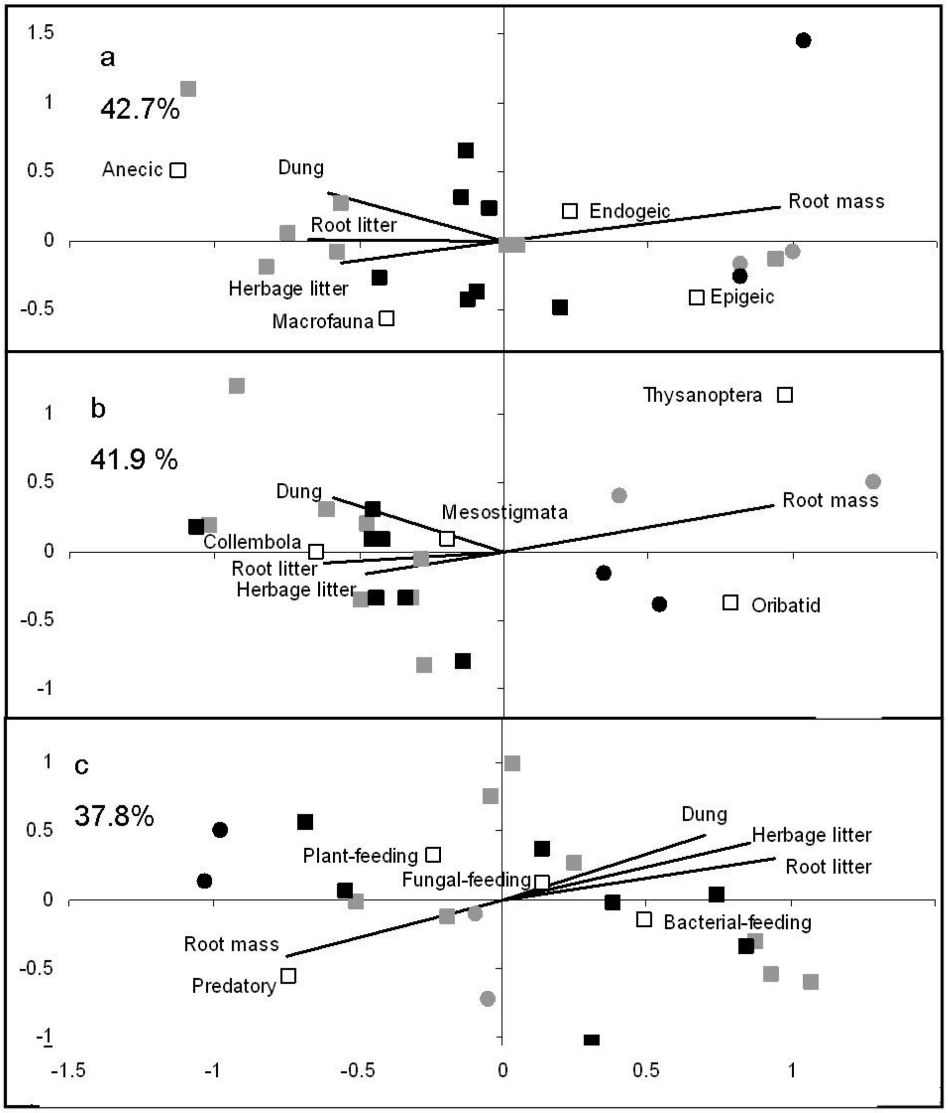

Fig. 5. Relationships between soil invertebrates (□), potential food resources and management type. (a) Macrofauna, (b) mesofauna, and (c) nematodes. The length of the lines represents the strength of relationship with potential food resources. For other symbols see Table 1. Cumulative % of data set explained by the two axes is given. The Monte Carlo test was significant for macrofauna and nematode assemblages.

Pastoral management can increase the quality of nutrients returning to the soil. This promotes the relative dominance of the bacterial (over the fungal) decomposition pathway, which is typically associated with faster nutrient cycling and may cause changes further up the food web (Wardle et al., 1998). Indeed, as dry matter input to the soil increased in non Allophanic soils, the NCR increased (Fig. 4). The NCR range in typical New Zealand sheep grazed and dairy grazed pastures was 0.70–0.95, which shows a dominance of bacterial mediated decomposition. Fungal feeding nematodes had a low abundance and biomass reflecting the relatively high fertility at all grazed sites, in comparison to ungrazed and unfertilised pastures where lower NCR values were found (Chapter 4).

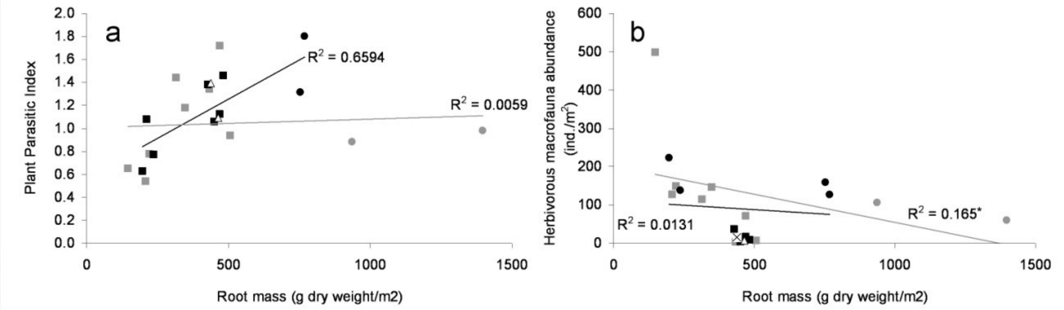

Fig. 6. Relationship between root mass and (a) the nematode Plant Parasitic Index and (b) abundance of herbivorous macrofauna. Trend line for Allophanic soils is grey, and non Allophanic soils is black. See Table 1 for symbols used. Significant regressions (α=0.1) are indicated by * after the R^2 value.

Pastures which were affected by weather disturbances (i.e., drought or alluvial deposition during flooding) had low abundances of earthworms, Oribatida, and nematodes. Even with increases in food resources invertebrate abundance did not change (triangle symbols in Fig. 4). This suggests that moisture limitations on invertebrate populations were not overcome by irrigation rates which stimulated plant growth.

Physical condition

Under pastoral agriculture treading pressures of ruminants may increase soil compaction and decrease soil porosity/habitable pore space (Elliott et al., 1980; Greenwood and McKenzie, 2001; Nielsen et al., 2008). Indeed, as live weight loading increased in non Allophanic soils, soil porosity decreased (Table 2, Fig. 3). This was not the case in more structurally resilient Allophanic soils. Soils tended to have lower porosity in dairy grazed than in sheep grazed pastures, even when structural vulnerability was similar. The management practice of mob stocking dairy cows can cause short term live weight loadings exceeding 50 tonnes/ha, creating greater treading pressures and greater likelihood of compaction in comparison to set stocked sheep pastures (Greenwood and McKenzie, 2001) (Table 1). The Allophanic Horotiu silt loam was an exception, having a low porosity even though its structural vulnerability was lowest, which may be a result of its alluvial parent material (Table 2).

Table 2. Effect of stock type, soil type and the soil structural vulnerability on soil porosity, as measured in resin embedded cores.

Soil Order	Soil Series	Parent material	Stock type	Porosity (%)[1]	Structural vulnerability[2]
Allophanic	Egmont black loam	Volcanic ash	Dairy	12	0.25
Brown	Ngamoka silt loam	Loess	Sheep	11	0.54
Allophanic	Dunmore silt loam	Volcanic ash	Sheep	8	0.55
Pallic	Marton silt loam	Loess + volcanic ash	Dairy	3	0.74
Allophanic	Horotiu silt loam	Alluvial (rhyolitic)	Dairy	2	0.19
Gley	Te Kowhai silt loam	Alluvial (fine rhyolitic)	Dairy	2	0.53

[1] Pores >50 µm ∅ as measured in resin embedded cores.

