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INFLUENCE OF LAND USE ON SOIL ORGANIC MATTER STATUS, MICROBIAL BIOMASS C AND SIZE AND COMPOSITION OF EARTHWORM COMMUNITIES IN NORTHERN KWAZULU-NATAL

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By

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ABSTRACT

The effect of land management including undisturbed native forest, native grassland, sugarcane (preharvest burnt or green cane harvested), exotic forest (gum, pine or wattle), orchard crops (banana, orange and avocado) and grazed kikuyu grass pastures on soil organic matter status, size of the microbial biomass and size and composition of the earthworm community was studied. The study locality was in the tropical, northern part of KwaZulu-Natal near the town of Eshowe and sites were on a number of sugar estates in the area.

Concentrations of soil organic C were notably high under kikuyu pasture, native forest and banana and lowest under burnt cane. Among the land uses, values followed the order : kikuyu pasture ≥ native forest > banana > native grassland = orange ≥ trashed cane = gum ≥ pine ≥ avocado > wattle ≥ burnt cane. Soluble C was considerably higher under kikuyu pasture than other land uses. Soils under native forest and banana also had relatively high values while lowest values were recorded under burnt cane. Values for microbial biomass C showed broadly similar trends with land use to soluble C. Very high values for microbial biomass C (> 2000 mg kg^{-1}) and microbial quotient (> 4.5 %) were recorded under kikuyu pasture, native forest, banana and orange whilst lowest values for microbial biomass C (250 - 750 mg kg^{-1}) and microbial quotient (1- 2 %) were found for soils under avocado, trashed and burnt sugarcane.

Earthworm numbers followed the order : kikuyu pasture > native forest > banana > orange > wattle = pine = gum = trashed sugarcane ≥ native grassland ≥ avocado > burnt sugarcane. Values for earthworm numbers and biomass were closely correlated. Earthworm numbers, microbial biomass C and soluble C were closely correlated with each other but none were significantly correlated with soil organic C content. Earthworm numbers were also positively correlated with soil pH and exchangeable Ca content.

A total of 11 species of earthworm were collected from the sample sites. Over 80 % of the individuals collected were accidentally-introduced exotic species which originated from India, South America and West Africa. Most land uses supported between 5 and 7 species. Wattle forest and sugarcane, however, had only 2 or 3 species. Juveniles dominated the community under all land uses except kikuyu pasture and avocado where the majority of earthworms were adults. Epigeic species dominated the community under native forest and native grassland and this was also the case under avocado and gum. For the other land uses endogeic species predominated.

The most numerous earthworm species present was *Pontoscolex coreththrurus* which was present under all the land uses. It is a peregrine, endogeic species originating from South America and is thought to have been introduced via India. The most common epigeic species was the Indian species *Amynthas rodericensis* which made up a particularly notable portion of the community under native and gum forests, avocado and banana. The third most numerous species was *A. minimus*, also from India, which is a polyhumic, endogeic species. It was particularly numerous under kikuyu pasture. In 8 out of 11 land uses, *P. corethrurus*, *A. rodericensis* and *A. minimus* coexisted together. Another polyhumic, endogeic species, *Dichogaster saliens*, which originates from West Africa, was present particularly under oranges, wattle and sugarcane. The only land use that contained mainly native species was native grassland where *Tritogenia douglasi* and *Acanthodrilidae sp* predominated.

It was concluded that organic matter content, microbial biomass C, soluble C and the size and composition of earthworm communities in soils of the study area are greatly affected by land management practice. As is the case in most other parts of the world, the earthworm community under agricultural land management is dominated by accidentally introduced exotic species and these have also emigrated into soils under native vegetation. The role of these species in influencing soil chemical, physical and microbial properties, and thus soil fertility, deserves further studying.

DECLARATION

I hereby certify that the research reported in this thesis is my own work, except where otherwise indicated in the text, and that the work has not been submitted for a higher degree at any other institution

Signed: ....

Thembisile Charity Dlamini

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

GENERAL INTRODUCTION AND STUDY OBJECTIVES

Current agricultural management practices and their role in soil degradation have raised concerns regarding the sustainability of agroecosystems and kindled interest in evaluation of soil quality through the use of chemical, physical and biological indicators (Karlen et al., 1997). Earthworms are an extremely important component of soil macrofauna and they are involved in many key soil processes. They play a vital role in nutrient cycling through organic matter decomposition (Lavelle, 1988), and have the potential to significantly improve soil properties (Lee, 1985). Thus, they enhance plant yield and positively affect crop productivity (Stockdill, 1982; Curry and Boyle, 1987) because of their beneficial effects on the soil environment (Edwards and Bohlen, 1996). Through their feeding and burrowing, earthworms can improve soil aggregate stability, incorporate surface organic matter, lime and fertilizers, create macroporosity, increase soil microbial activity and enhance nutrient availability (Edwards and Bohlen, 1996). Comparisons of field-collected earthworm casts with the surrounding soil have revealed casts usually have greater microbial populations, higher enzyme activity, larger concentrations of available nutrients and greater structural stability than surrounding soil aggregates (Blair et al., 1995; Edwards and Bohlen, 1996). In addition, their burrowing activities influence macroporosity and thus the transmission of water and air in soils (Tomlin et al., 1995). Owing to their key role in soil ecosystem functioning, their numbers and biomass can be used as indicators of soil quality (Doube and Schmidt, 1997).

Earthworms can be functionally classified according to the different roles they play in the ecosystem. These classes include epigeics that are litter feeding and dwelling, anecics which are litter feeding but build permanent subterranean burrows and live at depth, and endogeics that live in and feed on soil and which dig galleries and chambers within the plough layer (Edwards and Bohlen, 1996). As a result of the diverse roles that earthworms

1

play, it is not only the size of their community that is important but also the species composition. Whilst earthworms are found in many soils throughout the world, populations commonly range from less than 1 to greater than 850 m^{-2} (Lee, 1985). Populations are generally lower in acid soils and bare, fallow soils than in pasture soils. In the humid tropics earthworms are best represented in grasslands and are less abundant in forested and dry areas.

In most parts of the world, indigenous earthworms are more or less restricted to soils under natural vegetation and species present in agricultural soil are predominantly accidentally introduced (by man's activities) species (Fraser, 1994; Lavelle *et al.*, 1994). The size and composition of earthworm communities in South African agricultural soils is not well known. However, Plisko (2000) evaluated the role of nature reserves in protection of terrestrial earthworm fauna in KwaZulu-Natal, and found that indigenous species are remarkably limited to natural habitats. Hence, preliminary observations have suggested that there are a large number of introduced species in South Africa, most of which originated from Europe and India (Ljungström, 1972). In his observations, Ljungström (1972) noted that in the sugarcane belt of KwaZulu-Natal province the main populations are *Pheretima* spp., which were introduced from India (by the large Indian population). These species tolerate the subtropical climate of the region. A compendium of the introduced earthworms of South Africa and their taxonomy was compiled in 1972 (Ljungström, 1972) and a detailed collection is held at the Natal Museum (Pietermaritzburg) by Dr J.D. Plisko.

Very little research has been carried out on earthworm populations under sugarcane production. Research in South America (Lavelle *et al.*, 1994) suggested that sugarcane plantations could be considered essentially as humid grasslands and they support earthworm populations of similar magnitude to natural savannas (e.g. 33 - 35g m^{-2} or about 100 - 150g m^{-2}). In northern Queensland, Wood (1991) observed that under burning, earthworm populations averaged 75 m^{-2}. However, when fields were converted to green cane harvesting, with trash retention, populations increased rapidly to about 200 - 300 m^{-2}.

2

Nonetheless, observations in KwaZulu-Natal have suggested that there are very few earthworms under sugarcane production even when green cane harvesting is practised. Loss of soil organic matter content and soil compaction in the interrow spaces under long-term cane production (Haynes and Hamilton, 1999) are suspected to be the major causes of the low populations. Even so, no structured study has been carried out and populations may well change markedly across fields being much greater in, than between, sugarcane rows. The quantification of earthworm populations in agricultural soils is important for the following reasons :

(a)   Earthworms constitute a large proportion of soil mesofauna and have major positive effects on both nutrient availability and soil structural conditions.

(b)   Earthworms can be used as bioindicators of sustainable soil management practice (Lee, 1995). Their populations change rapidly in response to changes in C availability in the soil. For example, they rapidly increase under pasture and zero tillage and decline rapidly under conventional cultivation (Lee and Pankhurst, 1992; Edwards *et al.*, 1995).

(c)   Where indigenous earthworms are absent from agricultural land, and exotic species have been introduced by accident, there can often be localities where earthworms are not present due to lack of any introduction. In such cases, the introduction of earthworms can result in sustained stimulatory effects on crop yields under field conditions. This has been noted, for example, in New Zealand pastures (Stockdill, 1982) and reclaimed Dutch polders (Hoogerkamp *et al.*, 1983).

(d)   In situations of accidental introduction not all ecological types may have been introduced (Fraser *et al.*, 1996). For example, deep burrowing types may be absent and their introduction may well increase surface-connected macroporosity in soils.

In this study, the main objective is to investigate the size, composition and distribution of earthworm communities under different agricultural land uses compared to undisturbed native vegetation under South African conditions. The project was partly funded by the

3

South African Sugar Experiment Station and consequently the study was carried out on Sugar Estates in northern KwaZulu-Natal. The main land uses on these large estates, apart from sugarcane, are forest (gum, wattle and pine plantations), horticultural crops (citrus, banana and avocado) and permanent kikuyu pastures. Remnants of undisturbed land still exist as grassveld and indigenous forest.

CHAPTER 2

INFLUENCE OF LAND USE ON SOIL ORGANIC MATTER STATUS, MICROBIAL BIOMASS C AND SIZE AND COMPOSITION OF EARTHWORM COMMUNITIES IN NORTHERN KWAZULU-NATAL: REVIEW OF LITERATURE

2.1 Introduction

The soil is a habitat for a vast, complex and interactive community of soil organisms, whose activities largely determine the physical and chemical characteristics of the soil (Lee and Pankhurst,1992). Of the soil organisms, earthworms play an important and dominant role in the development and maintenance of the soil structure and fertility. Indeed, earthworms are an important biotic element of agricultural soils and contribute significantly to the physiochemical and microbiological formation of the soil environment. They affect the physical characteristics as they dig burrows, deposit casts on the soil surface and within, mix horizons and bury above ground- litter (Lee, 1985). The result of their activity is a general increase in porosity and aeration of soil and an improvement in hydraulic properties and structural stability (Lee, 1985). Soil characteristics are both the determinant and the consequence of earthworm activities (Edwards and Bohlen, 1996).

Earthworms find in the soil the energy, nutrient resources, water and buffered climatic conditions. They take an active part in energy and nutrient cycling through the selective activation of both mineralization and humification processes (Lavelle, 1988). By their physical activities and chemical effects, earthworms promote the cycling of nutrients within the soil system (Villenave *et al.*, 1999). Earthworms do not add any nutrients to the soil, but their activities and associations with microorganisms result in increased availability and rates of cycling of plant nutrients as well as changes in soil physical properties that promote plant growth.

5

Since earthworms often make up a large proportion of the biomass of the soil fauna and they are involved in soil chemical, physical and microbial processes they are used as an indicator of soil quality (Baker, 1998). Although earthworms are found in soils throughout the world, comparison between different studies can be complicated by differences in extraction methods and by seasonal changes in community size and composition at a particular site (Lee, 1985). However, there are generally few earthworms in acid soils, bare fallow and arable soils (Edwards and Bohlen, 1996). In the humid tropics earthworms are best represented in grasslands and are less abundant in forested and dry areas (Fragoso *et al.*, 1999b). Their role in soils of arid areas of the subtropics is often taken by termites and to some extent, ants. Earthworms appear to attain their highest populations in the pastures and deciduous woodlands of Europe and temperate regions of Asia (Lee, 1985). They are not uniformly distributed in the profile of soils. Indeed, different species inhabit different layers in soil. For example, *Lumbricus rubellus* is frequently found near the surface of pasture soils beneath the dung pats, *Dendrobaena octaedra* lives mainly in the surface organic horizon whereas *Lumbricus terrestris* commonly burrows down to 1m and sometimes to 2.5m (Lee, 1959). Subterranean species are often paler in colour than surface feeders (Edwards and Bohlen, 1996).

Among the soil fauna, earthworms are recognized as having the most significant effects on soil structure, soil microbial activity and nutrient availability. For this reason, earthworms have been intensively studied for their potential benefits to agriculture, waste management and land reclamation. Earthworm literature stretches back over 200 years to the taxonomic description of the European earthworm *Lumbricus terrestris* by Linnaeus (1758). Darwin (1881) began the modern era of earthworm research relating their activities to soil properties. Since then, a large amount of literature has accumulated. Several recent monographs have been prepared which discuss various aspects of this literature (Lee, 1985; Hendrix, 1995; Edwards and Bohlen, 1996; Edwards, 1998; Lavelle *et al.*, 1998). This short review chapter draws on these works and many research papers and provides a short overview of earthworm biology and ecology and their importance to soil fertility.

2.2 Classification of earthworms

2.2.1 Taxonomic classification

Earthworms are classified within the phylum Annelida and class Oligochaeta which consists of some 36 families. Some of these families consist of aquatic or semiaquatic worms while others are mostly, or all, terrestrial forms. There are 23 terrestrial families and there are reported to be 7254 species, both terrestrial and aquatic belonging to 739 genera (Edwards and Bohlen, 1996). The main earthworm families and their geographic distributions are shown in Table 2.1. The families Lumbricidae and Megascolicidae are ecologically the most important families in North America, Europe, Asia and Australia (Edwards and Bohlen, 1996). Species from both families have been introduced worldwide by human activities, and now dominate the earthworm fauna in many localities. These earthworms, with a worldwide distribution, are known as perigrine species and they often dominate agricultural soils. Earthworm species are identified by both visual and dissection methods. Many species of the family Lumbricidae can be identified from external body characteristics if specimens are sexually mature (Sims and Gerard, 1985). Most earthworms belonging to other than the Lumbricidae require dissection for taxonomic classification. Keys are used which take account of factors such as locations and characteristics of sexual organs, the gut and associated glands and other structures (Gates, 1972; Sims and Gerard, 1985).

2.2.2 Ecological classification

The main principle of the ecological classification of earthworms is based on the differences among species in their behaviour and activity. Ecological groups represent functional adaptations to the soil environment that allow different species of earthworms to co-exist by exploiting different food resources and habitat space (Edwards and Lofty, 1977). Earthworms are saprophagus soil animals, which can be differentiated into two main groups according to their feeding strategies.

7

Table 2.1 Systematics and global distributions / origin of major families of the terrestrial oligochaeta [Summarized from Wallwork (1983) and Reynolds and Cook (1993)]

Phylum : Annelida	
Class : Oligochaeta	
Order : Haplotaxida	
Suborders : Enchytraeina	
Family : Enchytraeidae	NH, SH
Suborder : Lumbricina	
Family : Lumbricidae	NH--NA, EU
Komarekionidae	NH–NA
Sparganophilidae	NH–NA
Lutodrilidae	NH–NA
Megascolecidae	NH, SH–SA, OC, AS
Glossoscolecidae	SH–SA
Eudrilidae	SH–AF
Acanthodrilidae	SH–AS
Octochaetidae	SH–OC
Oenerodrilidae	SH–SA, AF, AS, MA
Ailoscolecidae	NH–EU
Hormogastridae	NH–ME
Kynotidae	SH–MA
Microchaetidae	SH–AF
Almidae	SH–SA, AF, AS
Biwadrilidae	NH–JA

NH = northern hemisphere, SH = southern hemisphere; AF = Africa, AS = Asia, EU = Europe, JA = Japan, MA = Madagascar, ME = Mediterranean, NA = North America, OC = Oceania, SA = South America

The detritophages feed mainly at or near the soil surface on decaying vegetation whilst the geophages feed more or less selectively on mineral soil rich in organic matter and on decaying roots (Makeschin, 1997). Lee (1959), working with New Zealand Megascolecidae and later, Bouché (1971,1977) working with European Lumbricidae recognized three main ecological groups (Edwards and Lofty, 1977). Bouché named these groups epigeic (litter), anecic (topsoil) and endogeic (subsoil) species. Epigeic earthworms typically live on the soil surface or in the upper reaches of the mineral soil beneath the litter layer, have

relatively high reproductive rates and grow rapidly, and are heavily pigmented (Table 2.2). Anecic species live in vertical burrows in the soil that open at the surface, but feed on litter and other decaying organic materials. Endogeics inhabit the mineral soil horizon, and consume more soil than epigeics or anecics. They generally derive nourishment from humified organic matter. Endogeic species are better adapted to tolerate frequent and heavy perturbations and because of this they are very often the main earthworm group found in arable soils where only few species occur (Makeschin, 1997).

Bouché (1977) described these three major groups as being evolutionary extremes on the three corners of a triangle, with many species occupying intermediary positions with respect to these extremes. Lavelle (1979) proposed that endogeic earthworm species could be sub-divided into those that live in the upper soil horizon (epiendogeics) and those that live deeper in the soil profile (hypoendogeics). He later divided endogeics according to the food material ingested; polyhumic endogeic species ingest soil with a high organic matter content while mesohumics are those that feed indiscriminately on both mineral and organic particles in the upper 10-15 cm of soil. Oligohumic species, which are often found in tropical ecosystems, feed on soil from deep horizons (30-40cm) that is low in organic matter (Lavelle, 1988).