[2] from (Hewitt and Shepherd, 1997)

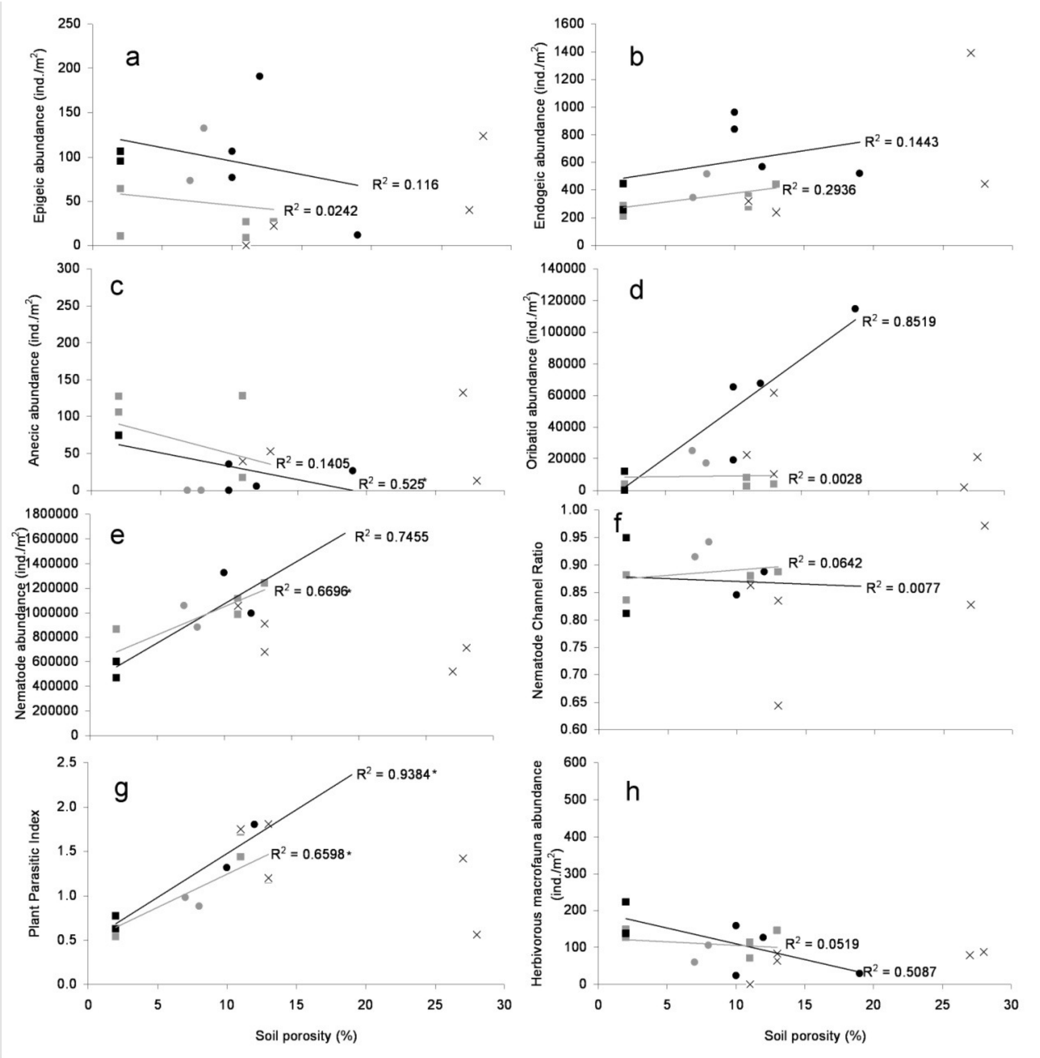

Fig. 7. Relationship between soil porosity as measured by resin impregnation and invertebrates. (a) Epigeic earthworm abundance, (b) endogeic earthworm abundance, (c) anecic earthworm abundance, (d) oribatid mite abundance (e) nematode abundance, (f) Nematode Channel Ratio, (g) nematode Plant Parasitic Index and (h) abundance of herbivorous macrofauna. Trend line for Allophanic soils is grey, and non Allophanic soils is black. See Table 1 for symbols used. Significant regressions (α=0.1) are indicated by * after the R^2 value.

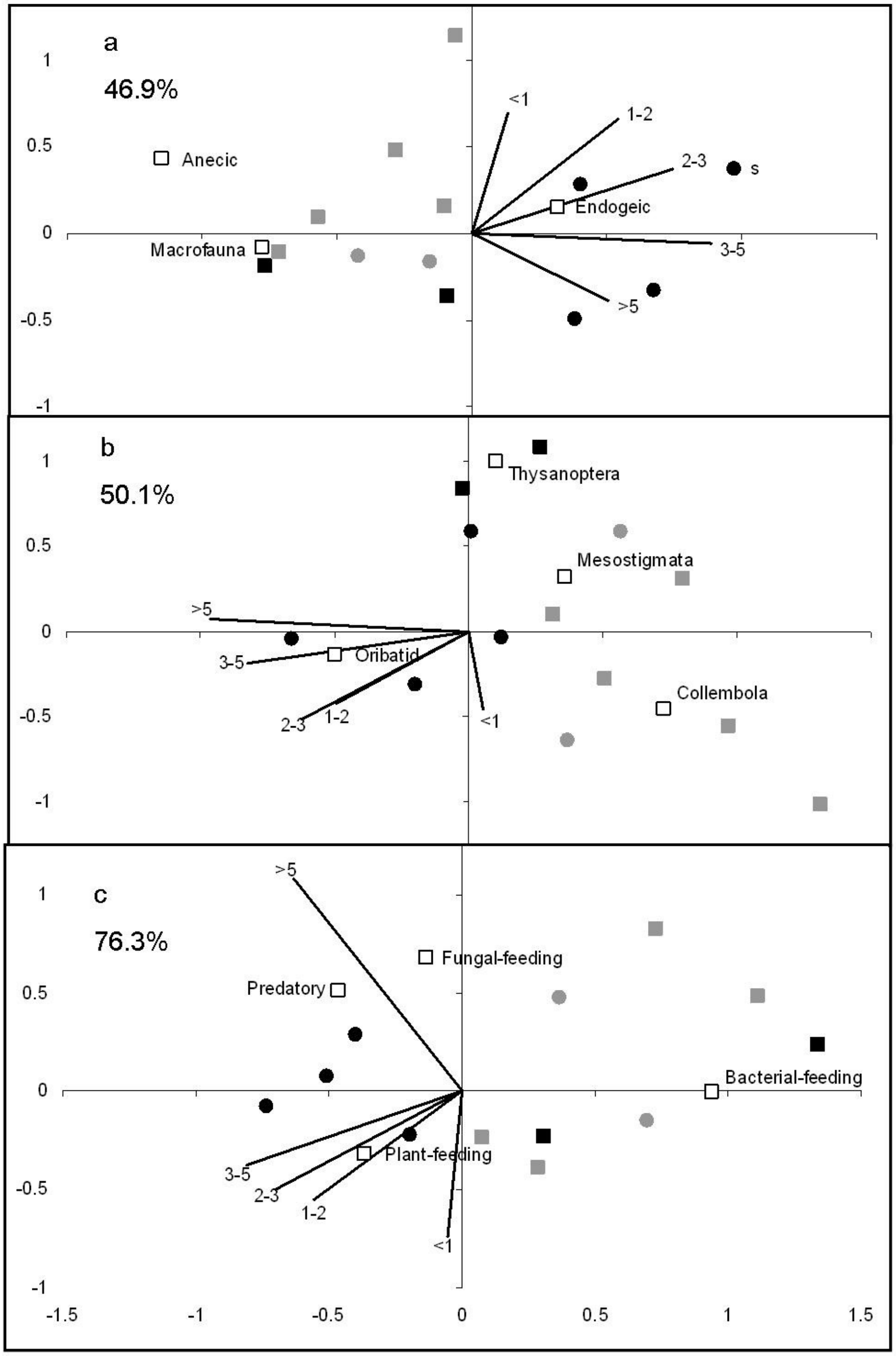

Fig. 8. Relationships between soil invertebrates (□), soil pore size and management type. (a) macrofauna, (b) mesofauna, and (c) nematodes. The length of the lines represents the strength of relationship with soil pores (<1–>5 mm ø). For other symbols see Table 1. Cumulative % of data set explained by the two axes is given. The Monte Carlo test was not significant for these three CCA.

Earthworm burrowing benefits soil porosity (Edwards, 2004) and there was some association between endogeic earthworms and soil porosity, especially pores 2–3 mm diameter (Fig. 7 & 8), typical of the burrows created by common *Aporrectodea* *caliginosa* (Springett, 1983). Epigeic and anecic earthworms appeared sensitive to a decline in soil porosity (in addition to live weight loading and dry matter input; Fig. 4), which may reflect the physical trampling effects on the topsoil habitat and the difficulty to burrow to depth.

Oribatida and nematodes are not capable of creating habitable pores and these non ecosystem engineers increase as soil porosity increases, especially on non Allophanic soils (Fig. 7).

In the soils in this study, oribatid abundance was higher in sheep grazed than in dairy grazed pastures. In support of this study, Oribatida, with their hard exoskeletons and typically long lifecycles (1–2 years), have been observed to have low abundance in physically disturbed systems elsewhere (Cianciolo and Norton, 2006; Cole et al., 2008). It was expected that oribatid size (body width) would reflect the availability of suitable pore sizes. There was some evidence of this in pastures where oribatid abundance was high (Chapter 7). However, the abundance of Oribatida was often low and thus it was difficult to draw inferences.

Plant feeding nematodes and the PPI were positively associated with pores 1–5 mm in diameter (Fig. 7 & 8). In contrast microbial feeding nematodes were not affected by soil porosity.

The less disturbed ungrazed pastures in this study had not been grazed for three to twenty years. They had porosities >10% and this may benefit soil invertebrates sensitive to stock treading. Indeed, oribatid abundance was higher under a permanent fence line where soil porosity was higher in comparison to the adjacent dairy grazed paddock (Fig. 9) (Chapter 6). Despite this, Oribatid abundance was not necessarily high under ungrazed pastures where soil porosity was high and this may be a reflection of their slow recovery time (Behan-Pelletier, 1999). That other invertebrates in ungrazed pastures did not necessarily follow the trends with porosity observed in typical sheep grazed and dairy grazed pastures, may be a reflection of differences in litter quantity and quality, and in root characteristics (Fig. 7 e, h).

Food resources and soil physical condition: overall effects

When examined separately, soil porosity had a larger and more predictable influence on soil invertebrates than did food resources across soil types (Fig 4 & 7). However, the CCA showed that invertebrates were not more sensitive to soil porosity than to food resources (Fig. 10). Anecic earthworms, Collembola and bacterial feeding nematodes were positively associated with potential dry matter inputs to the soil. Endogeic earthworms, Oribatida and plant feeding and predatory nematodes were associated with soil porosity.

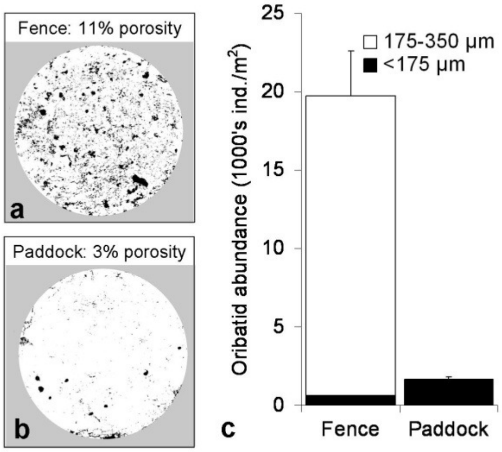

Fig. 9. Porosity as observed using resin embedding techniques between a (a) permanent fence line and (b) dairy grazed paddock on a Pallic soil (Chapter 6). White represents soil particles, black represents soil pores. (c) The differences in adult oribatid abundance and their size distribution.

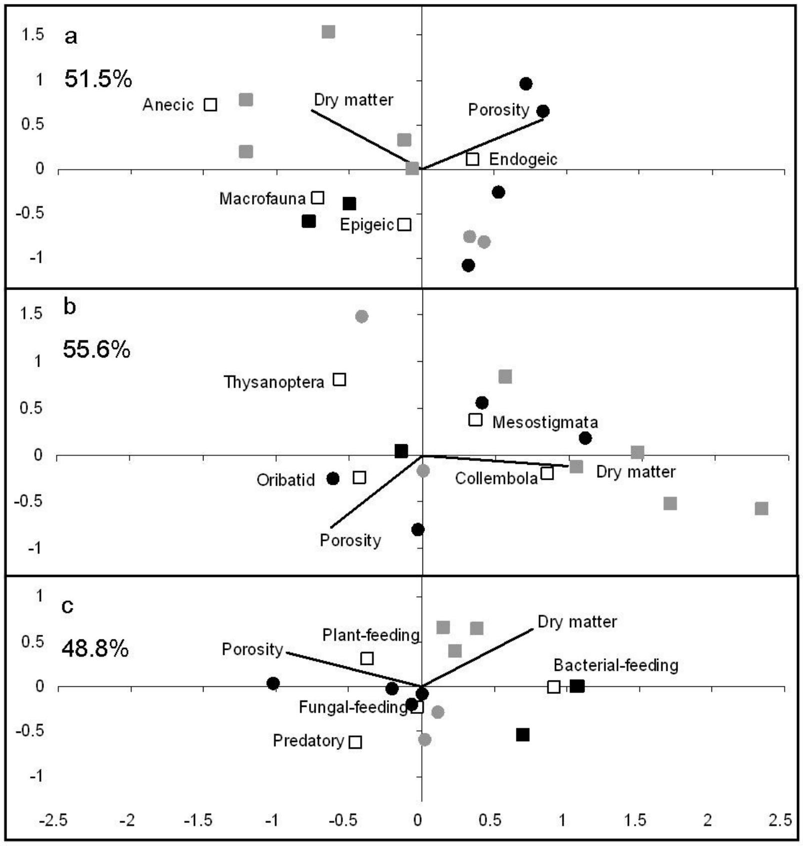

Fig. 10. Relationships between soil invertebrates (□), dry matter to the soil, soil porosity and management type. (a) Macrofauna, (b) mesofauna, and (c) nematodes. The lengths of the lines represent the strength of relationship with total dry matter to the soil and soil porosity. For other symbols see Table 1. Cumulative % of data set explained by the two axes is given. The Monte Carlo test was significant for macrofauna and mesofauna assemblages.

Whether invertebrates were sensitive to food resources or soil physical condition in the twelve soils under grazed New Zealand pastures depended on the invertebrate group, not just their size class (i.e., earthworm vs. nematode) but also their functional group (i.e., bacterial feeding vs. plant feeding). That there was a stronger relationship with porosity than with food resources may be due to the fact that in these productive pastures there are potentially large quantities of food entering the soil food web. The strong relationship between invertebrates and soil porosity highlights the importance of management practices which restore, maintain, or improve soil porosity, not only for plant growth, but also for sustaining biological communities and their role in soil services.

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Chapter Ten:

A proposed soil invertebrate threshold indicator of soil condition for New Zealand pastures

In Chapter Nine some consistent responses of soil invertebrates to changing food resources and soil physical condition were found and described. This forms the basis on which to construct an invertebrate threshold indicator which links to soil services, such as nutrient supply as shown in Chapter Eight.

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Abstract

Soil invertebrates influence a wide range of soil attributes and services on which pastoral agricultural systems are dependent. A soil invertebrate threshold indicator which uses three invertebrate size classes and is linked to soil services for use in New Zealand pastoral systems is proposed. The indicator extends current measures of soil attributes and services to provide land managers with an insight into how current practices affect soil biological populations and the soil processes they support.

Food availability to the soil food web and soil physical conditions are the key determinants of invertebrate abundance and community structure. Relationships developed between food availability, physical condition and invertebrates form the basis of the proposed invertebrate threshold indicator. The invertebrate threshold indicator includes the Nematode Channel Ratio, nematode Plant Parasitic Index, and abundances of all earthworm functional groups, Oribatida, nematodes and herbivorous macrofauna. The proposed indicator attempts to define threshold values for selected invertebrates, at which soil services may be either 'limited' or 'sustained' by the invertebrate community. Invertebrates are responsive to food resources and habitable pore space, and hence management can be manipulated to stimulate the desired invertebrate community in order to optimise the soil services.