Table 2.2 General diagnostic features of major ecological groups of European lumbricid earthworms as described by Bouché (1977). (Redrawn from Edwards and Bohlen, 1996).

Diagnostic features	Epigeic species	Anecic species	Endogeic species
Food	Decomposing litter on soil surface, little or no soil ingested	Decomposing litter on surface some of which is pulled into burrows	Mineral soil with preference for material rich in organic matter
Pigmentation	Heavy usually both ventrally and dorsally	Medium-heavy, usually only dorsally	Unpigmented or lightly pigmented
Size of adult	Small-medium	Large	Medium
Mobility	Rapid movement in response to disturbance	Rapid withdrawal into burrow, sluggish	Generally sluggish
Generation time	Shorter	Longer	Shorter
Drought survival	Survive in cocoon stage	Becomes quiescent during drought	Enters diapause
Burrows	None	Large, permanent, vertical into mineral soil horizon	Continuous, extensive, subhorizontal burrows in upper 10-15 cm
Predation	Very high, especially from birds, mammals & predatory arthropods	High when they eat at surface, protected in burrows	Low, some threat by ground dwelling birds & predatory arthropods

2.3   Environmental factors influencing earthworm abundance

Due to their relatively large size, fragile body, their mode of life and their spatial mobility, earthworms are susceptible to many environmental factors that affect their living conditions in soils. The most important factors are food supply (energy and nutrients), moisture and temperature regimes and texture and chemical status of soils.

2.3.1 Food supply

Earthworms are saprophagus animals, meaning that their diet comprises mainly organic detritus in various stages of decay and incorporation into the soil. Although the bulk food ingested is soil, dead plant tissue, living microorganisms, fungi, micro and mesofauna and their dead tissues are also ingested (Lee, 1985). The kind and amount of food available influences not only the size of earthworm populations but also the species present and their rate of growth and fecundity (Edwards and Bohlen, 1996). Lee (1985) divides earthworms into two groups. Detrivores are those that feed at, or near, the soil surface or on mammalian dung. Geophages are those that feed deeper beneath the surface, ingesting large quantities of soil, usually selecting portions with higher than normal organic matter content. It was shown in studies reviewed by (Edwards and Bohlen, 1996) that when earthworms are provided with decaying animal manure, cocoon production was higher than when fresh plant material was provided (Table 2.3). This was attributed to the higher nitrogen content of dung. It is not only the type of food available but also the particle size of food material that is important. Earthworms provided with barley straw fragments smaller than 0.2mm gained more than twice as much weight during 150 days as worms given fragments ranging from 0.2 - 1mm in size (Edwards and Lofty, 1977).

Most earthworms can distinguish between different kinds of litter. Satchell (1967) found that there was an order of preference for certain leaf species if uniform disks of a range of species of leaves were offered. Some species of leaves were unattractive to earthworms

11

because of their bitter alkaloid or noxious aromatic content. However, several studies revealed that the amount of water soluble polyphenols in litter was inversely proportional to the rate at which it was consumed, and that litter became much more palatable after a few weeks of weathering (Edwards and Bohlen, 1996). Other factors such as pesticides can render normally palatable leaves unpalatable (Edwards and Thompson, 1973). Vegetation can affect earthworm populations by altering the quality of their food supply. For optimal development and activity, earthworm populations require a sufficient quantity of high quality food.

Because of the importance of food supply for earthworm activity soil organic matter content can be an important factor influencing earthworm numbers. Indeed, soils poor in organic matter do not usually support large numbers of earthworms while soils with a high organic matter content often support a large community (Scullion and Malik, 2000). Conversely, if there are few earthworms the decaying organic matter usually lies in a thick mat of up to 4cm on the surface (Satchell, 1967). The development of organic horizons can, thus, often be attributed to the absence of earthworm activity as a result of acidity and / or wet conditions. Different sources of organic matter attract different species of earthworms. In different experiments several researchers found that animal droppings and dung readily attract some earthworms on the soil surface. In a long-term pasture fertilizer experiment in Park Grass at Rothamsted, the numbers were three times greater in plots receiving 3 tons/ha of dung than in unmanured plots (Table 2.4).

Table 2.3 Mean number of cocoons produced by five earthworms in 3 months (Evans and Guild, 1948). Redrawn from (Edwards and Bohlen, 1996).

Food	A. chlorotica	L. castaneus
Fodder	0.8	9.4
Oat straw	1.4	12.0
Bullock droppings	12.4	73.2
Sheep droppings	14.0	76.0

In another fertilizer experiment in an arable field at Barnfield (Table 2.4), there were about 15 times more earthworms in plots receiving dung annually than in unmanured plots. Decaying leaves in woodlands are also a source of organic matter that favour earthworm multiplication (Edwards and Fletcher, 1988). Provided that the leaf litter is palatable, a large part of annual leaf fall can be removed from the surface by earthworms (Edwards and Bohlen, 1996). Soil organic matter may be considered a poor quality food resource for earthworms as it is dispersed in the soil mineral matrix and includes up to 75% large complex, humic molecules that are bound with clay particles (Stout *et al.*, 1981) cited by (Edwards and Bohlen, 1996).

2.3.2 Soil moisture

When soil-inhabiting earthworms are kept in aerated fresh water, so that they become fully hydrated, their water content is about 80-90% of body weight (Lee, 1985). Terrestrial earthworms have no specialized respiratory organs. Gases diffuse through the cuticle and epidermal tissue into the blood, which contains haemoglobin, a respiratory pigment. In all respiratory systems, the oxygen must first dissolve in an aqueous layer on the respiratory surface. In the earthworm this is the whole body surface, from where it passes into the body by diffusion (Edwards and Bohlen, 1996). The cuticle is kept moist by secretions from mucous glands of the epidermis.

13

Table 2.4 Earthworm populations in plots with and without dung (from Edwards and Lofty, 1977).

Species	1. Grassland Park Grass, Rothamsted (Satchell, 1955a)		2. Arable land Barnfield, Rothamsted (Edwards and Lofty, 1977)	
	Unmanured	Dung	Unmanured	Dung
L. terrestris	13.1	22.5	0.23	10.8
L. castaneus	16.0	59.6	-	-
A. caligiriosa	2.9	8.0	0.8	15.4
A. chlorotica	1.6	-	3.2	44.6
A. rosea	10.0	21.3	-	0.23
A. longa	-	-	0.46	1.8
A. nocturna	1.3	18.9	-	-
O. cyaneum	6.9	24.5	-	-
Total	51.8	154.8	4.69	72.83

Thus, because of their cutaneous respiratory system that requires maintenance of a moist body surface, (and their excretion of nitrogen as ammonia and urea, which are toxic and therefore requires copious losses of hypotonic urine) earthworms are obliged to lose body water in large quantities. Most Lumbricidae worms can sustain a water loss of at least 50% (Edwards and Lofty, 1977). Water is also essential for earthworms in order to maintain coelomic hydrostatic pressure at levels that allow locomotion (Lavelle, 1988). Hence, the activity of earthworms depends greatly upon adequate availability of soil moisture (Edwards and Lofty, 1977). However, not all species have the same moisture requirement, and within the same species from different regions of the world the need for moisture may be different (Edwards and Lofty, 1977). For example, Lee (1985) reported that Lumbricids in Argentina were better able to tolerate drought than introduced and endemic

Megascolecidae and Glossoscolecidae species, while in South Africa the endemic Microchaetidae have the advantage over the Lumbricids. In both countries, however, Lumbricids apparently tolerate soil moisture levels lower than they do in Europe.

Earthworms that live in compost or dung heaps tend to prefer moister conditions than most soil-dwelling species (Edwards and Bohlen, 1996). Lack of moisture can cause some earthworms to become quiescent or go into diapause. For instance, *Aporrectodea sp.* are active in the upper 10cm of soil when it is moist, but when the soil is dry they are usually found below 20cm, where they estivate, tightly coiled within spherical, mucous lined cells (Lee, 1985). Cocoons of species such as *Lumbricus rubellus* may act as the main survival stage during drought. In early reports (see Edwards and Bohlen, 1996) cocoon biomass increased as drought severity increased during a severe drought in no-till agroecosystems in the USA, and many small immature earthworms of this species were observed immediately following drought. Most earthworms are more active in moist than dry soils, and during periods of considerable rain individuals of some species such as *L. terrestris* come to the surface at night (Edwards and Lofty, 1977).

2.3.3 Soil temperature

The metabolic rate, growth, reproduction and activity of earthworms are influenced by temperature. According to Edwards and Bohlen (1996) there is a strong interaction between temperature and moisture, and high surface temperatures and dry soils are much more limiting than low temperatures and waterlogged soils. Studies have shown cocoon production of *L. terrestris* to be highest at 15° C, and that at 20° C cocoons hatch most rapidly (Edwards and Bohlen, 1996). However, hatching success and number of hatchlings emerging per cocoon were greater at lower temperatures, which were more characteristic of these species natural habitat in Europe. Indeed, the temperature at which earthworms thrive best, and which they prefer, is not necessarily the same as that at which they grow fastest or are most active (Edwards and Lofty, 1977).

15

On the basis of field observations by Lee (1985), Lumbricidae in Europe generally have optimal temperatures in the range of 10 - 15° C, which corresponds with expected soil temperatures in the surface soil horizons during the spring and autumn months when earthworms are most active. However, European species that have become established in other parts of the world can have very different temperature optima (Lee, 1985). As expected, tropical earthworm species tend to have higher temperature optima than species from temperate regions (Edwards and Lofty, 1977). Earthworms are, however, capable of acclimatizing to different temperatures (Lee, 1985). Although there is no evidence that acclimatization to increasing temperatures can increase the absolute maximum temperature that can be tolerated, it can increase the duration of survival at temperatures approaching the lethal limit (Lee, 1985). The upper lethal temperature for earthworms is, in fact, lower than for many other invertebrates (Lee, 1985).

The lower lethal temperatures for temperate region earthworms are apparently close to freezing point (Edwards and Bohlen, 1996). Earthworms are also known to survive in surface soils that are frozen in winter and it is likely that species from extremely cold habitats posses some capacity to tolerate cold and resist freezing of their tissue. The lower thermal death point of tropical earthworm species was reported to be 7.5° C, which is well below the temperature these species encounter in their natural environment (Edwards and Bohlen, 1996). From the work of several authors (see Edwards and Bohlen, 1996) it is apparent that cocoons are not- freeze tolerant, but rather their cold hardiness strategy is to become extremely desiccated to prevent freezing of their tissues in frozen environments. Earthworms that live at, or above, the soil surface may find temporary shelter from high or low ambient temperatures under logs, stones or crevices in the soil, in the bark of trees or in deep litter layers (Lee, 1985). On the other hand, earthworms that burrow in the soil can escape temperature extremes by retreating to deeper soil horizons. Their high mortality is related more closely to seasonal variation in soil moisture than soil temperature.

16

2.3.4 Aeration and carbon dioxide

The effect of soil aeration on earthworm distribution is, at present, not well documented, and there is little experimental evidence that the soil oxygen tension affects earthworm distribution (Edwards and Bohlen, 1996). Satchell (1967) reported that in moorland bog and similar highly organic sites, the distribution of *Bimastos eiseni* and *D. octaedra* appears to be limited in some sites by the low oxygen tensions occurring in certain seasons. However, this was difficult to demonstrate because factors such as soil water content, presence of raw humus, plant cover and soil microfaunal activity can have independent effects on earthworms, but are also linked as causes or effects of variations in soil atmospheric oxygen concentration. In his unpublished work, Satchell showed that *B. eiseni* was relatively abundant in drier areas but scarce or absent in wetter areas (Satchell, 1967). Oxidation-reduction potentials measured after heavy rains showed that extremely low oxygen tensions sometimes occurred in the surface of horizon of wetter areas. As *B. eiseni* can survive in aerated water, it seems likely that the low oxygen tension rather than water was responsible for the scarcity of worms in these areas (Satchell, 1967).

Some earthworm species can survive for long periods at very low oxygen tensions, although not much is known about typical oxygen tensions that occur in the soil (Lee, 1985). The activity of deep-burrowing species can be limited in poorly-drained soils that have low redox potentials below the surface horizon (Edwards and Lofty, 1977). There is little evidence of the vertical distribution of earthworms being affected by carbon dioxide concentrations in soil, and the worms do not seem to migrate in response to high CO_2 concentrations (Edwards and Lofty, 1977). The limits of CO_2 concentrations in soil are normally between 0.01 and 11.5% and earthworms can survive much greater concentrations than this, even up to 50% (Russell, 1950 cited by Edwards and Lofty, 1977). Edwards and Bohlen (1996) reviewed several studies stating that many earthworm species can survive long periods submerged in aerated water. Examples of such species include *A. chlorotica, A. longa, L. rubellus* and *L. terrestris*. Some North American species

17

such as *Sparganophilus eiseni* are semi-aquatic and spend most of their life cycle submerged in water (Edwards and Lofty, 1977).

2.3.5 Soil pH

Because they are sensitive to hydrogen ion concentration in soil solution, it is not surprising that soil pH can limit earthworm numbers and species diversity in any particular soil (Edwards and Bohlen, 1996). Lee (1985) established that earthworms are rare in soils with pH less than 4.0 - 4.5, and where pH is less than 3.5 they are generally absent. There are, however, considerable differences between species in their preferred pH range (Lee, 1985). Many experiments (see Lee, 1985) have shown that *A. longa, L. terrestris* and *L. rubellus* will not burrow when placed on the surface of soils with pH values below 4.4 - 4.6, 4.1 - 4.3 and 3.8 respectively.

The inhibitory effects of low pH are that the activity of earthworms is limited by the low pH and in addition concentrations of other important ions (particularly calcium) are typically low. Soils can also be too alkaline for earthworm activity as demonstrated by a decrease in worm numbers when the pH was increased from 7.25 to 8.25 in some Egyptian studies (Edwards and Bohlen, 1996). Edwards and Lofty (1977) reviewed many papers on the effects of soil pH on Lumbricid earthworms, and concluded that the preferences and tolerances of most species appear to fall in the ubiquitous range (Fig. 2.1). In general, acid-tolerant species were usually surface dwelling while acid-intolerant ones were generally soil dwelling species (Fig. 2.1). According to Lee (1985) there is little information on the pH preferences of non-Lumbricids, but Megascolecids in New Zealand soils are absent in soils with pH values less than 4.0. Overall, Lee (1985) found no obvious relationship between species distribution and pH. However, several workers have stated that most species of earthworms prefer soils with a pH near neutral (pH 7.0) (Edwards and Bohlen, 1996).

18
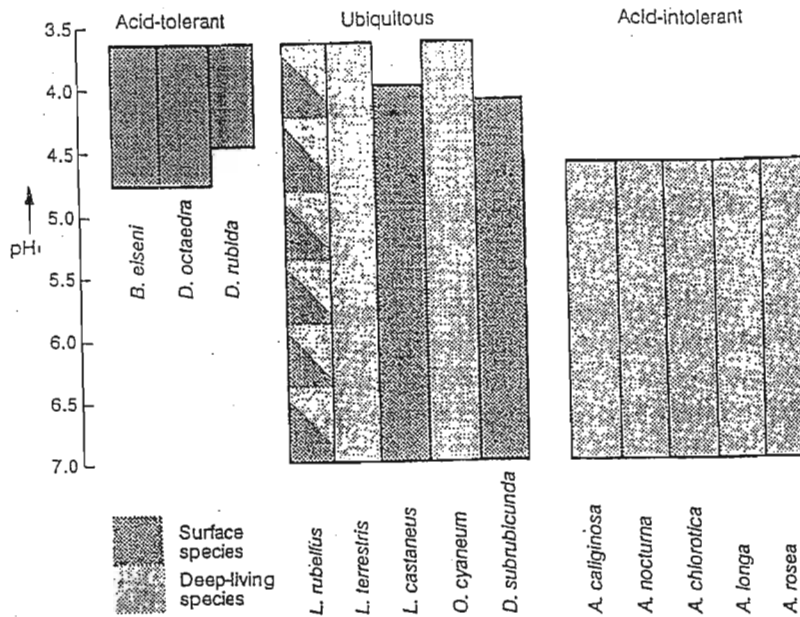
Figure 2.1 Classification of earthworms as a function of pH of litter (after Satchell, 1955a) from (Edwards and Lofty, 1977).

2.3.6 Soil texture

The abrasiveness of coarse-textured sandy soils and their susceptibility to drought, as a result of free drainage and low water holding capacity, can limit both the size and species diversity of earthworm communities (Lee, 1985). The clay content of soil is also important mainly because in areas of high rainfall or poorly drained soils (with high clay content) earthworms may be absent due to their susceptibility to waterlogged or anaerobic conditions. Light and medium textured loams generally have greater total populations of earthworms than heavier clays or more open gravelly sands and alluvial soils (Lee, 1985; Edwards and Bohlen, 1996). The effects of texture can be complex and involve interactions with other factors. For example, in a study by Hendrix *et al.* (1992), in south-eastern USA, it was reported that moderately and severely eroded sandy clay loams supported significantly more earthworms and greater biomass than slightly eroded soils with a higher sand content. Of the soil texture variables, silt content was correlated most closely with earthworm abundance. They attributed these findings to the lower organic matter content and water holding capacity of sandy soil.