Introduction

Soils need to be fertile and have good physical condition and biological activity for optimal pasture growth (Wall, 2004). To optimise soil productivity, organisms which promote these conditions need to be encouraged (van Eekeren et al., 2007). Through their actions of feeding, excretion, burrowing, casting, and litter incorporation it is well documented that soil invertebrates impact on a wide range of soil attributes and soil processes that contribute to soil services (Brussaard, 1998; Lavelle et al., 2006). Soil invertebrates have the potential to be useful indicators of soil services (Bardgett, 2005; Lavelle et al., 2006) and have, in various combinations, been regarded as indicators of 'soil condition'.

To be useful to land managers, biological indicators of soil condition need to be informative, providing an insight into the condition of the invertebrate community and their influence on soil services, as well as how their populations are influenced by management practices (Doran and Zeiss, 2000; Stockdale and Watson, 2009). Indices which use characteristics of the invertebrate assemblage or its constituent groups, such as trophic groups, life history strategies and body width, may fluctuate less than populations of individual taxa and thus provide a better insight into the provision of soil services (Bongers, 1990; Yeates, 1994; Paoletti, 1999; Yeates, 2003; Parisi et al., 2005). It is established that improved quality of food resources increases the relative dominance of the faster bacterial mediated decomposition pathway over fungal mediated decomposition in the soil food web, and this is captured in indices such as the Nematode Channel Ratio (NCR) (Yeates, 2003; Bardgett et al., 2005). Further, disturbances can influence community structure by favouring populations of smaller, short lived organisms, as described in maturity indices of nematodes and Acari (Bongers, 1990; Yeates, 1994; Bongers and Korthals, 1995; Siepel, 1996; Ruf, 1998; Ferris et al., 2001; Cianciolo and Norton, 2006). While each of the indices mentioned above looks at a single invertebrate group, according to Breure et al. (2005) an indicator of soil quality should include information about the soil microflora, earthworms and one mesofauna group. In The Netherlands, a biological indicator of soil quality (BISQ) uses this approach, listing important soil services ('life support functions') and the biology important to these services (Rutgers et al., 2008).

Here, an invertebrate threshold indicator is proposed to assess the soil's capacity to provide and maintain the services required by pastoral agriculture. The indicator builds on the approach used to develop the biological indicator of soil quality in The Netherlands, where they selected invertebrates underpinning the services required under pastoral land use. The indicator, which is based on relationships described in Chapter 9, aims to add to the current measures of soil attributes (e.g., Visual Soil Assessment (Shepherd, 2000)) and soil services (e.g., nutrient supply) for New Zealand, providing land managers with a greater knowledge of their soils' condition and a better understanding of how current management affects soil invertebrates and the soil services to which they contribute. This may guide land managers to ensure their management practices sustain the required biological community.

Methods

Sites and treatments

The invertebrate threshold indicator was developed using data collected during a series of studies on the influence of pastoral management on soil invertebrates (macrofauna, mesofauna and nematodes) at nine field sites and 21 treatments. These included six managements in sheep grazed pastures and 15 managements in dairy grazed pastures (Table 1). Other sites sampled in this thesis, which were affected by drought, flooding, or were ungrazed, are not included in the development of the indicator. The proposed indicator is based on samples collected in winter from 0–7.5 cm depths from flat pastoral land or from low slopes in hill country. Sites were located on experimental research farms and commercial farms in temperate New Zealand climates in Waikato, Taranaki and Manawatu. At each location the invertebrate community was described and the influence of management practices on potential food resources and soil physical condition was assessed (see Chapter 9). The findings of each field investigation have been reported in other Chapters of the thesis (Table 1).

Indicator development

Chapter 9 showed that the response of invertebrates to changes in habitable pore space and food availability was independent of soil type, so for the purposes of this indicator, the data for all soil types were combined. For each of the invertebrates included in the indicator, an estimate of abundances or indices values at which the activity of this invertebrate may ‘limit’ soil services and abundances that should ‘sustain’ soil services was calculated. This was done arbitrarily, by using the 25th and 75th percentiles of the abundance; further research should be conducted to determine abundances below which their role in soil services is limited. Thresholds were chosen as a way to reduce the spatial and temporal variability in abundances that can be expected between sites (rather than giving an optimal range). Difficulties in comparing absolute values between different sites are recognised, and to be comparable samples need to be collected during the winter months.

Table 1. Sites, their soil, treatments and number of replicates (‘reps’) sampled for soil fauna.

Site (n=9)*	Soil Order**	Soil Series	Grazing	Treatment (n=21)	Reps
Whatawhata[1]	Allophanic	Dunmore	Sheep	Low fertility	1
				High fertility	1
Whareroa[2]	Allophanic	Egmont	Dairy	3 cows/ha	5
				4 cows/ha	5
				5 cows/ha	5
Newstead[3]	Allophanic	Horotiu	Dairy	2.3 cows/ha	1
				3 cows/ha	1
				3.8 cows/ha	1
Manawatu[4]	Allophanic	Kiwitea	Dairy	Organic	1
				Conventional	1
Ballantrae[5]	Brown, Pallic (non Allophanic)	Mangamahu, Ngamoka	Sheep	Low fertility	1
				High fertility	1
Ballantrae[6]	Brown (non Allophanic)	Ngamoka	Sheep	Organic	2
				Conventional	2
Newstead[3]	Gley (non Allophanic)	Te Kowhai	Dairy	2.3 cows/ha	1
				3 cows/ha	1
				3.8 cows/ha	1
Manawatu[4]	Pallic (non Allophanic)	Tokomaru	Dairy	Organic	1
				Conventional	1
Manawatu[4]	Recent (non Allophanic)	Manawatu	Dairy	Organic	1
				Conventional	1

*The study is described in: [1]Chapter 7, [2]Chapter 1, [3]Chapter 2, [4]Chapter 3, [5]Schon et al. (2008), [6]Chapter 4.

**Soil order according to New Zealand Soil Classification (Hewitt, 1993). Allophanic soils had a P retention of >60%, and non Allophanic soils had a P retention of <60%.

Soil invertebrate threshold indicator

The components and potential application of the invertebrate threshold indicator are outlined in Fig. 1. Management practices carried out at a particular site are examined with particular focus on their effects on food resources and soil physical condition (for relationships see Chapter 9). Invertebrates which influence soil attributes and processes, and hence regulate soil provisioning and regulating services (Dominati et al., 2010), are characterised. Thresholds which attempt to define levels at which invertebrates may ‘limit’ or ‘sustain’ soil services, based on percentiles, are given in Table 2 and expanded on below. Earthworm abundance has been reported to be an important component of ecosystem functioning (Faber et al., 2008), and hence defining abundance thresholds would appear to be suitable for an indicator of soil function. Invertebrates which may be limiting soil services are identified. The knowledge of soil invertebrates, their effect on soil services, and how they are affected by management potentially allows land managers to manage soils to enhance the desired services (Pankhurst and Lynch, 1994).

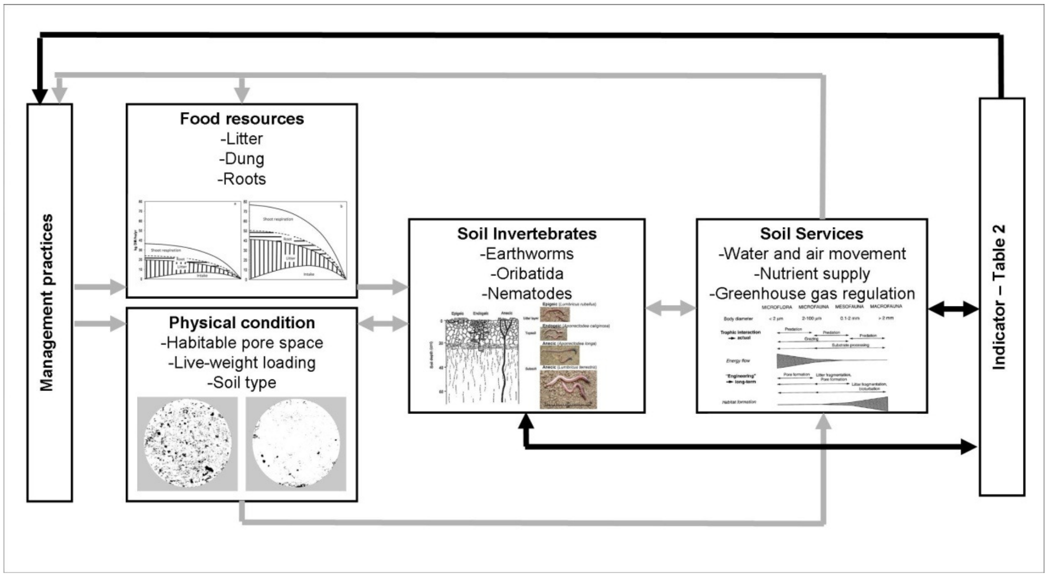


Fig. 1. Components of the proposed invertebrate threshold indicator. The current management practices influence the potential food resources entering the soil food web and the soils' physical condition, these in turn influence soil invertebrates and the services they regulate (grey arrows). The threshold values in the indicator (Table 2) are suggested to determine which invertebrates may be limiting soil services; the management can be altered to improve the contribution of invertebrates to the desired soil services (black arrows).

Earthworms

All three functional groups of earthworms (epigeic, endogeic and anecic) were included in the indicator as they have differing effects on soil services important for pastoral agriculture (Lee, 1959; Bouche, 1977; Springett, 1983). Epigeic earthworms live in the surface soil and feed on litter (e.g., *Lumbricus rubellus* with body width 2–6 mm). Endogeic earthworms form semi permanent burrows (~3 mm ø) in the top soil and feed on soil (e.g., *Aporrectodea caliginosa* with body width ~4 mm). Anecic species form deep vertical burrows (~5 mm ø) which open up to the soil surface where they feed on litter (e.g., *Aporrectodea longa* with body width 6–9 mm). Earthworms may be particularly useful as indicators for land managers, because not only are they visible to the naked eye, but also they contribute to the majority of soil services required in pastoral agriculture.

Earthworms, sometimes described as ecosystem engineers, assist in aggregate building and create burrows in the soil, helping to maintain, restore or improve soil porosity (Edwards, 2004). The combination of endogeic and anecic earthworms is particularly beneficial to soil porosity and water infiltration, with endogeic earthworms forming extensive burrow systems in the topsoil, and anecic earthworms forming few burrows which open at the soil surface (Lee and Foster, 1991). Through their actions on soil structure, earthworms assist in the services of water/air movement, physical support and flood mitigation. Aerobic conditions in the soil may increase nitrate availability (Chapter 8). Anaerobic conditions in earthworm casts may increase nitrous oxide emissions (Rizhiya et al., 2007; Speratti and Whalen, 2008), however, as earthworm activity increases soil aeration on the whole, the reduced nitrous oxide emissions from the bulk soil may offset the increased emissions from the casts. When earthworm abundance becomes extremely high (>1200 ind./m^2) there are concerns, especially for anecic earthworms, of increased bypass flow/nutrient leaching (Sparling et al., 2008).

Earthworms also play an important role in organic matter incorporation into the soil profile, particularly epigeic and anecic earthworms which feed on organic matter. Organic matter incorporation is an important process in nutrient supply and carbon storage. Earthworms produce casts rich in nutrients and, in addition to their value for soil structure, are important for plant growth (Lee and Foster, 1991; Haynes et al., 2003). In comparison to epigeic earthworms, anecic earthworms have the ability to incorporate more litter, and to greater depths (Edwards and Bohlen, 1996; Felten and Emmerling, 2009).

In pastoral systems high earthworm abundances are desirable, with all three functional groups represented. Introductions may be necessary to help establishment if certain groups are not present at a site. Introduction of the topsoil dwelling species has been achieved successfully in New Zealand (Stockdill, 1982), and the introduction of anecic species is also possible (Springett, 1984; Butt et al., 1992; Baker et al., 1994). In pastoral systems, where soil moisture and physical condition are not limiting earthworms, their populations may be stimulated by increased food supply if high quality (i.e., low C:N ratio) food is limiting (Fraser, 1994). Increasing pasture production increases plant residues, while associated increases in stocking rates increase dung deposition to the soil surface. Organic fertilisers (i.e., composts and mulches) may also provide a valuable food resource to earthworms (Edwards and Lofty, 1982).

Earthworms can be sensitive to treading, so pugging events should be avoided during wet periods when soils are most vulnerable to soil compaction. Pastoral soils in New Zealand tend to have a pH of 5–7 (Sparling and Schipper, 2002) so pH may not limit earthworm abundance as they have a pH optimum of 6–7 (Fraser, 1994; Edwards and Bohlen, 1996).

Table 2. Soil invertebrates involved in the delivery of the provisioning and regulating services for pastoral agricultural soils under sheep and dairy management. Limiting and sustaining thresholds (25th and 75th percentiles) for the abundance of invertebrates indicate when their role in supporting soil services is limiting and when their presence is sustaining. Whether food resources (F) or soil physical condition (P) has the greater 'influence' on the invertebrates is given.

Soil service/process	Important invertebrates[1]	Limiting	Sustaining	Influence
Water and air movement/supply				
Creation of soil pores	Endogeic earthworms	<350	>600	F & P
	Anecic earthworms	<20	>120	F & P
Sensitive to physical condition	Oribatid mites	<800	>17 000	P
Physical support				
Aggregate size and strength	Endogeic earthworms	<350	>600	F & P
	Anecic earthworms	<20	>120	F & P
	Total oribatid mites	<800	>17 000	P
Nutrient supply				
Organic matter incorporation	Anecic earthworms	<20	>120	F & P
	Epigeic earthworms	<25	>110	F & P
Nutrient rich faecal pellets	Total oribatid mites	<800	>17 000	P
Microbial population - control	Total nematodes	<636 000	>1 070 000	F
- pathway	NCR	<0.78,>0.89	0.78–0.89	F
Green house gas regulation				
Carbon storage	Anecic earthworms	<20	>120	F & P
	Epigeic earthworms	<25	>110	F & P
Nitrous oxide production	Endogeic earthworms	<350	>600	F & P
	Anecic earthworms	<20	>120	F & P
Flood mitigation				
Water infiltration	Endogeic earthworms	<350	>600	F & P
	Anecic earthworms	<20	>120	F & P
Pest regulation				
Plant growth	Nematode PPI	>1.4	<0.9	F
	Herbivorous macrofauna	>180	<70	F

[1] All values are abundances (ind./m^2), except NCR (Nematode Channel Ratio) and PPI (Plant Parasitic Index).

Oribatida

Of the organisms sampled, it is Oribatida, with their hard exoskeletons, which are particularly sensitive to physical disturbance and changes in habitable pore space, especially as a result of dairy cow treading, but also earthworm burrowing (Maraun et al., 2001; Cole et al., 2008; Schon et al., 2008). An increase in oribatid abundance is likely to reflect improved soil structure.

Oribatida contribute to the fragmentation of organic matter, producing nutrient rich faecal pellets (Barratt, 1971a,b; Lee and Foster, 1991). Increased oribatid abundance is likely to coincide with increases in other mesofaunal abundances, such as Collembola, and should have positive effects on nutrient supply.

Oribatid abundance should increase when there are physical habitats to reside in and the food resources are stimulated (Gupta, 1994). Reduced physical disturbance will favour their populations as they tend to have long lifecycles.

Nematoda

Increasing nematode abundance *per se* may not be beneficial to the soil services, but will likely be a reflection of a more productive system. Microbial feeding nematodes contribute to nutrient cycling by controlling and stimulating abundances of bacteria and fungi, which are important for soil structure (Miller and Jastrow, 2000), decomposition and nutrient supply (Yeates and Pattison, 2006). Further, nematodes grazing on bacteria and fungi increase available plant nutrients by excreting excess nitrogen (Yeates and Pattison, 2006). These microbial feeding nematodes can be useful in examining the relative dominance of bacteria mediated decomposition vs. fungi mediated decomposition, as approximated by the Nematode Channel Ratio (Yeates, 2003).