19

2.4   Management factors influencing earthworm abundance

2.4.1 Land use and cropping system

(a) **Deforestation**. Many European temperate earthworm species that naturally inhabit forest soils adapt well to grassland conditions on cleared forest sites (Curry, 1998). There is a characteristic decline in epigeic species, due to the loss of the forest litter layer, but anecic and particularly endogeic species may benefit from improved soil fertility and food quality. Indeed, temperate pastures tend to support a greater earthworm biomass than do temperate forest soils (Lee, 1985). Nonetheless in some temperate localities (e.g., New Zealand) forest clearance resulted in the loss of all native species and the improved grass / clover pastures that replaced the forests now support a large population of introduced European species (Lee, 1985). Similarly, most tropical forests have nutrient-poor soils and support predominantly epigeic species which largely disappear following forest clearance (Fragoso *et al.*, 1999a). In more fertile forest soils, where endogeic and anecic species are more abundant, some may survive conversion to pasture (Fragoso and Lavelle, 1992). When introduced perigrine endogeic species become established, pastures in cleared tropical forest areas can support a very large earthworm biomass (Fragoso *et al.*, 1999a).

It is interesting to note that in Mexico and Guadeloup, Sugarcane plantations have been shown to support similar earthworm biomasses (i.e., 30 - 50g m^{-2}) as grasslands (Barois, *et al.*, 1988; Patrón, 1993). This led Fragoso *et al.* (1999a) to suggest that in terms of soil-fauna relationships sugar plantations are comparable with humid grasslands. Land clearing for tree plantations such as palm trees, herbaceous legume cover or cocoa, results in trees with a litter layer below, a situation similar to a secondary forest. As a result, many of the original native earthworm species survive. Nevertheless, the soil disturbance and establishment of exotic trees and bushes provides an opportunity for exotic species to also colonize (Fragoso *et al.*, 1999a). As discussed below, where forests are cleared for arable crop production, there is always a large depletion of the earthworm communities.

(b) **Afforestation.** The response of earthworm populations to afforestation depends very much on the tree species planted and the quality and quantity of litter produced (Curry, 1998). In general, broad-leaved forests support substantial earthworm communities although differences can occur due to differences in the palatability and quantity of litter (Parmelee *et al.*, 1990). By contrast, afforestation of fertile soils with coniferous forests can be accompanied by significant decreases in earthworm numbers reflecting the poor litter quality, declining pH and deterioration in soil structure (Curry, 1998).

(c) **Cultivation.** Earthworm populations in arable land are generally much lower than those in undisturbed habitats (Fragoso *et al.*, 1999a). Cultivation itself can cause direct mortality but the extent of this depends on the severity and frequency of soil disturbance. Rotary cultivation is a drastic form of cultivation and it was shown by Wilson-Rummenie *et al.* (1999) to reduce earthworm numbers in semi-arid central Queensland by 60 - 70%. Ploughing is much less drastic. For example, Doran (1980) estimated that about 5 - 10% of the earthworm biomass was brought to the surface by ploughing and only about 25% of this was killed. Discing is less damaging to earthworms than conventional ploughing (Doran and Werner, 1990).

Tillage is particularly damaging to earthworms when cultivation is followed by dry or frost periods (Lal, 1987; Beare *et al.*, 1994a). Indeed, Beare *et al.* (1994b) showed that ploughing before a dry period leads to a high earthworm mortality rate. Earthworms are brought to the surface where they can be easily attacked by beetles, chilopods and particularly birds (Doran, 1980). When natural forest or grassland is converted to arable agriculture there is a pronounced decline in soil organic matter content and arable soils characteristically have a low organic matter content (Lamarca, 1996). The main reasons for this are an increased rate of organic matter decomposition caused by repeated cultivation, low organic matter returns induced by removal of biomass as harvested product and often a lack of crop cover (and thus organic matter returns) during part of the year (Lamarca, 1996). The general lack of a food source, in the form of organic residues,

generally results in arable soils supporting a small earthworm biomass with narrow species diversity (Lamarca, 1996).

Larger species such as *L. terrestris*, that require a supply of surface litter, and have permanent burrows are the species most adversely affected by repeated soil disturbance and there is also usually a lack of epigeic species (Edwards and Bohlen, 1996) due to the lack of surface litter layer. Endogeic species may even benefit from ploughed-in crop residues and endogeic species generally dominate the earthworm community structure under arable agriculture (Fraser, 1994).

(d) **Zero and minimum tillage**. Arable agriculture which uses minimum or zero tillage, tends to promote earthworm populations. These techniques have generally been shown to increase earthworm densities by a factor of two or three (Edwards and Lofty, 1982; House and Parmelee, 1985; Wilson-Rummenie *et al.*, 1999). Results presented in Fig.2.2 show the effect of converting a pasture to arable crops under zero or conventional tillage. Earthworm numbers remained considerably higher under zero tillage (direct drilling) during the eight year duration of the experiment. Under minimum and zero tillage, a layer of decaying litter remains at the soil surface. This not only acts as a food source for anecic and epigeic species but the surface mulch conserves soil moisture and provides insulation from temperature extremes (Lee, 1985). Deep burrowing anecic species are particularly benefitted from zero tillage (Edwards and Lofty, 1982) since the soil is not disturbed and their permanent burrows remain intact.
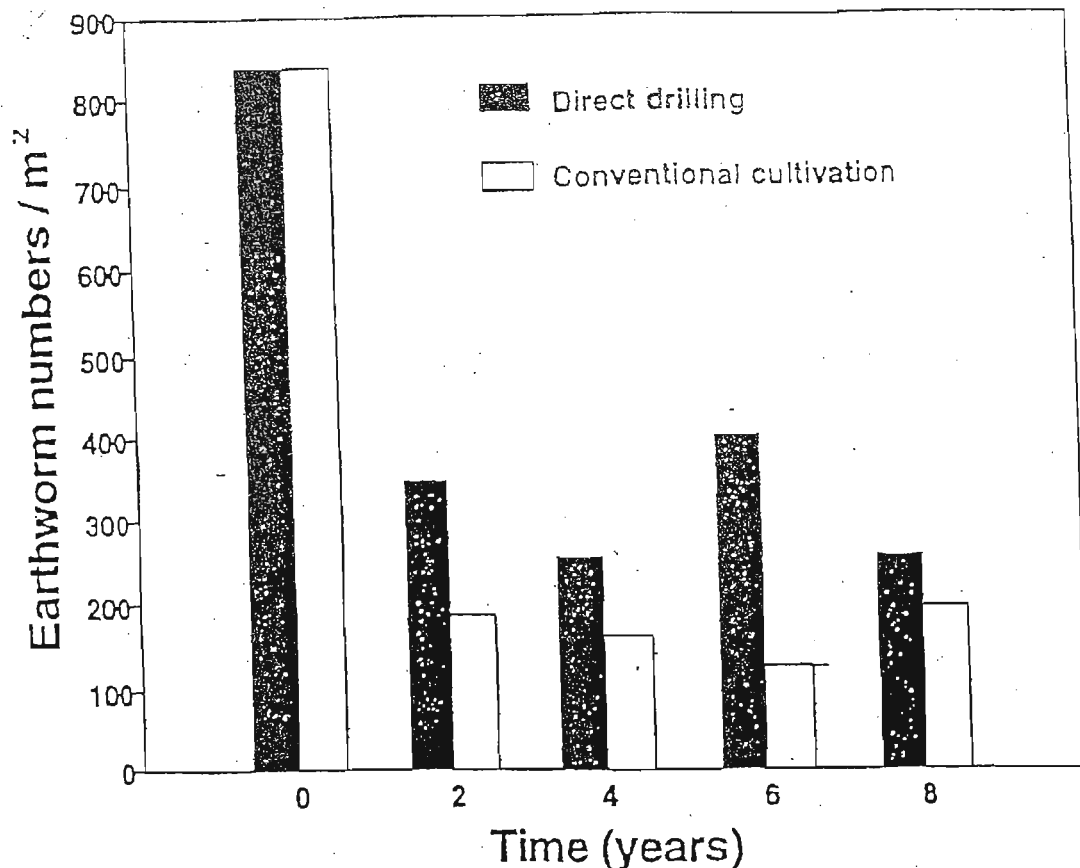
Figure 2.2 Effect of converting pasture land to arable land using direct drilling or conventional cultivation (Redrawn from Fraser, 1994).

(e) **Crop type and rotation**. Crops such as cereals, where significant amounts of residues are left behind promote earthworm numbers when compared with root crops where most of the plant parts are removed (Edwards, 1983; Lofs-Holmin, 1983a; Hendrix *et al.*, 1986). Edwards (1981), for example, found on the long-term Broadbalk experiment at Rothamsted that soil under wheat, cropped continuously for more than 120 years, had more earthworms than soils under crop rotations that contained root crops (e.g., sugar beet and potatoes). A wheat crop following potatoes and beans had about half the population of the continuous wheat treatment while in an annual fallow followed by wheat no earthworms were found. Hopp and Hopkins (1946b) found earthworm abundance was higher under cereals than under row crops such as soybean or maize.

23

In rotations in which arable crops are grown in rotation with pastures, earthworm populations fluctuate greatly (Fraser, 1994). They increase rapidly under the pasture phase (due to increased food supply and lack of soil disturbance) but then decrease rapidly under the arable phase.

2.4.2 Fertilizers, manure and lime

The use of fertilizers is mainly aimed at improving crop growth and yield. As a result, in the long term, fertilizer additions result in increases in organic material returns to the soil in the form of decaying roots, litter and crop residues (Fraser, 1994). Earthworms benefit directly from this as the increased organic material becomes their source of food. In the long-term Broadbalk experiment at Rothamsted Experimental Station earthworm numbers increased in proportion to the amount of N applied (Edwards and Bohlen, 1996). Fraser (1994), however, noted that when food supply does not limit earthworm populations, increased organic returns due to added fertilizer will have little effect on earthworm numbers.

The effect of fertilizer on soil pH is, however, another important factor determining the impact that fertilizer has on earthworm abundance (Lee, 1985). The long-term influence of repeated applications of ammonium-containing or forming fertilizers is often soil acidification (Lee, 1985). This occurs during the nitrification process in which two moles of H^+ ions are produced per mole of ammonium that is converted to nitrate. Since earthworms are particularly sensitive to low soil pH (see section 2.3.5) repeated applications of nitrogenous fertilizers can sometimes reduce earthworm numbers (Edwards, 1983). Although usually a short-term effect, high concentrations of electrolyte in the soil solution due to high rates of inorganic fertilizer applications can also sometimes reduce earthworm abundance (Lee, 1985). Method of fertilizer application has also been reported to affect the composition of earthworm community. For example, epigeic species may be more affected by surface broadcasting than if fertilizer is banded or injected (Lee, 1985). By contrast endogeic species are more likely to be affected by localized regions of high salt

24

concentrations close to where fertilizers are banded or injected.

Earthworms generally respond more positively to applications of organic manures than to chemical fertilizers. Additions of manure have been shown to increase earthworm biomass and numbers in both pastoral and arable soils (Paoletti, 1999). Applications of farmyard manure have been shown to be particularly beneficial to earthworm abundance and densities although composts, sewage sludge and mulches show similar positive effects (Makeschin, 1997). The reason for this is that in addition to adding nutrients, organic manures provide a food source for earthworms in the form of organic residues added to the soil. Heavy applications of animal wastes to soils in slurry form can cause death of topsoil-dwelling earthworms. The toxic components of slurries can include ammonium, benzoic acid, potassium sulphite and copper. Any adverse effects of moderate slurry applications are transitory and the net population response is positive (Curry, 1976).

As noted in section 2.3.5, earthworms are rare in acid soils (<pH 4.0 - 4.5) so that one would expect applications of lime to increase earthworm numbers. Indeed, several workers have shown that liming can increase earthworm abundance (Edwards and Lofty, 1977). Springett and Syers (1984) argued that when lime is applied to soils it is the change in pH *per se.* that influences earthworms rather than the increase in soil calcium levels. Edwards and Lofty (1977) concluded that population responses to lime do not normally occur if the initial soil pH is greater than 4.5 - 5.0 since above these values most species are insensitive. In a review of Australian research, Baker (1998) showed that the increase in earthworm density in response to liming varies considerable depending on soil type, the earthworm species present and the range of pH involved.

2.4.3 Earthworm Introduction

As noted previously, peregrine exotic earthworm species tend to be present, and often are predominant, in agricultural soils throughout the world. For example, in a worldwide survey

of earthworms in the humid tropics, Fragoso et al. (1999b) found that 51 exotic and 151 mature species were commonly found in tropical agroecosystems. Of the 51 exotics, 15 were temperate Lumbricidae of European origin that were restricted to high altitude mountain localities. The remainder were tropical species which mainly belonged to the Megascolecidae, Glossoscolecidea and Dichogastrini families. Similarly, in the USA (Edwards et al., 1995) and Australia (Lee, 1985) earthworm species belonging to the family Lumbricidae are not endemic but have been introduced from Europe. They are now distributed widely and are usually predominant in agricultural soils.

For the most part, introduction of exotic earthworm species by man has been accidental. It has been greatly favoured by the spread of plants (and associated soil) worldwide and also such practices as the use of soil as ballast for sailing ships in the days of long sea voyages (Lee,1985). Over a period of several years Gates (1972) intercepted the earthworms that arrived in the USA in pots containing imported plants. He found a wide range of exotic species mainly belonging to the Lumbricidae and Megascolecidae. Presumably, the same situation occurred in the past on repeated occasions and this is the main cause for the predominance of exotic earthworms in the USA (Fragoso et al., 1999b). Exotic earthworms tend to become dominant in ecosystems to which they were introduced either because of lack of endemic species in previously disturbed areas or because they are strong competitors for available resources (Edwards et al., 1995).

Where removal of native vegetation resulted in loss of native earthworms, the presence or absence exotic species is dependent on the extent of their accidental introduction by man. Some soils, particularly in remote regions, can be devoid of earthworms. For that reason, soils may need to be inoculated with exotic species. For example, in New Zealand, addition of introduced European earthworm species to pastures was common in the 1940s and 50s and resulted in increased pasture yields (Stockdill, 1982).

2.5   Effects of earthworm activity on soil fertility

2.5.1 Soil turnover

Earthworms can ingest and turnover large amounts of soil (Edwards and Shipitalo, 1998) but it is difficult to make accurate estimates of the total amounts of soil that they turn over annually at any given location. The total annual production of casts by earthworms is difficult to quantify. Mostly surface production has been reported. Mean annual above-ground cast deposition in temperate pastures and broadleaf forest soils is within the range of 3 - 7 kg m^{-2} (Lee,1985). In arable soil, Graff (1969) measured an annual surface cast production up to 4 - 5 kg m^{-2}. However, many endogeic species cast predominantly below-ground rather than at the surface. Only a few estimates of cast deposition within the soil matrix are available. In a pasture soil an annual cast production on soil surface and in the topsoil to a depth of 10cm of 25 kg m^{-2} or about one quarter of soil volume, was estimated (Graff, 1971).

From available field data, Makeschin (1997) concluded that annually about 30 - 70 Mg ha^{-1} of soil material will be ingested and deposited by earthworms in moderately populated soils. This may be a conservative estimate and in tropical soils annual soil ingestion up to 400 Mg ha^{-1} was reported by Barois *et al.* (1993). Makeschin (1997) concluded that under temperate climatic conditions, within 50 - 100 years the whole top layer of agricultural soils will pass through the gut of earthworms.

2.5.2 Nutrient cycling

Earthworms can influence the size and activity of the soil microbial biomass in ways that impact on nutrient availability. The earthworm gut provides suitable conditions for vigorous multiplication of microorganisms that are stimulated to decompose ingested organic matter (Parmelee *et al.*, 1998). Earthworms secrete large amounts of water soluble organic

27

compounds into their gut and this material can be readily assimilated by n

in the gut (Parmelee *et al.*, 1998). This is described as a mutualistic dig

where microbes benefit from the earthworm secretions and the earthworm i

the enhanced microbial decomposition of ingested organic matter (Lavelle,

increased microbial activity and mineralization continues for some time after the gut

contents have been egested as casts. As the casts age, the rate of decomposition is

lowered due to physical protection of organic matter in the compact structure of casts

(Lavelle, 1988).

Plant nutrients, particularly extractable N and P, often occur in higher concentrations in

fresh earthworm casts and around the lining in their burrows than in bulk soil (Edwards and

Bohlen, 1996). This increased availability in fresh casts usually lasts for a relatively brief

period of time (Lavelle and Martin, 1992). The increased concentrations of available N and

P are attributable to increased mineralization of soil organic N and P during gut transit

(Parmelee *et al.*, 1998). Increased N availability in casts can have a large positive effect

on soil N availability since the direct N flux through the earthworm biomass is substantial.

It was estimated to be 63 kg N ha^{-1} yr^{-1} in no-till systems in Georgia (Parmelee and

Crossley, 1988). Earthworms also return N to the soil in the form of urine and

mucoproteins which are both readily assimilatable forms of N. Lee (1983) estimated that

an average population of lumbricids may produce around 18 - 50 kg N ha^{-1} yr^{-1} in urine.

Nutrients in earthworm tissues turn over rapidly and nitrogen in dead earthworm tissue is

rapidly mineralized (Satchell, 1967). Earthworm death can contribute to the soil N pool

significantly since they have a high protein content in their tissues. Makeschin (1997)

estimated 24 g N m^{-2} would be released by death of earthworms annually in highly

populated soils.

Increased concentrations of extractable K, Ca, Mg and some trace elements have

sometimes also been observed in freshly egested casts (Pashanasi *et al.*, 1996).