A NCR <0.78 indicates a fungi dominated, low fertility system, while a NCR >0.89 suggests a bacteria dominated system with fast nutrient cycling; such systems are often "leaky", losing nutrients. The NCR within the range of 0.78–0.89 is ideal for pastoral soil, indicating good soil structure and good level of fertility, but associated with slower nutrient cycling and better nutrient retention. To stimulate the fungal decomposition pathway, fungi need to increase. Attempts to inoculate the soil with fungi are not always successful (van Veen and Heijen, 1994). Instead, it is more appropriate to stimulate conditions which enhance fungal growth. For example, decreased stock grazing frequency and soil compaction, and phosphorus and nitrogen applications can benefit mycorrhizal fungi; changes in soil acidity can have varying effects depending on the fungal species (Abbott and Robson, 1994; Entry et al., 2002; Erland and Taylor, 2002). Effectively whole system changes are required to stimulate fungi.

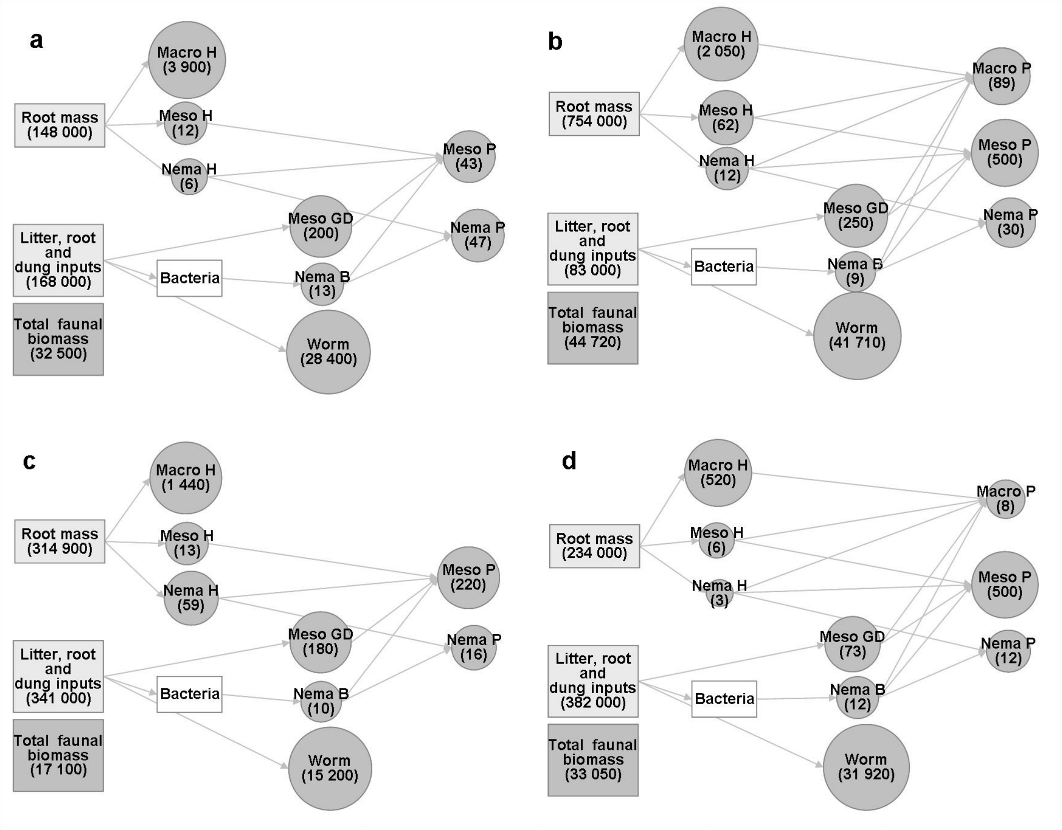
Plant feeding nematodes and macrofauna

Herbivorous fauna tend to be positively associated with food availability. Herbivorous macrofauna (grass grub, porina, clover root weevil) affect plant growth and can cause large declines in pasture productivity through their grazing. High densities of grass grub (>400 ind./m^2) and clover root weevil (>320 ind./m^2) can suppress net plant growth (East et al., 1982; Gerard et al., 2007). Similarly, high populations of plant feeding nematodes can have negative influences on pasture growth (Yeates, 1976). The prevalence of plant feeding nematodes is described in the Plant Parasitic Index (PPI) (Bongers, 1990). Ultimately, stresses caused by high densities of herbivorous fauna make plants susceptible to other stresses such as drought. However, low amounts of root herbivory may cause leakage of nutrients from roots to the rhizosphere and increased microbial populations (Yeates et al., 1998). It has been found that populations of *Longidorus* may contribute to increased root turnover (Yeates et al., 2003).

Plants bred to be resistant to herbivorous fauna may have reduced susceptibility to these stresses (Chen et al., 2004). Further, pasture diversity (Yeates and Pattison, 2006), and the application of organic composts (Oka 2010) may be beneficial for resistance to plant feeding nematodes. Grass grub populations may be reduced by grazing to a herbage height of <5 cm during the summer – reducing the roots on which they feed (East and Willoughby, 1980). Mob stocking may also reduce porina populations (French, 1973). Insecticides may help control target organisms (e.g., clover root weevil) but may disrupt natural biocontrol mechanisms and lead to increases in other pasture pests (e.g., grass grub, clover cyst nematodes) (Gerard et al., 2007).

Using the invertebrate threshold indicator: A case study

The influences of management practices on potential soil food resources, soil physical condition and soil invertebrates, form the basis of the proposed indicator. To explore the potential influence of the invertebrate community on soil services, the proposed thresholds were applied to four pastoral sites considered in this thesis (see Chapters 1, 2, 4 and 7 for the detailed descriptions). Two of these pastures were located on an Allophanic soil, and two on non Allophanic soil. They had similar inputs of phosphorus fertiliser but differed in stock type, associated live weight and soil biological communities. The results for four pastoral sites are presented in Fig. 2 and Table 3.



Food-web	a	b	c	d
Stock type	Sheep	Sheep	Dairy	Dairy
Stocking rate (SU/ha)	17	12	25	25
Liveweight (kg/ha)	935	720	1 350	1 350
Soil porosity (%)	8	10	11	2
Soil type	Allophanic	Pallic	Allophanic	Gley
P inputs (kg P/ha)	50	33	47	50
Pasture production (kg DM/ha)	12 500	9 600	14 000	15 900
Total dry matter to the soil (kg DM/ha)	18 000	17 100	34 100	38 200

Fig. 2. Soil food webs of selected soil faunal groups and associated site properties in: sheep grazed pastures on (a) Allophanic soil, (b) non Allophanic (Pallic) soil, and dairy grazed pastures on (c) Allophanic soil and (d) non Allophanic (Gley) soil. Macrofauna (Macro), mesofauna (Meso) and nematode (Nema) herbivores (H) feed on plant material. Earthworms (Worm), general detritivores (GD), bacterial feeders (B) and fungal feeders (F) feed on detrital inputs and associated microflora. The macrofauna, mesofauna and nematodes are in turn consumed by predators (P). The area of circles represents the log of the faunal biomass (mg dry weight/m^2) and litter, dung and root returns are given in mg dry weight/m^2. Soil physical condition and pasture production are also given. Only (d) received nitrogen as fertiliser (170 kg N/ha/yr).

In both sheep grazed pastures (Fig. 2 a, b) the high abundance of epigeic earthworms ensures good litter incorporation (Table 3). However, the absence of anecic earthworms may have implications for organic matter incorporation deeper into the soil, and for creation of soil pores, affecting water/air movement, nutrient supply and carbon storage (Table 3). The absence of peregrine anecic earthworms is the general situation for New Zealand hill country pastures. The reason for the absence is suspected to reflect their restricted distribution in New Zealand rather than management practices (Springett, 1992). Introducing anecic earthworms to hill country should have positive effects on soil services such as water infiltration, water/air movement, physical support, nutrient supply, greenhouse gas regulation). In the non Allophanic sheep grazed pasture both the nematode PPI and herbivorous macrofauna are reaching levels which may limit soil services (Table 3). The NCR suggests that the fungal based decomposition pathway is relatively small with few decomposer fungi present in these soils.

Table 3. Soil invertebrates linked to the soil services in two sheep grazed and two dairy grazed pastures. Pastures and their food webs are described in Fig. 2. Bold font indicates that the value may be "limiting" that soil service. For limiting and sustaining thresholds for abundance, NCR and PPI see Table 2.

Soil service/process	Important invertebrates[1]	Sheep pastures		Dairy pastures	
		(Fig. 2a)	(Fig. 2b)	(Fig. 2c)	(Fig. 2d)
Water and air movement/supply					
Creation of soil pores	Endogeic earthworms	516	837	**278**	**254**
	Anecic earthworms	**0**	**0**	**18**	74
Sensitive to physical condition	Oribatid mites	17 100	19 200	8 100	**100**
Physical support					
Aggregate size and strength	Endogeic earthworms	516	837	**278**	**254**
	Anecic earthworms	**0**	**0**	**18**	74
	Total oribatid mites	17 100	19 200	8 100	**100**
Nutrient supply					
Organic matter incorporation	Anecic earthworms	**0**	**0**	**18**	74
	Epigeic earthworms	132	106	**8**	106
Nutrient rich faecal pellets	Total oribatid mites	17 100	19 200	8 100	**100**
Microbial population - control	Total nematodes	881 200	1 322 800	985 300	**599 700**
- pathway	NCR	**0.94**	**0.90**	0.87	**0.95**
Green house gas regulation					
Carbon storage	Anecic earthworms	**0**	**0**	**18**	74
	Epigeic earthworms	132	106	**8**	106
Nitrous oxide production	Endogeic earthworms	516	837	**278**	**254**
	Anecic earthworms	**0**	**0**	**18**	74
Flood mitigation					
Water infiltration	Endogeic earthworms	516	837	**278**	**254**
	Anecic earthworms	**0**	**0**	**18**	74
Pest regulation					
Plant growth	Nematode PPI	0.88	1.31	**1.44**	0.77
	Herbivorous macrofauna	106	159	71	138

[1] All values are abundances (ind. /m^2), except NCR (Nematode Channel Ratio) and PPI (Plant Parasitic index)

Of concern in both dairy grazed pastures is the low abundance of endogeic earthworms (Fig. 2 c, d). In the Allophanic soil all earthworm functional groups are low and nematode PPI high. This suggests that the positive influence of earthworms on soil porosity and organic matter incorporation may be limited, while plant feeding nematodes may be suppressing plant growth. In the non Allophanic soil oribatid and nematode abundance are low. Potential food resources to the soil are unlikely to be limiting their populations and it may be that stock live weight loading of dairy cows is exerting significant pressure on this non Allophanic soil which is vulnerable to compaction. The NCR suggests that there are few fungi in these soils, with little contribution by the fungal decomposition pathway.

Conclusion

Food resources and soil physical condition influence soil invertebrates. These relationships, which were independent of soil type, form the basis of the proposed indicator. The contribution of soil invertebrates to soil services is formalised. Invertebrate threshold values are suggested as a tool to determine which invertebrates may be limiting soil services. The invertebrates used in the indicator include all three functional groups of earthworms, Oribatida mites, nematodes (including Nematode Channel Ratio and Plant Parasitic Index), and herbivorous macrofauna.

When applied to four different pastures the invertebrate threshold indicator highlighted some invertebrates which may be limiting soil services. At least one functional group of earthworm was found in low abundances in each pasture. This is concerning as earthworms contribute to many of the soil services important in pastoral agriculture by improving soil porosity, water infiltration, aggregate size and strength, as well as organic matter incorporation and carbon storage. In applied use of invertebrate threshold indicator, a particular focus may be given to earthworms, as they are visible with the naked eye and have a role in a wide range of soil services. It is the “limiting” and “sustaining” thresholds of earthworm abundance which may be most valuable to land managers. With further validation, the invertebrate threshold indicator may give land managers a basis on which to alter management practices to stimulate the desired invertebrate community in order to optimise the soil services.

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General discussion and conclusions

General discussion

Invertebrates living in the soil are difficult to observe and study but they can provide us with knowledge far greater than their actual size would suggest (Coleman, 2008). The presence and activities of invertebrates contribute to and support a wide range of soil services which are essential for pastoral agriculture (Lavelle et al., 2006). They, in turn, are influenced by the quantity and quality of the food supply and the soils physical environment, which change as pastures become intensified.

Previous work in New Zealand has examined the influence of pastoral management on selected invertebrate groups, particularly earthworms and nematodes (McMillan, 1969; Yeates, 1978a,b; Fraser et al., 1996). Little work has been conducted on the influence of management practices on all three size classes of invertebrates (macrofauna, mesofauna and nematodes), or attempted to link responses of invertebrates to soil services. To be useful to land managers, biological indicators of soil services need to be understood and linked to pasture management practices (Stockdale and Watson, 2009).

This thesis tested the hypothesis that consistent responses of soil invertebrates to changing pasture management practices can be used in the development of a biological indicator that is linked to soil services. In the thesis, a particular focus was given to developing an improved understanding of the impact of food availability (calculations of potential food resources, constructions of soil food webs) and physical condition (determination of habitable pore space and stock live weight loading) on the invertebrate community at a diversity of sites and soils. Sampling a diversity of sites was chosen over sampling one site in detail, this allowed for general trends to be observed across the diverse New Zealand agricultural landscape. One of the main limitations of sampling a diversity of sites, rather than one study site in detail is the temporal variability; to minimise this samples were only collected in winter. Field sites included nine different managements in sheep grazed pastures (i.e., fertiliser, stocking rates, irrigation, organic vs. conventional), 17 different managements in dairy grazed pastures (i.e., fertiliser, stocking rates, organic vs. conventional) and 15 in ungrazed pastures (i.e., fallow, cut and carry).

This thesis had three main aims to address this hypothesis:

1) Explore the response of soil invertebrates to pastoral management under a variety of agricultural systems.
2) Determine the contribution of invertebrates to the availability of nitrogen in pastures.
3) Develop a biological indicator for New Zealand pastures linked to soil services.

1. Response of invertebrates to changing food availability and soil physical condition resulting from changing pastoral management

It was predicted that more productive pastures, with increasing inputs of litter and excreta to the soil food web, would stimulate invertebrate populations. This was supported for some invertebrates including anecic earthworms, bacterial feeding nematodes (an important component of the Nematode Channel Ratio) and plant feeding nematodes (summarised by the Plant Parasitic Index). Anecic earthworms increased in abundance and biomass with increases in stocking rate in the Andosol (Chapter 1), and this was suspected to be due to their deep burrowing which enables them to avoid treading damage. These deep burrowing, surface litter feeding earthworms may be a suitable substitute, but also support, for epigeic earthworms which are more sensitive to treading pressure.

Further, it was suspected that the increased live stock numbers, treading pressures, and associated declines in habitable pore space would be more pronounced in soils with limited physical structure, and would be reflected in decreased abundances of more sensitive invertebrate groups. Indeed, Oribatida with limited mobility and a hard exoskeleton were sensitive to stock treading pressures. Oribatid abundance declined in both sheep and dairy grazed pastures as stock live weight loading increased, and was especially low in abundance in dairy grazed pastures (Chapters 1 and 2). Other invertebrates were also sensitive to stock treading pressure, and while the Oribatida with their long lifecycles did not recover once treading pressure was removed, the shorter lived predatory nematodes recovered (Chapter 6). Lower dairy cow stocking rates under organic management resulted in higher abundances of endogeic earthworms and calculated N mineralisation than on paired conventional systems (Chapter 3), despite food availability being greater under conventional systems. There was no decline in earthworm abundance from conventional to organic management when sheep stocking rate and fertiliser application was consistent (Chapter 4), highlighting the importance of these two management practices (stocking rate and fertiliser application) on the soil fauna.

2. Contribution of invertebrates in nitrogen supply availability to pastures

It was hypothesised that in pastures where nitrogen was not limiting pasture growth, the invertebrates would have a reduced influence on nitrogen (N) supply. Contrary to our hypothesis, in an artificially constructed legume based pasture mesocosm (Chapter 8), it was observed that invertebrates stimulated N availability to plants even in N fertilised and compacted systems. Through their activities of pore construction and organic matter fragmentation, invertebrates produce plant available nutrients in their faecal pellets and casts.