Materechera *et al.* (1998), for example observed increases in extractable P,

28

exchangeable K, Ca, Mg and Na in casts of *Microchaetid* species. These elevated levels have been attributed to selective feeding of earthworms on fresh organic materials that are high in these nutrients (Lavelle *et al.*, 1998). In addition, many earthworms possess calciferous glands in esophageal regions which are involved in production of $CaCO_3$ spherules (Blair *et al.*, 1995). Egestion of this material in cast material can lead to temporary increases in Ca availability in fresh casts and increases pH (Materechera *et al.*, 1998) which could affect the availability of other soluble nutrients (Edwards and Bohlen, 1996).

2.5.3 Soil Aggregation

One of the main ways in which earthworms can influence soil properties is through soil ingestion and cast production, resulting in continuous turnover of the soil and intimate mixing of mineral and organic constituents (Curry and Baker, 1998). Soil aggregation is affected mainly through the production of casts, which can make up the majority of structural aggregates in the uppermost (10 - 20cm) horizon in some pasture soils (Edwards and Shipitalo, 1998). Earthworm burrows can also contribute to aggregate stability since they are often lined with oriented clays and humic materials that can form a stable structure (Edwards and Bohlen, 1996).

Several authors cited by Edwards and Bohlen (1996) have agreed that casts contain more water stable aggregates than the surrounding soil, since they are lined with clays and humic material which can form a stable structure due to cementation by clay of mineral particles. Particle size analysis of casts shows that earthworms preferentially ingest the smaller particle fractions of soil, so that casts contain higher proportions of clay and silt and lower proportions of sand than the surrounding soil. During gut transit soil components undergo various transformations such as decomposition and humification and release or protection by clay mineral particles (Barios *et al.*, 1993). These processes of destruction and construction occur within a few hours (2 to 8 hours). The large quantities of soil

29

ingested and egested by geophagus endogeic earthworms means they have a true impact on the soil structure, as the soil aggregates are regenerated after passage through the gut (Haynes and Fraser, 1998).

Shipitalo and Protz (1988) in their study found that fresh casts of *Lumbricus terrestris*, *L. rubellus* and *Aporrectodea caliginosa* had a higher dispersion index than the dry casts. However, they also confirmed the idea of soil structural renovation through casting. Most authors agree, that casting activity results in more water stable aggregates (Lee and Foster, 1991). Casts have for instance been shown to withstand up to 54 times more kinetic energy from raindrop impact and possess greater tensile strength and stability than soil aggregates (De Vleescheuwer and Lal, 1981). Often casts have a higher bulk density and lower porosity than uningested soil aggregates. There are at least two possible explanations for this. Firstly, casts contain greater proportions of clay and silt fractions. Secondly, the thorough mixing of soil in the gut results in dispersion of clay, which improves surface contact between particles and eliminates planes of weakness. In addition, Beare and Bruce (1993) showed that the stability of earthworm casts largely depends on the nature and concentration of organic matter they contain.

2.5.4 Soil porosity

The burrows of earthworms are important contributors to soil porosity, because average pore space is being increased by large channels that are created through burrowing and by the deposition of casts as loosely packed aggregates within the soil matrix. The resulting pores are termed biopores and are usually cylindrical and relatively long. In nearly all soils, earthworm burrows are thought to be the most numerous and important pores of animal origin. Several authors quoted by Edwards and Bohlen (1996) reported that the number of pores in the soil is correlated with the number of earthworms. Soil porosity influences properties such as water infiltration and gaseous exchange. Macropores formed from earthworm burrows, such as those of the anecic species

30

Lumbricus terrestris, which have a large diameter (>5 mm) and are open to the soil surface, can act as pathways for the preferential flow of water. Water that flows down earthworm burrows has been referred to as bypass flow, because it bypasses the soil matrix. Burrows do not transport water to the same degree during all rainfall events. The moisture status at the time of rainfall, intensity of rain, soil type and residue cover, and micro-relief all influence the degree to which water will flow down burrows (Trojan and Linden, 1992). Zachmann *et al.* (1987) found that the presence of surface residue resulted in double the number of burrows open to surface relative to incorporated residues.

Clements (1982) showed the importance of earthworms on hydraulic conductivity by eliminating earthworms from an English grassland using heavy treatments of pesticides phorane (a toxin to earthworms). He noted a decrease in water infiltration rate of 93%. The presence of earthworms thus positively affected the movement of water through the soil. Increases in water infiltration due to earthworm activities can translate into a decrease in surface runoff, especially when burrows are open to the surface. Changes in soil porosity and water infiltration due to earthworm activities can also increase the water-holding capacity of soil (Lee, 1985). In New Zealand the introduction of *Lumbricid* species of earthworms to pastures led to a 17% increase in the moisture content at field capacity (Lee, 1959). Clearly, earthworms influence both drainage of water from the soil and moisture retention capacity of soil, both of which are important factors for plant growth (Edwards and Shipitalo, 1998).

Except after heavy rain or where water table levels are seasonally high, the burrows of earthworms are air-filled. The increased macro porosity through burrowing activity directly improves aeration in unsaturated soils. Calculations revealed that earthworm burrows would account for 13.3%, 18.8% and 10.4% of the minimum required air-filled pore space at 0-20, 20-40 and 40-60 cm depths respectively in the soil (Edwards and Bohlen, 1996). Depending on the dominant species in a soil, improved aeration could be observed to greater depths.

31

2.5.5 Crop productivity

The importance of earthworms for plant growth has been recognized for over 100 years, since the publication of Darwin's work in 1881. Earthworms play a variety of roles in agroecosystems and thus positively affect crop productivity. Through their feeding and burrowing activities, earthworms incorporate organic residues and amendments into the soil, enhancing decomposition, humus formation, nutrient cycling, and soil structural development (Kladivko *et al.*, 1986). Thus, it is not surprising that there are many pot and field experiments that have demonstrated plant growth responses to the presence of earthworms (Parmelee and Crossley, 1988; Baker,1998).

Results from pot and field experiments by Brown *et al.* (1999) showed a greater increase in above-ground biomass (including shoot and grain yield) than in roots in response to earthworm activities. Similarly, Pashanasi *et al.* (1996) found that grain production was stimulated to a greater extent than root production as a result of earthworm activities. Other studies (Edwards and Bohlen, 1996; Fragoso *et al.*, 1999a) showed that in C-rich soils earthworms tended to have a slight negative effect on roots compared to a positive effect in C-poor soils. *P. corethrurus* , the dominant species present in these studies, is known to be able to exploit highly stable organic reserves in C- poor soils, with the help of microorganisms, thus liberating and cycling nutrients that would otherwise be tied-up and unavailable to plants (Brown *et al.*, 1999).

Brown *et al.* (1999) found that the yield response to earthworms was dependent on the type of crop. The plants most positively affected by earthworm activity were all perennials which included trees (760.7%), tea (162%) and pasture grass (103%) as shown in (Fig 2.3). However, the palm tree responded negatively to earthworm activity, due to its coarse root system which was unable to take advantage of worm structures which decreased soil compaction and increased water infiltration (Brown *et al.*, 1999).

32
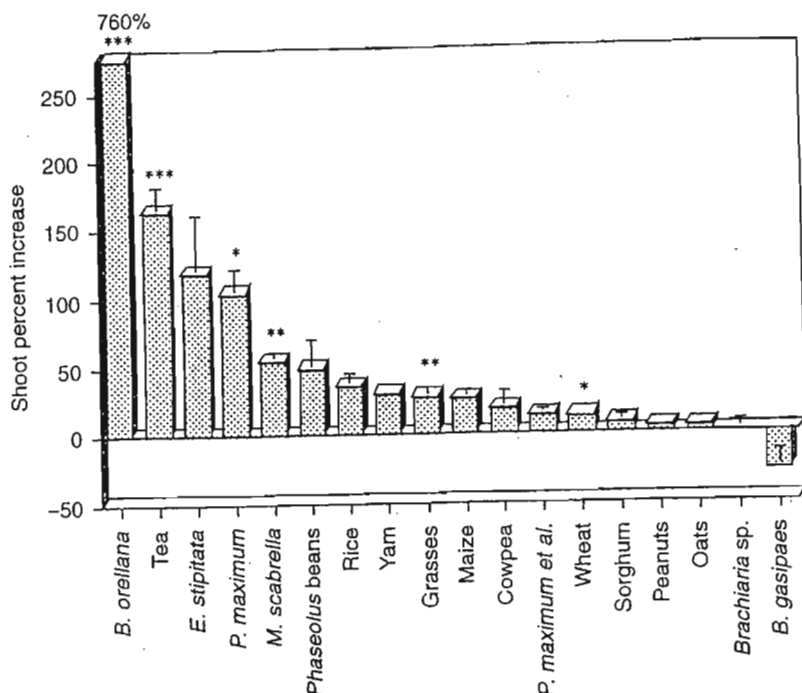
Figure 2.3 Percentage increase (mean ±SE bars) due to all earthworm species combined, of above-ground biomass of 17 plant species. Statistical significance of the F-test comparing the means of earthworm and non-inoculated treatments are shown as follows: ***P<0.001; **P<0.01; *P<0.05. Redrawn from Brown *et al.* (1999).

In their study, Zaller and Arnone (1999) found there was no apparent effect on above ground production of plant communities due to earthworm activities. The lack of an earthworm-effect was puzzling since earthworm activity and nutrient availability to plants did vary significantly between earthworm density treatments. They concluded that the lack of a stimulatory effect of increased earthworm activity on plant biomass production was because increases in plant nutrient availability were insufficient to promote the growth of the plants. They also suggested that, the longer-term effects that earthworms have on soil physical properties maybe as important, or even more important, than their shorter-term effects on plant nutrient availability. The results of Zaller and Arnone (1999) are not isolated since there are a number of studies where increasing earthworm densities had no significant effect on plant growth (Willems *et al.*, 1996; Zaller and Arnone, 1997). Where nutrient availability and / or soil physical conditions are not limiting plant growth, the activity of earthworms is unlikely to have a substantial positive effect on crop growth.

2.5.6 Use of earthworms as indicators of soil quality

Soil quality is generally defined as the continued capacity of the soil to function as a living system, within ecosystem and land use boundaries, to sustain biological productivity, promote the quality of air and water and maintain plant, animal and human health (Doran et al., 1996). Soil quality is usually assessed by using chemical (e.g. organic matter, pH, extractable nutrients, mineralizable N), physical (e.g. bulk density, penetrometer resistance, soil water retention characteristics) and biological (microbial biomass, basal respiration, enzyme activity and earthworm numbers) indicators. These soil quality indicators are used to assess the effects of agricultural management on the ability of the soil to function both now and in the future. Earthworms have been suggested as important indicators of soil quality for a number of reasons (Doube and Schmidt, 1997). Indeed, since ants, termites and other litter-dwelling macrofauna are not sufficiently abundant in most agricultural soils, and also not clearly linked to soil productivity, earthworms remain the sole potential soil quality indicators among the soil macrofauna. Earthworms are usually the dominant soil faunal biomass and their activity influences soil chemical, physical and microbial properties. In turn, soil properties influence earthworm numbers and their activity. In addition, as noted previously, a number of studies have demonstrated the beneficial effects of earthworms on plant growth.

Earthworms have relatively long life-spans and generation times and so populations are relatively stable and their abundance can be estimated with one or two samplings per year. Further, the number of species in any one location is commonly low and the communities are usually dominated by one to three species. Thus, the use of total numbers or preferably biomass avoids the difficulties associated with differences in earthworm size and taxonomy. Earthworm biomass may be more stable than numerical abundance as a measure of their impact (Doube and Schmidt, 1997). For example, unpublished data by Williams and Doube showed that biomass was superior to abundance as a predictor of the impact of earthworms on plant growth (Doube and Schmidt, 1997). There are, however

34

practical problems with using earthworms as quality indicators. Earthworms are very patchily distributed within fields which makes sampling methods used labour intensive and fraught with inaccuracies (Baker, 1998). In addition, soil moisture content can change within short periods and this can greatly affect the numbers of earthworms collected. Another important drawback is the absence of critical values for earthworm numbers or biomass in different soils. This is a particularly complex issue since the species dominant in agricultural soils often differ from those that predominate under native vegetation.

Since the key agronomic factors which determine plant yield and soil conservation are not necessarily those that influence earthworm abundance, their numbers cannot be used as a universal indicator of soil health. There are some factors (e.g. chemical fertilizers, waterlogging, root diseases) which can be of overriding importance in determining yield and which do not have a corresponding effect on earthworm abundance and vice versa. Although some management practices promote both earthworm abundance and crop growth, there are other examples when the two were disassociated (Doube and Schmidt, 1997). The presence of a diverse community of earthworms would normally be considered a sign of healthy soil. However, there is a strong risk that low numbers or indeed absence of earthworms might be misinterpreted as a "problem" at a particular site. The real problem may not be the soil but that earthworms have not been dispersed to it (Baker, 1998). As already noted, in agricultural soils introduced exotic species often predominate. Most introductions have been accidental. The lack of earthworms does not necessarily mean soil factors will limit crop production. Indeed there are highly productive fertile soils that are devoid of earthworms (Robertson, 1994).

Lavelle *et al.* (1992) concluded that earthworm activities are not merely a consequence of high soil fertility, but they contribute to its build up and maintenance. This is undoubtedly the case and as a consequence the size of the earthworm community can be an important soil quality indicator. However, the patchy distribution of the more common exotic species in agricultural soils means that comparisons will be more meaningful at a local rather than

35

regional level (Baker, 1998). Earthworm numbers and / or biomass values should not, however, be used in isolation but in association of other biological, physical and chemical indicators of soil quality.

EFFECTS OF AGRICULTURAL LAND MANAGEMENT ON SOIL ORGANIC MATTER STATUS AND THE SIZE OF EARTHWORM COMMUNITIES

3.1 Introduction

Concerns regarding soil degradation, agricultural sustainability and environmental quality have stimulated interest in assessment of soil quality (Doran and Parkin, 1994; Doran *et al.*, 1996). Soil organic matter is an important component of soil quality because it affects soil physical, chemical and biological properties. It helps determine soil characteristics such as nutrient mineralization potential, cation exchange capacity, aggregate stability, trafficability and water retention as well as being a substrate for soil microflora (Janzen *et al.*, 1997; Paustian *et al.*, 1997). Recent concerns over world climate change have also increased interest in soil organic matter and its role in the global C budget through sequestration of atmospheric CO_2 in the soil (Carter *et al.*, 1997).

Management-induced changes in soil organic matter status that occur over relatively short periods are difficult to quantify because of the large background organic C pool. Measurements of smaller more active (labile) fractions of organic matter (e.g. soluble C and microbial biomass C) have, however, been used successfully because they can respond more rapidly to changes in C supply (Gregorich *et al.*, 1994). For example, microbial biomass C has been proposed as an early indicator of changes in total soil organic matter (Sparling, 1997). With its dual role as a pool of labile nutrients and as an agent of decomposition of organic materials in soils, microbial biomass may be a sensitive indicator of changes in active soil organic matter. Soluble organic matter is the main energy source for heterotrophic soil microflora, it is a primary source of mineralizable N, S and P, and it influences the availability of metal ions in soils by forming soluble complexes (Stevenson, 1994). Its concentration has been shown to change rapidly in

response to changes in soil C supply induced by changes in soil management (Campbell et al., 1999; Haynes, 1999a).

The abundance of earthworms can be used as another indicator of soil quality (Doube and Schmidt, 1997). Earthworms are involved in key soil processes such as litter and soil organic matter decomposition, nutrient turnover, aggregate formation and stabilization and formation of macroporosity. Soil disturbances, such as conventional tillage can result in massive reductions in earthworm abundance whilst pastoral management commonly results in a large, diverse earthworm community (Fraser et al., 1996). There is normally a substantial increase in the dominance of accidentally introduced exotic species in agricultural ecosystems (Lee, 1959; Fraser et al., 1992).

The impacts of agricultural management on soil organic matter status and the size of soil microbial and faunal communities has received very little attention in South Africa. The initiative was taken to address some of these issues in this study which was conducted in the tropical, northern part of KwaZulu-Natal. The major land use in the area is sugarcane production but most large sugar plantations also have substantial areas planted in orchard crops, exotic forests and grazed pasture. The purpose of this study was to compare the soil organic matter status and the size of the soil microbial biomass and earthworm community under undisturbed native forest or grassveld with that under long-term sugarcane (preharvest burn or green cane harvested), exotic forests (gum, wattle and pine), orchard crops (banana, orange and avocado) and grazed kikuyu grass pastures.

3.2 Materials and Methods

The study area was within a 10 km radius of the town of Eshowe (28° 51' S; 31° 24' E) in northern KwaZulu-Natal. Fields on commercial sugar plantations were chosen that had a long-term (>15yr) history of permanent grazed kikuyu grass (*Pennisetum clandestinum*) pasture, pine (*Pinus elliottii*), gum (*Eucalyptus grandis*) or wattle (*Acacia mearnsii*) forest, orange (*Citrus sinensis*), banana (*Musa accumunata*) or avocado (*Persea americana*) orchards, or sugarcane (*Saccharum* spp) under preharvest burning or green cane harvesting. Areas of undisturbed indigenous rainforest and native grassland were also identified. A preliminary soil survey was carried out to ensure that sites were all on the same soil type. The soils in the area are classified as Inanda form (Glenariff series) (Soil Classification Working Group, 1991) or as Humic ferralsols (FAO). The soils have a clay, silt and sand content of 10-30, 5-10 and 60-80% respectively. The mineralogy of the clay fractions is dominated by kaolinite plus halloysite and there are also appreciable amounts of sesquioxides, gibbsite and interlayered chlorite. Mean annual rainfall is 1166 mm which falls mainly in summer (December - March) and mean monthly temperatures range from a maximum of 20.7°C in January to a minimum of 16.4°C in June.

A total of 66 fields (6 replicates of each of the land uses), located on 12 commercial sugar estates were sampled in late summer autumn (Feb. to May) which was towards the end of a wet season. Within each field area (approximately 10 ha), four plots (about 60 m² in area) were randomly chosen. In each plot 10 soil samples (0-10 cm) were taken and bulked for subsequent analysis. Field-moist soil was sieved (< 2 mm) and a sub-sample was stored at 4°C prior to analysis of microbial biomass C. Another sub-sample was air-dried and ground (< 0.5 mm). Microbial biomass C was analyzed by fumigation extraction method using a K_c factor of 0.38 (Vance *et al.*, 1987). The quantity of K_2SO_4-extractable C from unfumigated soil was used as an index of soluble organic C. Organic C was analyzed on ground soil by the Walkley and Black dichromate oxidation method (Blakemore *et al.*, 1972). Soil pH was measured in a 1:2.5 soil water slurry using a glass

electrode. Exchangeable cations were extracted with 1M ammonium acetate (1:4 soil-extractant ratio) for 2 hours (Beater, 1962) and K, Ca and Mg were measured by atomic absorption and Na by atomic emission spectrophotometry.

Within each of the 4 plots in each field, a soil sample (25 x 25 x 25 cm) was taken randomly and transported to the laboratory. In total 264 samples were taken. Earthworms were removed from the soil by hand-sorting. Recovered earthworms were held in water for 6 hours to allow time for gut voidance before being weighed and then preserved in 70% ethanol. Earthworms were later identified to species level (see Chapter 4).

Data relating soil physical, chemical, microbial properties and earthworm numbers and biomass to each other were fitted to linear, quadratic, cubic and exponential regression functions using the Genstat 4.1 statistical package. For the most part, linear functions gave equal or better fits than the other functions and they are presented throughout the chapter.

3.3   Results

3.3.1   Soil chemical properties

Mean values for soil pH and extractable macronutrients under the various land uses are presented in Table 3.1. The pH under native forest was 5.6 and that under native grassland was 5.3. Soils under horticultural management (avocado, orange and banana) had been limed and had a pH of 5.8 or 5.9. Substantial acidification had occurred under pine, wattle and sugarcane, all of which had pH values below 5.0. The lowest soil pH was observed under wattle forest. Soil acidification under wattle is commonly observed and is related to the fact that they are leguminous trees and thus absorb a cation excess during nutrient uptake.

Truog P concentrations were relatively low under native forest, native grassland and soils under gum and wattle forests had similar or lower values. The other land uses had elevated extractable P levels reflecting the substantial inputs of fertilizer P that are applied to agricultural soils. Truog P levels were notably high under orange and banana (i.e. > 60 mg kg^{-1}). Exchangeable cation concentrations were variable and presumably the result of the interaction of a number of factors. Where lime has been applied at substantial rates exchangeable Ca concentrations will be elevated (e.g. orange, banana and avocado). Where soil acidification has occurred, cation concentrations (particularly Ca and Mg) will be decreased due to leaching losses (e.g. pine, gum and wattle forests and burnt sugarcane). Fertilizer applications of K and Mg and crop uptake of nutrients will also have influenced values.

3.3.2   Soil organic matter and microbial biomass

Concentrations of organic C (Figure 3.1) were notably high under kikuyu pasture, native forest and banana and lowest under burnt cane. Among land uses, values followed the

41

Table 3.1. Mean values for pH and extractable macronutrients for soils from different land uses.

| Land use	pH (water)	Extractable macronutrients (mg kg^{-1})				
		Truog P	K	Ca	Mg	Na
Native Forest	5.6	14.5	229.7	1272.5	378.3	55.2
Native grassland	5.3	17.6	176.6	394.0	122.6	34.7
Kikuyu pasture	5.5	46.7	288.2	497.3	161.2	55.0
Avocado	5.8	32.7	173.2	905.0	236.2	35.0
Orange	5.9	64.3	235.0	1268.5	196.2	42.6
Banana	5.8	69.7	252.5	1357.5	246.5	35.4
Gum	5.2	16.8	131.8	638.4	200.2	46.0
Pine	4.8	25.2	122.3	502.3	125.8	70.5
Wattle	4.6	10.8	99.2	288.2	123.2	46.0
Burnt cane	4.8	40.8	124.0	395.5	91.8	31.8
Trashed cane	4.9	22.2	219.8	760.0	212.8	34.8
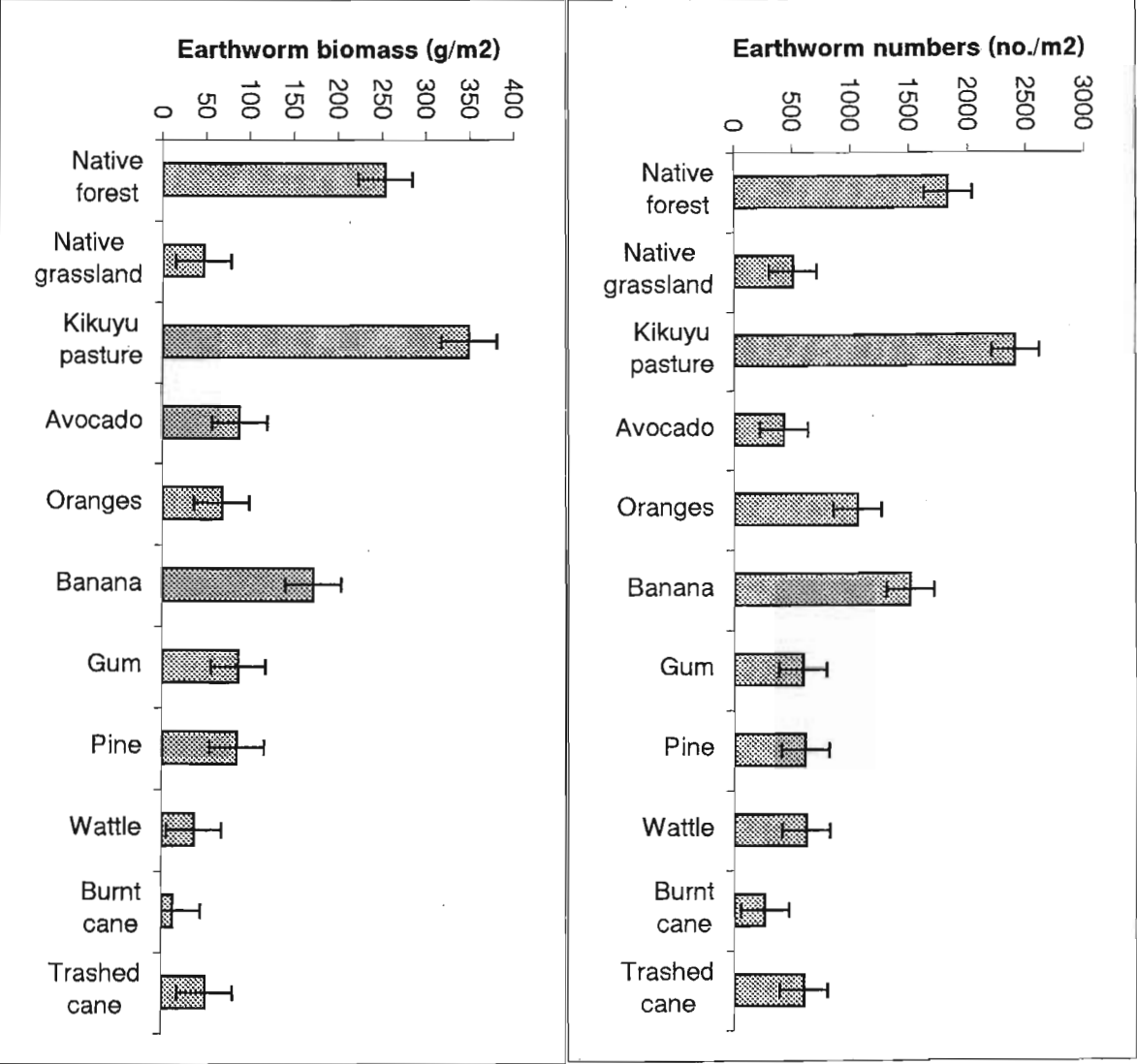
Figure 3. 2. Earthworm numbers and live biomass for the different land uses
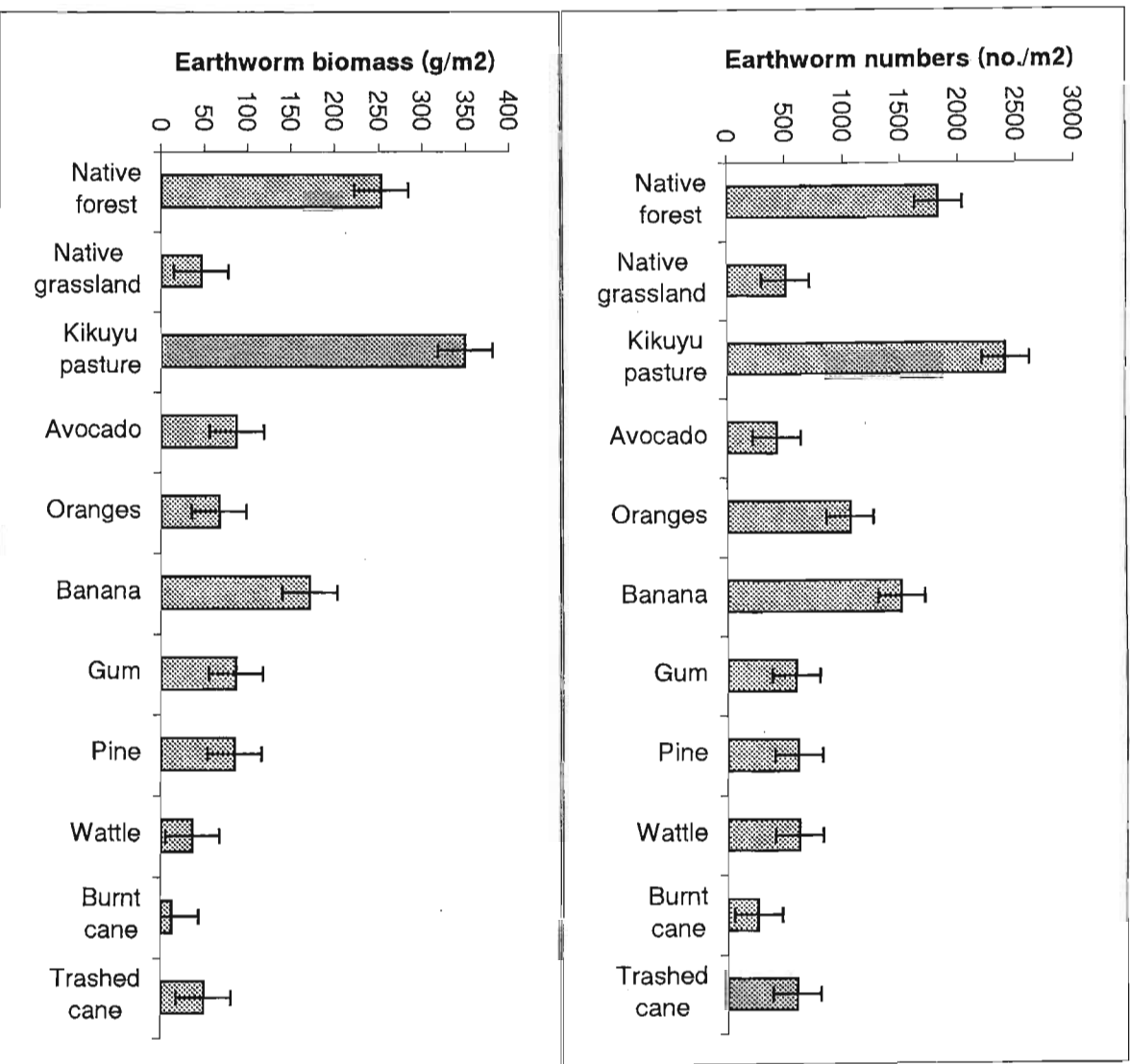
Bars show ± SE

44

Figure 3. 2. Earthworm numbers and live biomass for the different land uses

Bars show ± SE

44

order : kikuyu pasture≥ native forest >banana > native grassland ≥ orange > gum > trashed sugarcane > pine > avocado > wattle > burnt sugarcane. Soluble C was considerably higher under kikuyu pasture than any of the other land uses (Figure 3.1).

Soils under native forest and banana also had relatively high concentrations. Lowest values were recorded for burnt sugarcane, and like those for organic C, values were markedly higher under trashed than burnt sugarcane. Very high concentrations of microbial biomass C (i.e. > 2000 mg kg^{-1}) were found under kikuyu pasture, native forest, banana and orange (Figure 3.1). These four land uses also had high values for the microbial quotient (i.e. > 4.5 %). Intermediate, but still high, levels of microbial biomass C (1000 - 2200 mg kg^{-1}) were recorded under native grassland, gum, pine and wattle. Lowest values for microbial biomass C (250 - 750 mg kg^{-1}) and microbial quotient (1 - 2 %) were found for soils under avocado, trashed and burnt sugarcane.

Earthworm numbers followed the order : kikuyu pasture > native forest > banana > orange > wattle = pine = gum = trashed sugarcane ≥ native grassland ≥ avocado > burnt sugarcane. Numbers were very large under kikuyu pasture (Figure 3.2) and were also large (> 1500 m^{-2}) under native forest and banana. Orange groves also supported communities of > 1000 m^{-2}. In comparison with values for soluble C, microbial biomass C, earthworm numbers were surprisingly low under gum, pine and wattle forests (cf. Figures 3.1 and 3.2). Earthworm numbers were considerably higher under trashed than burnt cane. Earthworm biomass showed broadly similar trends with land use to those for numbers. The relatively small biomass under orange groves indicates there were a large number of small earthworms under that land use. Similarly, the extremely high biomass under kikuyu pasture reflects the large percentage of large adult earthworms found under this land use.

3.3.3 Regression analysis

Linear correlation coefficients (r) between the various measured soil properties and earthworm numbers and biomass are presented in Table 3.2. Microbial biomass C was highly correlated with soluble C but neither were significantly correlated with total organic C content. Microbial biomass C was positively correlated with pH and sand content and negatively correlated with clay content. As expected, earthworm numbers and biomass were closely correlated with each other (Table 3.2, Figure 3.3) and were both strongly correlated with microbial biomass C (Figure 3.3) and soluble C but not with organic C content. Earthworm numbers were also positively correlated with exchangeable Ca content and soil pH.

Table3. 2. Linear correlation coefficients (r) between various parameters measured in the study

	Earthworm biomass	Earthworm numbers	Microbial biomass C	Soluble C	Organic C	Exchangeable Ca	Clay %	Sand %
pH $_{(water)}$	0.16	0.38**	0.34**	0.07	0.06	0.82***	- 0.32*	0.29*
Sand %	0.05	0.31*	0.53***	0.28	0.04	0.10	- 0.97***	
Clay %	- 0.12	- 0.31*	- 0.50***	- 0.40**	- 0.12	- 0.15		
Exchangeable Ca	0.14	0.37**	0.24	0.10	0.11			
Organic C	0.15	0.11	0.21	0.30				
Soluble C	0.58***	0.65***	0.68***					
Microbial biomass C	0.40**	0.64***						
Earthworm numbers	0.81***							

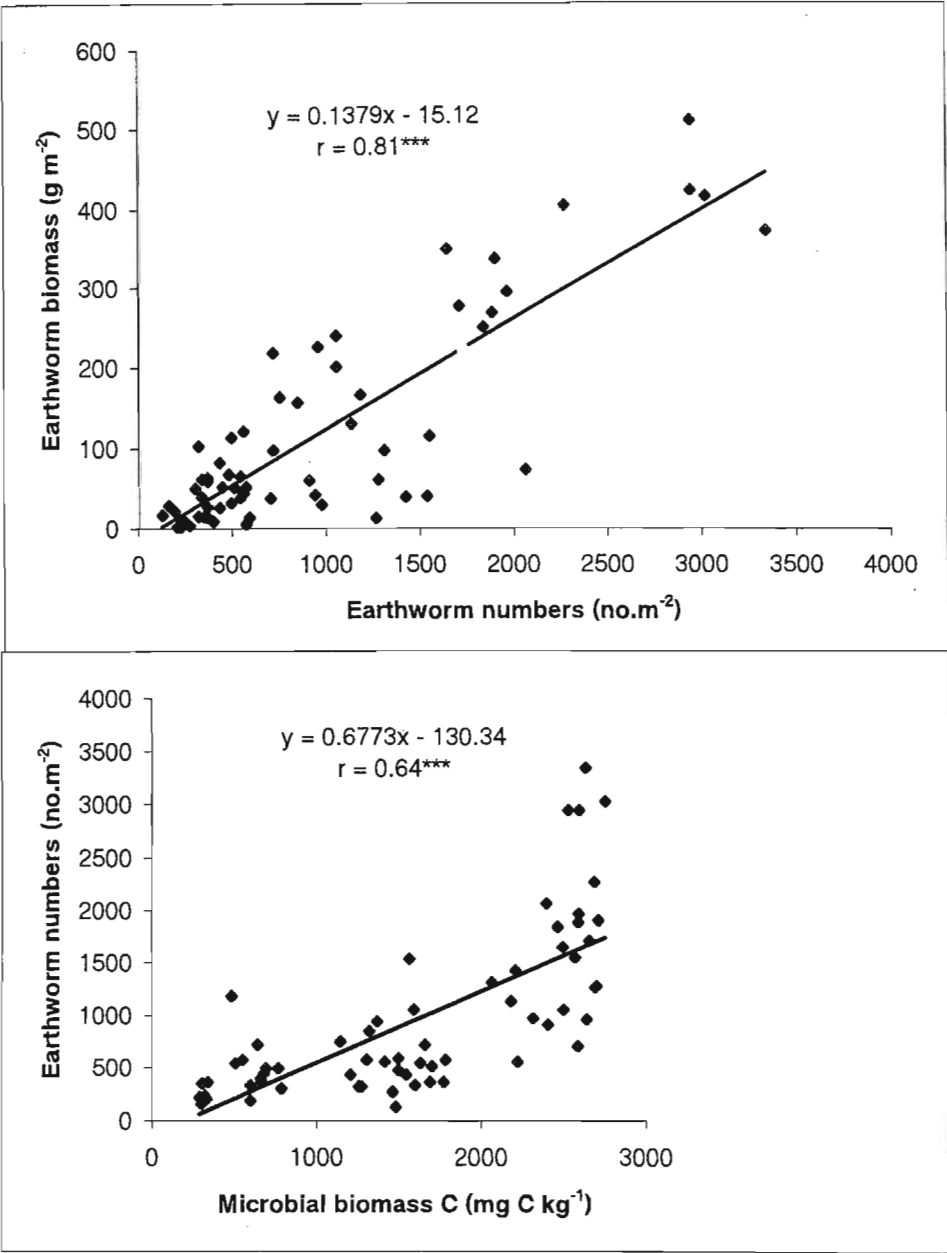*$P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Figure 3.3. Linear regressions between earthworm numbers and biomass for the different land uses

3.4 Discussion

3.4.1 Soil organic C

Native vegetation in the locality is rainforest and equilibrium soil organic C concentrations were about 56 g C kg^{-1}. In areas where forest had been cleared but the land had been allowed to revert back to native vegetation, the dominant cover was native grassland. The lower organic matter content under these grasslands reflects the degrading effect of clearing forest, burning remaining vegetation and cultivating the soil. Through the process of secondary succession, this land will presumably eventually return to forest cover and organic matter will accumulate until it reaches that present under the undisturbed forest.