This highlights the importance of soil invertebrates even in modified (compacted and fertilised) systems. Importantly, the study provides a direct link between the invertebrate community and nutrient supply, demonstrating to land managers the importance of preserving invertebrate populations as part of the strategy for sustaining nutrient supply to pastures.

3. Development of an invertebrate threshold indicator linked to soil services for land managers of New Zealand pastoral soils

As was hypothesised, there were some consistent responses of invertebrates to pastoral management. In two contrasting soils where phosphorus fertiliser and sheep stocking rates increased, the earthworm abundance increased and oribatid abundance decreased (Chapter 7). Other fauna, such as herbivorous macrofauna, did not behave predictably, with their distribution sporadic, but were still an important component of the soil fauna, having a direct and significant influence on plant growth when abundant.

While soil type was important in structuring invertebrate communities, the overall responses of invertebrate functional groups tended to be consistent independently of the soil type (Chapter 6 and 9). When explored across all sites, soil porosity appeared to have a larger and more consistent influence on soil invertebrates in comparison to changes in the potential food resources (Chapter 9). Soil porosity even limited earthworms, which contribute to maintaining and restoring soil porosity. The large quantity of food potentially available to the belowground soil food web, a quantity of dry matter similar to what is consumed by aboveground herbivores, suggests that food supply was not limiting invertebrate populations. Further, this response to soil porosity reflects the combined influence of soil type and management practice on the environment of soil invertebrates (soils vulnerable to compaction will be more affected by increases in stock treading pressure). The strong relationship between invertebrates and soil porosity highlights: 1) the importance of considering soil physical characteristics when studying the invertebrate community, 2) the potential for invertebrate activities and their contributions to soil services to be limited in compacted soils, and 3) the importance of employing management practices which restore, maintain, or improve soil porosity, biological communities and their role in soil services.

However, invertebrates can be expected to respond predictably to management practices only in soils where they are not limited by strong seasonal moisture fluctuations. In the summer dry environment of Canterbury, annual periods of extended soil moisture deficit was associated with a decline in earthworm activity and more short lived organisms which showed little response to sheep stocking rate or fertiliser application (Chapter 5). Under conditions where invertebrate populations are more influenced by a stress than by management practices, the stress needs to be overcome before invertebrates can benefit soil services.

The consistent responses of soil invertebrates and their characteristics to pastoral management (described in Chapter 7 and 9) provided the basis for developing a soil invertebrate indicator (Chapter 10). By linking the role of the invertebrates to soil attributes (e.g., pore size distribution) and processes (e.g., N mineralisation rates) that support the soil services important in New Zealand pastoral soils, the indicator has a direct application to land managers. The proposed indicator attempts to define threshold values for selected invertebrates, at which soil services may be either 'limited' or 'sustained' by the invertebrate community.

Included in the threshold indicator were: 1) all three earthworm functional groups (epigeic, endogeic and anecic), which contribute to the maintenance of soil structure and/or litter incorporation. 2) Oribatida, a group sensitive to treading disturbance. 3) Nematodes, with their abundance responding to productivity and the Nematode Channel Ratio providing information on the relative contribution of the bacterial over the fungal decomposition pathway. 4) The nematode Plant Parasitic Index and the abundance of herbivorous fauna, which assess the likelihood of reductions in plant growth. The linking of invertebrate thresholds to soil services, with further validation, may be a useful tool for land managers.

This thesis focused on determining the relationship between invertebrates and pastoral management. Well established links between invertebrates and soil services (Bardgett, 2005; Lavelle et al., 2006; Rutgers et al., 2008) were not measured directly in this study, but further studies should be carried out to determine more accurately at which critical abundances the invertebrate activity will limit selected soil services. The invertebrate threshold indicator operates on the basis that when there are no or very low numbers of selected invertebrates, they will have no or limited contribution to soil services. Further, the indicator attempts to overcome the limitation of natural variability in invertebrate abundances between sites by setting thresholds which may influence soil services at any site. The proposed invertebrate threshold indicator has advantages over existing indicators (Bongers, 1990; Yeates, 1994; Paoletti, 1999; Yeates, 2003; Parisi et al., 2005) by considering more than one invertebrate group, having a strong focus on soil services, and being linked to pasture management practices. Further, by understanding the relationship between invertebrates and management practices we are able to give suggestions on how to manipulate invertebrate abundances.

In particular, the thresholds for different functional groups of earthworms (potentially combined into a tool such as the Visual Soil Assessment) may have the largest practical application. Not only do earthworms, with their large biomass in the soil, contribute to a range of soil services, they are visible with the naked eye, and may be one of the invertebrate groups which are more easily manipulated. For example, the absence of peregrine anecic earthworms from most of the hill country pastures sampled in this study may be remedied by their introduction. Further their establishment in dairy grazed pastures may benefit surface active earthworms and be crucial for litter incorporation and carbon storage, as epigeic species are more vulnerable to treading pressures.

Future Research

This thesis contains a comprehensive data set on the behaviour of all size classes of soil invertebrates under a wide range of pastoral management practices. The relationships derived from these data and the methodologies developed to quantify food resources and physical condition form a critical part of the proposed invertebrate indicator linked to soil services. The proposed biological indicator adds to the current measures of soil attributes (i.e., Visual Soil Assessment) and soil services (i.e., nutrient supply), to give land managers greater knowledge of how their actions are affecting soil invertebrates and the processes to which they contribute. The hope is that this may guide land managers to change their current management to ensure the desirable biological community is obtained and sustained to underpin soil services required in the long term.

This thesis has identified some future topics for research, including:

- Determining the potential of different earthworm functional groups to incorporate litter and dung from the soil surface into the soil profile (the amount and depth), and the implications of this on carbon storage and soil physical attributes.
- Assessing the potential of anecic earthworms to reduce the pressure on surface active invertebrates, and to assist the role of epigeic earthworms in litter incorporation.
- Exploring the potential of large scale introductions of anecic species in New Zealand for improving carbon storage and sustaining soil physical attributes.
- Assessing possible deleterious effects of anecic earthworms on ‘by pass’ flow of nutrients to ground water.
- Investigating the relationship between different habitable pores and requirements of invertebrates, establishing which habitable pore sizes, when lost, have the greatest influence on invertebrates that are not ecosystem engineers.
- Exploring the influence of soil type and bulk density on pore sizes created by earthworm burrowing, and these pores influence on water and air movement.
- Further assessing the influence of stock treading pressures on the soil invertebrate community (i.e., treading pressure, stocking rate, frequency of treading, vulnerability of soil to compaction in relation to engineering properties of soil). What degree of ‘treading’ can invertebrates withstand and when?

- Extending the mesocosm study (which indicated that invertebrates stimulated nitrogen cycling in compacted and high nitrogen soils) under field conditions.
- Establishing critical limits at which invertebrate activity in soil attributes and processes declines to the point that the underlying service (i.e., nutrient availability) diminishes or fails in different soils.

Conclusions

Soils under New Zealand pastures are coming under increasing pressures as farmers increase fertiliser application and stocking rates to increase productivity. The soil is important, storing water and nutrients and providing a habitat for soil invertebrates. Through the actions of feeding on the soil organic matter and burrowing through the soil, invertebrates make important contributions to nutrient supply and water movement. In this thesis, it was observed that invertebrate contributions to nutrient supply in pastures remained important even in fertilised soils where nutrients were not limiting.

Soil invertebrates are very diverse, ranging in both size and function and it is important for all functional groups to be represented within the soil food web. The functional diversity of invertebrates ensures their differing responses to agricultural management practices, but those with similar characteristics tended to behave consistently in response to pastoral management in New Zealand, particularly to changes in soil porosity. The relationship between invertebrates, soil services and pastoral management allowed the development of the invertebrate threshold indicator. In the future this threshold indicator could become a useful tool for land managers to manage their soils, to obtain desirable communities of invertebrates, and to benefit from their actions within the soil. Soils which have low abundances of invertebrates will not benefit from the contribution of invertebrates to soil services, for example, low abundances of litter incorporating invertebrates may result in more surface applied carbon lost directly to the atmosphere.

This thesis highlights the importance of soil invertebrates in New Zealand pastoral systems and the need for their management, which extends to include invertebrate introductions.

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