Low organic C and soluble C contents were observed under burnt sugarcane. Substantial losses of soil organic matter content under preharvest-burnt sugarcane have been noted by a number of workers (Wood, 1985; Blair et al., 1998; Dominy and Haynes, 2002; Dominy et al., 2002). A decline in organic matter under arable systems can be traced to three main factors. These are (i) a much lower allocation of carbonaceous residues to the soil (due to relatively wide spacing of crop plants, removals of harvested products and burning of crop residues, (ii) tillage-induced aggregate disruption and exposure of organic matter that was previously physically-protected against microbial action and (iii) more favourable conditions for decomposition (e.g. tillage induced aeration, irrigation and fertilizer additions (Haynes and Beare, 1996; Paustian et al., 1997). The substantial loss of soil organic matter is surprising since cultivation is infrequent only occurring at replanting (every 7 - 10 years). However, much of the field is effectively fallow (i.e.. the interrow spaces) and receives very sparse inputs of organic matter (Haynes and Hamilton, 1999). That is, because the fields are preharvest-burnt (causing large losses of C, N and S via volatilization) and the above-ground biomass is then harvested and removed, inputs of organic matter over the whole field are very small. The main organic matter inputs will be via root turnover in the row area.

49

Larger soil organic matter contents under green cane harvesting than burning have been observed by a number of other workers (Wood, 1991; Blair *et al.*, 1998; Blair, 2000; Graham *et al.*, 2002) and occur because of greater organic matter inputs. Green cane harvesting involves the return of all the crop residues to the soil and a blanket of trash mulch is left at the soil surface after harvest. Annual deposition of trash can be substantial commonly ranging from 10 - 20 Mg ha^{-1} (Graham *et al.*, 2002). Even so, levels of soil organic matter attained were considerably lower than those under native forest.

The highest organic C, concentrations were recorded under grazed kikuyu pastures. A substantial accumulation of organic matter under kikuyu pastures (often with higher concentrations than under native vegetation) has been observed previously (Haynes *et al.*, 2002; Milne and Haynes, 2002). The accumulation of organic matter under high-producing grazed pastures is common and is attributable to the large inputs of organic matter that occur under grazed pastures in the form of root turnover plus inputs of leaf litter and animal dung (Haynes and Williams, 1993). Application of fertilizer and irrigation may also play an important role since the greatly increased dry matter production results in larger returns of organic matter than under unfertilized conditions (Fraser *et al.*, 1993). The much higher soluble C under pasture than native forest is indicative of the large turnover of organic matter that occurs under highly productive, grazed pasture (Haynes and Williams, 1993) which maintains high concentrations of organic matter in soil solution (Sarathchandra *et al.*, 1988; Haynes, 1999a).

The three horticultural crops were under markedly different soil management. In banana plantations, trash from the banana plant (vegetative growth from the previous year) is piled on the soil surface at the centre of the interrow spaces where it decomposes. Thus, organic matter inputs to the soil are large. Orange orchards are grassed-down with narrow herbicide strips down the tree rows. Organic matter inputs will therefore occur mainly through turnover of grass root material and irregular inputs of grass clippings following mowing. In the avocado orchards the canopy had closed, thus shading the orchard floor.

50

As a result, the floor was essentially bare (fallow) apart from thin layer of decaying a\
leaves. Thus, organic matter inputs to the orchard floor increased in the order : avocado
< orange < banana and this is reflected in the increasing levels of organic C and soluble
C (Figure 3.1).

The pine and gum forest floors are covered with a thick layer of litter while the floor of
wattle plantations is essentially bare as there is sparse litter fall except after flowering. As
a result, soil organic C content under wattle was lower than that under the other two tree
species. Likewise, soluble C under wattle was lower than under gum and pine forests.

3.4.2 Soluble C

Although 0.5 M K_2SO_4 extracts slightly less dissolved organic C than water (Bolan et al.,
1996; Haney et al., 1999), the K_2SO_4-extractable fraction is often used as a measure of
"labile, soluble" C (Janzen et al., 1997; Chan and Heenan, 1999; Haynes, 1999a; Graham
et al., 2002). In general, the soluble fraction is considered the most dynamic C fraction in
soils and as a readily-available substrate for heterotrophic microbial activity (Burford and
Bremner, 1975; McGill et al., 1986). In fact, typically less than 50% of it is readily
degradable (Wagai and Sollins, 2002). The refractory fraction is thought to consist of
mainly soluble humic material while the degradable part is mainly present as
carbohydrates (Qualls and Haines, 1991; Jandl and Sollins, 1997; Wagai and Sollins,
2002).

The organic matter in soil solution may be replenished by leaching from above-and below-
ground litter, the synthetic activity of soil microbes involved in decomposition of the litter,
desorption from soil colloids and hydrolysis of insoluble soil organic polymers (Moore,
1997). Even so, it accounted for only a very small proportion (0.20 - 0.90%) of total soil
organic C. This small, labile C fraction changed much more markedly in response to
changes in land management than total organic C content. For example, in comparison

51

with burning, green cane harvesting of sugarcane resulted in a 1.3-fold increase in organic C content but a 3.1-fold increase in soluble C. Similarly, soils under banana had 1.4 times more organic C than those under avocado but 2.1 times more soluble C. In comparison with native forest, the decrease in organic C under burnt sugarcane was 1.7-fold while the equivalent decrease in soluble C was 5-fold. Furthermore, concentrations of soluble C were not significantly correlated with those of organic C. The lack of any correlation may well reflect seasonal fluctuations in soluble C that commonly occur in response to changes in C supply, and / or rates of decomposition (Sarathchandra *et al.*, 1988; Janzen *et al.*, 1997; Campbell, 1999).

3.4.3 Microbial biomass C

Because of the dynamic nature of the soil microbial biomass, it responds rapidly to changes in C supply and therefore can be a good indicator of early changes in soil organic matter status (Gregorich *et al.*, 1994; Sparling, 1997). Effects are often evident long before changes in organic C can be detected. In a similar way, in this study changes in microbial biomass C in response to changes in land management were much more pronounced than those of organic C. For example, the 1.7-fold decrease in organic C content under burnt sugarcane (compared to native forest) contrasted with the 8.3-fold decrease in microbial biomass C. Since changes in microbial biomass C with land use were much more marked than those for organic C, values for microbial quotient showed very similar trends to those for microbial biomass C (Figure 3.1).

The microbial quotient ranged from 0.9 to 4.9% which is in the range of 1 -5% commonly found in soils (Sparling, 1997). However, the absolute values for microbial biomass C were, in general, high. For example, under banana plantations, native forest and kikuyu pasture they exceeded 2500 mg C kg^{-1}. These high values are presumably attributable to the luxuriant plant growth and thus large organic matter inputs that occur in the warm, moist conditions that prevailed in this tropical area. In temperate regions, microbial

biomass C commonly ranges from 100 - 500 mg C kg^{-1} under arable crops and 800 - 1500 mg C kg^{-1} under native forests and long-term grazed pastures (Sparling, 1997; Dalal, 1998).

The close correlation between soluble C and microbial biomass C was expected since, as already noted, soluble C represents a readily-available substrate for soil microbial activity. In addition, much of the soluble C fraction is, itself, of microbial origin. For example, part of it consists of the products of microbial synthesis (e.g. microbial polysaccharides, aliphatic organic acids, polyphenols and humic substances) (Moore, 1997).

3.4.4 Earthworms

The influences of soil management practice on earthworm communities are complex and act by affecting food supply (location, quality and quantity), insulation of the soil through the presence of mulches (effects on soil water content and temperature) and alteration of the chemical environment (fertilizers, pesticides) (Edwards and Lofty, 1977). The use of earthworm numbers as an indicator of soil quality is complicated by the fact that when native vegetation is removed to form agricultural fields, commonly most, or all, of the native earthworm species die out (Lee, 1985). Accidently introduced exotics become the dominant species and the extent of their introduction and dispersal can influence their consequent abundance. In addition, sampling for earthworms is notoriously labour intensive (Baker and Lee, 1992), they can be very patchily distributed in fields and soil moisture can vary within short periods of time and greatly affect the numbers of earthworms collected (Baker, 1998). Despite these drawbacks, earthworm numbers and / or biomass have been used successfully as indicators of soil quality in a number of recent studies (e.g. Fraser *et al.*, 1996; Haynes and Tregurtha, 1999; Paoletti, 1999; Didden, 2001; Jongmanns *et al.*, 2001).

The community of earthworms under native forest was very large (~1800 m^{-2}). The smaller earthworm community under native grassland than forest is presumably due to loss of earthworm species when the land was cleared and cultivated. Earthworm numbers and biomass were markedly greater under kikuyu pasture than native rainforest despite organic C content being similar under the two land uses. The large inputs of organic matter in the form of root turnover and deposition of dung pats at the surface provides a suitable environment to support a large earthworm community (Lee, 1985; Fraser, 1994). In addition, pasture plants act as a type of mulch which buffers the soil against rapid changes in temperature whilst the lack of tillage means burrow systems are left undisturbed. The large inputs of decomposable organic matter enables earthworms to develop rapidly (Lee, 1985) so the majority were present as adults (see Chapter 4). This explains the particularly high earthworm biomass present under kikuyu pasture (Figure 3.2).

The fact that the pastures were grazed with cattle may have, to some extent, actually limited earthworm populations. Lobry de Bruyn (1993), for example, suggested that trampling of irrigated pastures by livestock (and consequent compaction) can increase earthworm mortality and reduce their abundance. The presence, or extent, of such an effect was not investigated in this study. However, the extremely large community under pasture suggests such an effect was minimal.

According to Lavelle *et al.* (1994), earthworm biomass under sugarcane at two sites in tropical Mexico and Guadeloupe was similar to that under pastures. They, therefore, suggested that in terms of faunal relations, sugar plantations are essentially humid grasslands. Results presented in Figure 3.2 are in direct contrast to such an ascertion since earthworm numbers and biomass were the lowest recorded under any land use. Indeed earthworm numbers under kikuyu pasture were 8 times those under burnt cane whilst earthworm mass was 18 times as great. Low earthworm numbers under burnt cane were also noted by Wood (1991). Under burning, inputs of organic matter to the soil surface are small and, in addition, soil in the interrow space often becomes compacted

54

(Hartemink, 1998; Haynes and Hamilton, 1999) and this would further discourage earthworm activity. The 2.4-fold increase in earthworm numbers under trashing compared to burning of cane was not unexpected. Not only does the decaying trash blanket at the soil surface act as a food source but the surface mulch conserves moisture and provides insulation from temperature extremes. Similarly, in northern Queensland, Wood (1991) noted that earthworm numbers were 2.7 fold higher under a trash blanket than under burning.

In comparison with the relatively high values for organic C and microbial biomass C recorded under exotic forests, earthworm numbers and biomass were surprisingly small. The response of earthworm populations to afforestation has been shown to be very much dependent on the tree species planted and the quantity and quality of litter produced (Curry, 1998). In general, most coniferous litter is unacceptable or marginally palatable to the majority of earthworms (Bernier and Ponge, 1994) and, as a result, coniferous forests usually support a small earthworm community (Curry, 1998; Paoletti, 1999). Similarly, most *Eucalyptus* species produce litter that is not attractive to earthworms and most invertebrates and planting such forests tends to cause disappearance of many species (Paoletti, 1999). Thus, the low numbers under pine and gum are not surprising. Under wattle, the forest floor is almost bare since litter inputs are minimal. As a result, a shortage of food probably limited earthworm populations. The very low pH $_{(water)}$ (4.6) and low exchangeable Ca concentrations (288 mg kg^{-1}) may well have been additional limitations under wattle.

Under orchard crops, earthworm numbers increased in the same order as organic C, soluble C and microbial biomass C (i.e. avocado < orange < banana). Thus, the greater the organic matter inputs that occurred to the orchard floor, the larger was the earthworm community. The decaying plant residues at the soil surface in banana plantations evidently provided a particularly favourable environment for earthworms.

In general, the earthworm numbers in this study were high. For example, in regions of the humic tropics, Lavelle *et al.* (1994) suggested that earthworm numbers were in the general range : tropical rainforest, 4 - 401 (mean 77); pastures, 93 - 740 (mean 310); crops, 10 - 42 (mean 19) and tree plantations, 84 - 341 (mean 170 m^{-2}). The smallest numbers recorded here were under burnt sugarcane (~ 250 m^{-2}). Numbers under kikuyu pasture were exceptionally high (~2400 m^{-2}) but are in agreement with the very high levels of microbial biomass C recorded under this land use. Earthworms were sampled towards the end of the rainy season when numbers were expected to be highest (J.D. Plisko, personal communication, 2000) so numbers and biomass probably represent maximum levels. The warm, wet climate in the study area and high inputs of organic matter to the soil presumably provide excellent conditions for earthworm populations to flourish.

The positive correlations between earthworm numbers and both pH and exchangeable Ca are not uncommon (Edwards *et al.*, 1995; Makeschin, 1997) and reflect the generally low pH (mean pH $_{water}$ for all land uses was 5.3) and in some cases low exchangeable Ca levels (i.e. < 500 mg kg^{-1}) found in these soils (Table1). Soil acidity can limit earthworm activity and their abundance in acid soils is often increased by liming (Edwards and Bohlen, 1996). The importance of exchangeable Ca has been underlined by a number of workers and may be related to the need for Ca because of its excretion from calciferous glands (Lee, 1985).

Although earthworm numbers were not significantly correlated with organic C they were closely correlated with both soluble C and microbial biomass C contents. Similarly, in a study of earthworm communities in cropping soils in New Zealand, Fraser *et al.* (1996) found that earthworm biomass and numbers were not significantly correlated with organic C content but they were correlated with microbial biomass C. Earthworm communities are often food-limited and they increase greatly following the addition of organic amendments (Curry, 1998). The main sources of organic matter for earthworms are decaying above- and below-ground litter and the associated soil microbial biomass. Both epigeic and

56

endogeic species contribute to the earthworm community in these soils (see chapter 4) so the quantity and quality of surface litter and that deposited below ground will both greatly affect earthworm numbers. Values for microbial biomass C and soluble C in the surface 10 cm of soil are presumably greatly dependent upon the extent of C inputs via above and below-ground litter. As a result the size of earthworm communities is closely related to the size of these labile C pools.

In this discussion, only the effects of land use on the size of the earthworm community have been considered. Certainly, both numbers and biomass were greatly affected, and changes were related to differences in the size of labile soil C pools. The composition of the earthworm community is another important aspect of soil quality and will be discussed in Chapter 4.

CHAPTER 4

EFFECTS OF AGRICULTURAL LAND MANAGEMENT ON
THE COMPOSITION OF EARTHWORM COMMUNITIES

4.1 Introduction

In a recent, detailed review of the effect of land-use on earthworm ecology in tropical agroecosystems, Fragoso *et al.* (1999a) concluded that when native forests or savannas are converted to agroecosystems, earthworm communities change in abundance, biomass, number of species, ecological categories and species composition. The composition of the community is important because earthworms can be grouped into three broad ecological categories (Edwards and Bohlen, 1996). Epigeic earthworms do not have burrows, they are litter dwelling and pigmented and their main role is in litter decomposition. Endogeics are unpigmented and burrow through the upper 15 - 30 cm of soil; they ingest mineral soil (with a preference for material high in organic matter) and deposit their casts below ground in burrows and other voids. They are important in creating macroporosity, and increasing soil microbial activity and nutrient availability (Smettem, 1992). Anecic species have semi-permanent vertical, surface-connected burrows; they inhabit the subsoil but come to the soil surface to feed on litter and other decaying materials. They are important in litter decomposition, downward movement of organic residues and in creation of surface-connected macro pores to depth.

In temperate regions, accidentally introduced exotic earthworm species dominate in agricultural soils (Lee, 1985). However, in tropical regions Fragoso *et al.* (1999b) observed that a group of ubiquitous exotic species are common in the majority of countries and these usually co-exist with native species common to a particular locality or region. However, agricultural land use has major effects on both the size and composition of earthworm communities. In general, the community structure most resembles that under

58

native forest under tree plantations and a diverse community dominated by endogeics exists under improved pastures (Lavelle *et al.*, 1994; Fragoso *et al.* (1999 a, b). Annual arable crop production generally results in poorest communities in relation to both abundance and ecological categories (Fragoso *et al.*, 1999b).

Little is known regarding the composition of earthworm communities in agricultural soils of South Africa or how agricultural land use effects composition. As part of the study described in Chapter 3, the species composition of earthworm communities under 11 land uses in northern KwaZulu-Natal was determined and the results are described and discussed below.

4.2   Materials and Methods

Earthworms were identified under the supervision of Dr J.D. Plisko of the Natal Museum, using the keys of Gates (1972), Sims and Easton (1972) and Plisko (1992; 1997). The criteria for classification are mainly focussed on the reproductive organs as they affect evolution of earthworm species, and the digestive tract organization that influences the ecological activities of worms. The earthworms were classified according to the presence or absence of clittelate disregarding their body size in terms of length. Individuals with clittelate were identified as adults on the basis of the position and shape of clittelate, and those without clittelate as juveniles. Some specimens were only collected as juveniles and thus, were only identified to genus level.

4.3 Results

4.3.1 Total earthworm collection

A total of eleven species were collected from the sample sites surveyed. Averaged across all land uses sampled, the dominant species was *Pontoscolex corethrurus* (Müller, 1856) which represented approximately 40 % of the total number of earthworms collected in the survey (Figure 4.1). *Amynthas rodericensis* (Grube, 1879) and *A. minimus* (Horst, 1893) represented about 28 and 19 % respectively. *Dichogaster saliens* (Beddard, 1893) represented about 6 % of the total number of earthworms collected. Together *A. diffringens* (Baird, 1869), *D. bolaui* (Michaelsen, 1891), *Tritogenia douglasi* (Plisko, 1997), and *Acanthodrilidae* sp. from the Microchaetidae family comprised 2 % each. The remaining 0.6 % was shared by the remaining 3 species each having about 0.2 % of the total 0.6 %. These consisted of *A. hawayanus* (Rosa, 1891), *A. aeruginosus* (Kinberg, 1866) and *Proandricus* sp. from the Microchaetidae family that is indigenous to South Africa. *Acanthodrilidae* sp. and *Proandricus* sp. were both collected as juveniles and thus could be identified only to genus level. *T. douglasi* is also an indigenous species of the Microchaetidae family. The other species were all accidentally introduced exotic species originating from South America, Asia and West Africa (Table 4.1).

4.3.2 Effect of land use

The total number of species identified under the various land uses is shown in Figure 4.2 a. Most land uses supported between five and seven species. The exceptions were wattle forest and sugarcane that had only two or three species present. The maximum number of species present was seven under orange groves. Juveniles dominated under all land uses except kikuyu pasture and avocado orchards where the majority of the community were adults (Figure 4.2 b). Epigeic earthworms dominated the community under native

60
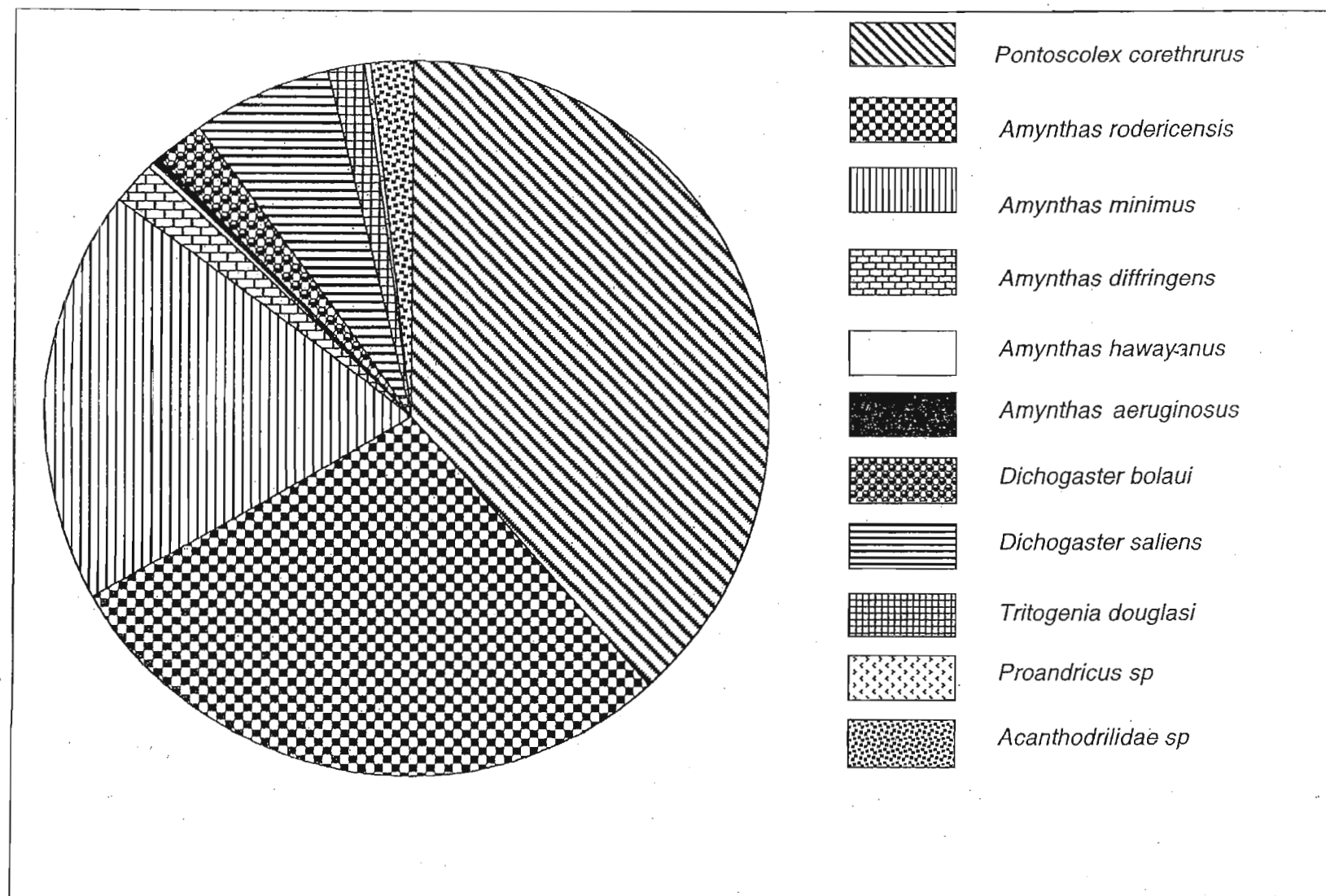
Figure 4.1 Species composition (percentage of total number of individuals) of the total collection of earthworms

Table 4.1. Family, continent of origin and ecological classification of exotic species found.

Species	Family	Origin	Categories	Habitats	Food
Pontoscolex corethrurus	Glossoscolecidae	South America	Endogeic (mesohumic)	Upper 0 - 20 cm	Soil from 0 - 10 cm
Amynthas rodericensis	Megascolecidae	Asia	Epigeic	Litter	Leaf litter
Amynthas diffrengens	Megascolecidae	Asia	Epigeic	Litter	Leaf litter
Amynthas hawayanus	Megascolecidae	Asia	Epigeic	Litter	Leaf litter
Amynthas aeruginosus	Megascolecidae	Asia	Epigeic	Litter	Leaf litter
Amynthas minimus	Megascolecidae	Asia	Endogeic (polyhumic)	Surface soil and rhizosphere	Soil with high organic matter
Dichogaster bolaui	Megascolecidae	West Africa	Epigeic	Litter	Leaf litter
Dichogaster saliens	Megascolecidae	West Africa	Endogeic (polyhumic)	Surface soil and rhizosphere	Soil with high organic matter
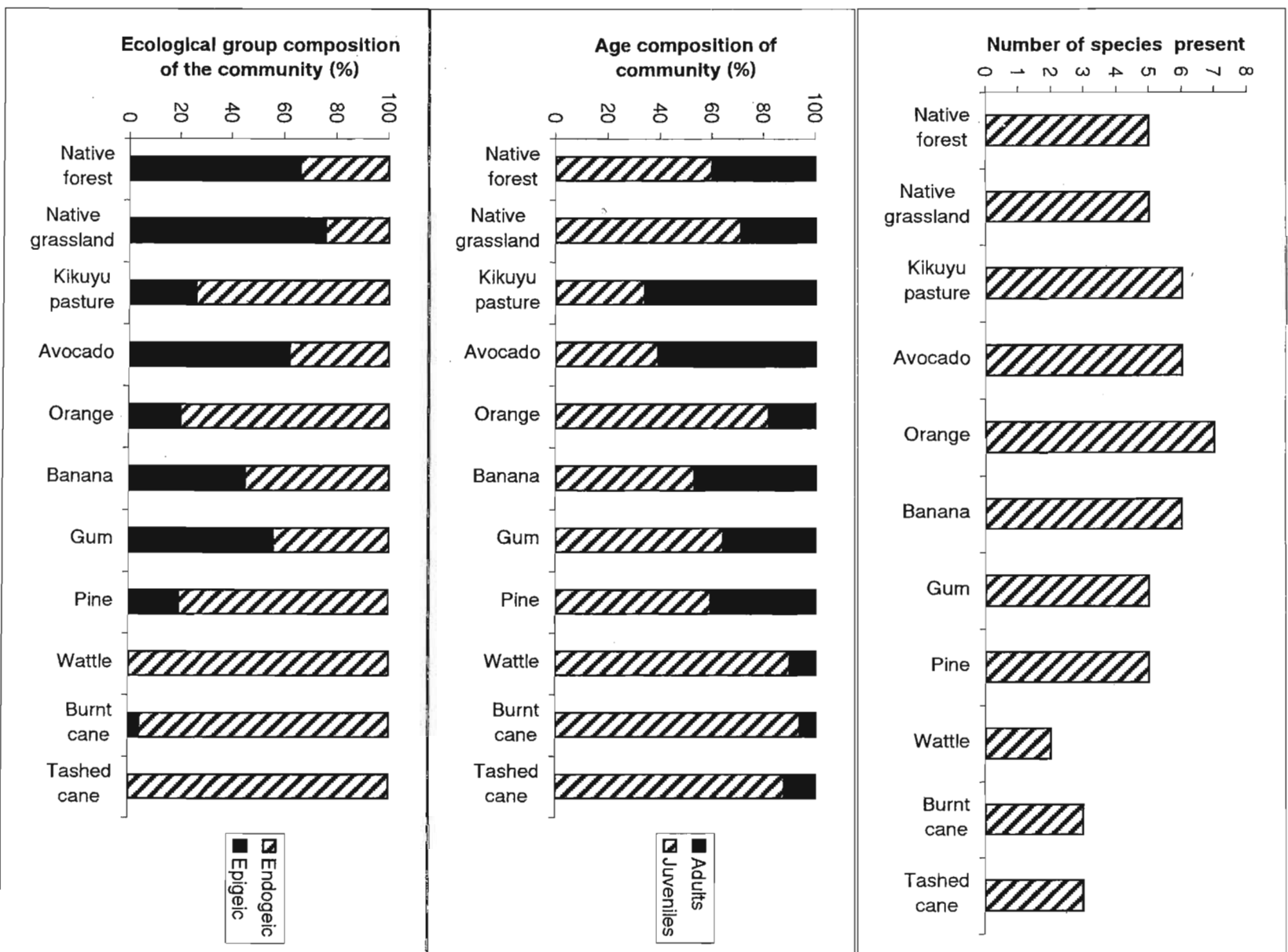
Figure 4.2 Composition of earthworm communities under various different land uses in terms of (a) number of species present, (b) percentage of adults and juveniles present and (c) percentage of endogeic and epigeic species present

63

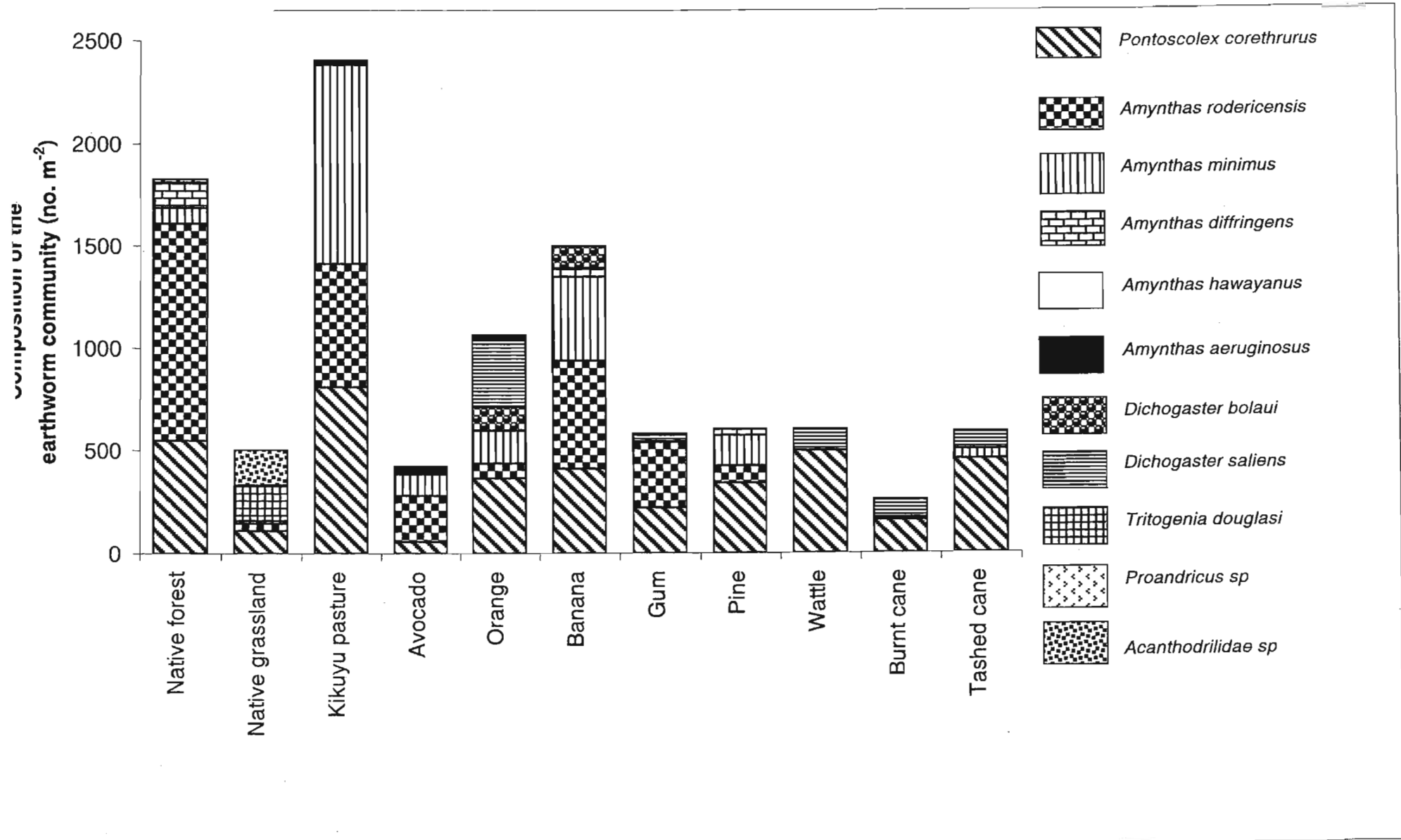**Figure 4.3 a** Species composition of earthworm communities under various land uses expressed as number m^{-2} of the total individuals in the community
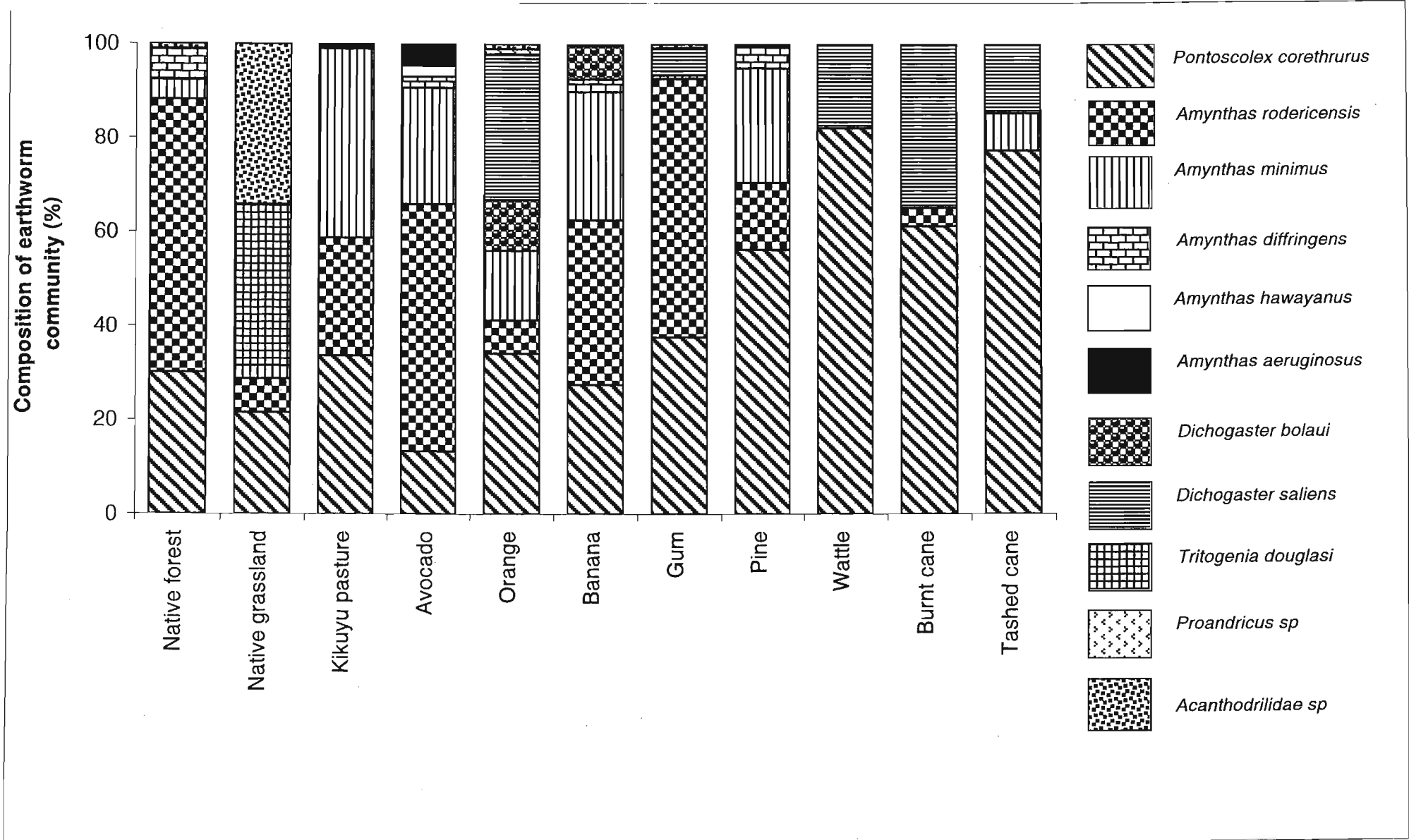
Figure 4.3 b Species composition of earthworm communities under various land uses expressed as percentage (%) of total number of individuals in the community

forest and native grassland (Figure 4.2 c) and this was also the case under avocado orchards gum forests. Under the remainder of the land uses endogeic species predominated.

The composition of the earthworm communities under the 11 land uses is shown in Figure 4.3 a, b. It is clear that *P. corethrurus* was the dominant species being present under all the land uses. It made up more than 50 % of the community under pine and wattle forest and sugarcane. *A. rodericensis* was present in nine of the 11 land uses and it made up 50 % or more of the community under avocado, native and gum forests. *A. minimus* was present in nine of the land uses and made up the highest proportions of the community (40 %) under kikuyu pasture. *D. saliens* was present in six, *T. douglasi* in two and *Proandricus* sp. in one land use.

In order to investigate, in more detail, the distribution of earthworms within sugarcane fields, data from samples taken within the row area and in the interrow were separated and presented in Figure 4.4. It is evident that earthworm numbers were much higher in soils in the row than interrow area under both burnt and trashed cane and higher numbers were recorded in both areas under trashed than burnt cane.

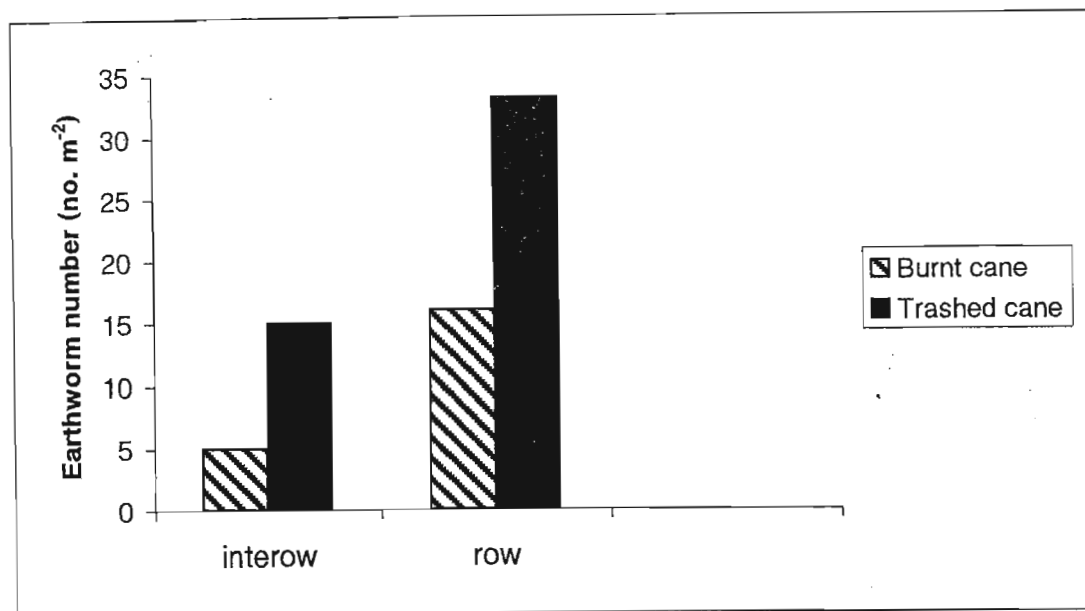**Figure 4.4.** Effect of burning and green cane harvesting with trash retention on the numbers of earthworm below the row and in the interrow space of sugarcane fields

4.4 Discussion

4.4.1 Community structure

Populations of exotic earthworms are generally spread by man, when planting gardens or trees or transporting soil (e.g., as ballast for soiling ships up to four centuries ago) (Lee, 1985). The exact mode of entry of exotic earthworms to South Africa is unclear but the Asian species are thought to have been brought in with the large Indian community that emigrated to KwaZulu-Natal in the 1860's (Ljungström, 1972). Similarly *P. corethrurus* is also thought to have been brought in from India after first establishing there. The mode of entry of the West African *Dichogaster* species is unknown. Once introduced, they were then spread by man's activity and probably particularly by the sugar industry. The ingress of exotics is common in agricultural soils throughout the world. They generally tend to have shorter generation times and higher fecundity rates than natives (Fragoso *et al.*, 1999b). They are all at least facultatively parthenogenetic. Their ability to rapidly increase the density of their population by parthenogenesis, which allows a single individual to build a population, contributes greatly to their success particularly in disturbed soils in agricultural ecosystems.

Earthworm biodiversity is dependent on many factors including the diversity of habitats and food sources in the soil (Fragoso and Lavelle, 1992). For example, conventional tillage results in loss of a surface litter layer and characteristically results in loss of both anecic and epigeic species that feed on surface litter (Lofs-Holmin, 1983b; Curry, 1998). As a result, the community in arable fields is generally dominated by endogeic species (Lal, 1987b; Hendrix *et al.*, 1986; 1992). By contrast, under an improved pasture, a large diverse community typically exists since there is no tillage and large inputs of C occur below ground via root turnover and above ground as leaf litter and animal dung. Nevertheless, endogeic species usually predominate (Fragoso *et al.*, 1999a).

Thus, in this study, although epigeic species were predominated under native forest and native grassland, endogeics were dominant under both kikuyu pasture and sugarcane. The ample supply of food and nutrients under fertilized kikuyu pasture enables earthworms to develop rapidly and so unlike the communities under most other land uses, those under pasture were dominated by adults. Haynes *et al.* (2002) also observed at two sites in the KwaZulu-Natal midlands that earthworms were present mainly as adults under kikuyu pasture whereas under arable crops and exotic forests they were present predominantly as juveniles. In avocado orchards, the epigeic species *A. rodericensis* dominated and the high proportion of adults present may well reflect the high palatability and nutrient content of avocado leaves, particularly in comparison with that of forest litter. Although Fragoso *et al.* (1999a) suggested that the community structure under tree plantations often resembles that under native forests, in this study communities under orange, banana and particularly pine and wattle forests, were dominated by endogeic species. Avocado orchard and gum forest communities were, however, dominated by the epigeic species *A. rodericensis* as was that under native forest.

Certain earthworm species tend to be associated with one another. Edwards and Bohlen (1996) reported some associations are casual and others are dependent upon similarities or differences between species in ecological requirements. Some associations may be a form of commensalism and independent of habitat. The most common association noted here was the coexistence of *P. corethrurus*, *A. rodericensis* and *A. minimus* together in eight of the 11 land uses. This is a combination of three species that exploit different layers of the soil volume; *A rodericensis* the litter at the soil surface, *A. minimus* the surface humus layer and *P. corethrurus* the mineral soil of the upper 20 cm.

It is important to recognize that the diversity of earthworm communities will, to a certain extent, be dependent on the accidental introduction, or otherwise, of individual species to specific localities. That is, as Baker (1998) suggested, although a diverse community of earthworms can only be a healthy sign, low numbers may indicate lack of dispersal of

exotic species rather than a problem with the soil or site. Lack of introduction and / or dispersal may well be the reason why no anecic earthworms were found in this study. Such earthworms form semi-permanent, surface-connected burrows that can extend to a depth of 1m or more. They feed on surface litter and can move large quantities of litter into their burrows and thus into the soil profile. In addition, their burrows form surface-connected macropores and are important for water infiltration. Bypass flow of water down such macropores can also reduce leaching losses of nutrients held within the soil matrix (Edwards *et al.*, 1993). Under some agricultural management practices (e.g. zero tillage) introduction of anecic species could be a practicable way of increasing infiltration and reducing runoff of water.

4.4.2 Dominant species present

In tropical and subtropical areas, most earthworms tend to have limited geographic distributions. Species with a pantropical distribution are often small and live in environments rich in organic matter (Fragoso and Lavelle, 1992). One of the few exceptions is *P. corethrurus* which is a peregrine, endogeic, unpigmented earthworm typically 7 -10 cm long and 3 - 4 mm in diameter. Adults may weigh up to 600 - 3500 mg fresh weight and the cocoon's mean fresh weight is about 40 mg (Lavelle *et al.*, 1987). The origin of this species is probably the forests of Guyanese plateau in South America (Righi, 1972; 1996) and it has been transported by man all over the humid tropics. It has been identified in 56 countries in four different continents (Fragoso *et al.*, 1999b). *P. corethrurus* has an ability to live in a great variety of soils differing in pH, organic matter content and texture. It is found in soils with a pH range 2.8 - 8.2, clay content of 4 - 41 %, organic matter content of 0.9 - 12.6 %, exchangeable Ca content of 8 - 165 m mol_c kg^{-1} and in areas with annual rainfall ranging from 268 - 5000 mm (Lavelle *et al.*, 1987; Fragoso *et al.*, 1999a).

P. corethrurus is a fast colonizer compared to most native African and Indian species

(Lavelle *et al.*, 1987). There are several reasons for this. Parthenogenesis reduces the time for sexual maturity to cocoon deposition since there is no need to seek a partner of the same physiological state. Growth is very rapid and individuals can produce cocoons after as little as 82 days. Fecundity of adults is also exceptional and values of more than 50 cocoons per adult per year are common in most soils. In addition, *P. corethrurus* has been shown to possess a very efficient mutualistic digestion system (Barois and Lavelle, 1986). In the anterior part of the gut, large amounts of water and intestinal mucus are secreted and mixed well with the ingested soil. As a result, soil microflora are strongly activated and become able to digest the complex organic compounds in the soil. Thus, simple organic solutes are released and absorbed in the posterior part of the gut. This digestion system is very efficient since up to 19 % of total soil organic C may be digested in 2.4 h, the duration of gut transit (Barois and Lavelle, 1986). By comparison, the assimilation of soil C by common tropical earthworms is only 1 - 5 %.

Presumably, due to its efficient digestion system and rapid colonizing ability *P. corethrurus* has become the dominant species in agricultural soils in the study area. Under sugarcane, which is the major agricultural land use in the locality, it made up about 70 % of the earthworm community. Interestingly, Spain *et al.* (1990), working on sugarcane soils in northern Queensland, found that *P. corethrurus* was the major earthworm species present. As with this study, they also observed that *P. corethrurus* numbers were considerably higher in the rows than between the rows and that they were found to be intimately associated with the root system of sugarcane. They suggested that the rhizosphere is the major source of tissue C for these earthworms. In this study, *P. corethrurus* numbers were markedly increased by trash retention, compared to burning and in fact the proportion of the community present as this species increased from 58 % to 79 % due to trash retention. This is somewhat surprising since the return of organic residues to the soil surface would be expected to increase the proportion of epigeic litter dwelling species (Lee, 1985). Nonetheless, Spain *et al.* (1990) also observed that *P. corethrurus* numbers were greatly increased by conversion from burning to trash retention.

71

They suggested that this endogeic species tends to inhabit the deeper layers of more humified trash during its latter stages of decomposition.

The presence of *P. corethrurus* is likely to be of great importance to the fertility of agricultural soils in the district. Endogeic earthworms ingest large amounts of soil and only occasionally come to the soil surface to feed or cast. They constantly extend their burrows which ramify through the upper 10 to 15 cm of soil, and they deposit their casts mainly in their old burrows and other voids. Because these earthworms are continually burrowing, they ingest and excrete large amounts of soil and can significantly affect properties of the plough layer of agricultural soil by increasing soil microbial activity, nutrient availability, aggregation and macroporosity (Lee, 1985; Lavelle and Martin, 1992). Indeed, *P. corethrurus* has been recognized as having the potential to ameliorate poor soil structure such as compaction (Barois *et al.*, 1993; Tomlin *et al.*, 1995) and improve soil structure and drainage in the wet tropics (Robertson *et al.*, 1994). In addition, its activity can greatly increase N and P availability since concentrations of mineral N and extractable P are elevated in cast material (Lavelle *et al.*, 1992; Pashanasi *et al.*, 1992; Lopez-hernandez *et al.*, 1993).

The most numerous epigeic species was *A. rodericensis* which was particularly numerous in native and gum forest litter layers, below the sparse litter of avocado orchards and in the decomposing trash in the banana plantation interrows. It has been accidentally introduced from India. The large numbers of *A. rodericensis* found under native forest are not surprising since it has been identified in 26 tropical countries on three continents and is characteristically numerous in natural ecosystems with an undisturbed litter layer (Fragoso *et al.*, 1999a). It is a fast colonizer of natural ecosystems where it is involved in decomposition of the litter layer. It was evidently also an important species involved in degradation of litter in gum forests, avocado and banana plantations. Its relatively large numbers under grazed kikuyu pasture indicate it is involved in decomposition of pasture litter and possibly animal dung.

72

The third most numerous species was *A. minimus* which is an Indian polyhumic endogeic species (i.e. lives and feeds in the organic-rich surface soil). It was particularly numerous under kikuyu pasture, banana, avocado and orange plantations and pine forest. Another, endogeic polyhumic species originating from West Africa, *D. saliens*, was also present in significant numbers under oranges and burnt cane. These species live in the humic layer of these systems. *A. minimus* made up the highest proportions of the community under kikuyu pasture which, indeed, had the highest organic matter content of all the land uses studied. *D. saliens* was a significant contributor to the relatively small earthworm community present under sugarcane. It was found predominantly in the row area and probably feeds on humified organic matter formed in the sugarcane rhizosphere.

The only land management that contained mainly native species was the native grassland, where *T. douglasi* and *Acanthodrilidae* sp. predominated. The areas of grassland sampled were more or less separated from adjoining agricultural land by wasteland. By contrast, the native forest areas sampled adjoining agricultural land were sampled at least 100 yards inside the forest. Sampling the native forest soils as far away as possible from agricultural land would be most likely to reveal native earthworm populations. Nevertheless, other workers have also observed that exotic earthworm species dominate soils in forest nature reserves in KwaZulu-Natal (Plisko, 2000).

Thus, it is clear that land use not only affected the size of the earthworm community but also greatly altered its composition. Changes in composition could be broadly related to alterations in vegetation cover and the degree of soil disturbance.

CHAPTER 5

GENERAL CONCLUSIONS

Individual farmers follow their own management systems to suit their particular needs, so that a large number of combinations of land uses and soil management practices are used. Each of these undoubtedly has its own individual effects on earthworms, although it is often difficult to separate the differences due to the operation of a large number of interacting factors. In addition, considerable natural population fluctuations occur between seasons adding to the complexity of the system. However, a large population of earthworms will be maintained by providing an adequate food supply and an environment conducive to their needs (e.g. moisture, temperature and soil chemical properties at acceptable levels and soil that is disturbed as little as possible). In this study, these conditions were observed in land uses that retained high levels of organic residues with little soil disturbance (i.e. grazed kikuyu pasture, native forest, banana and orange).

Undisturbed soils under native vegetation support a relatively stable assemblage of indigenous earthworm species. The abundance and diversity of the community is determined primarily by the interactions of soil and climate. These factors determine the physicochemical parameters of the soil, the nature of the vegetation it can support and the quantity and quality of the litter produced. Hence, major environmental factors affecting the distribution and activity of earthworms in natural systems are soil temperature, soil moisture and food supply.

Human intervention influences earthworm populations greatly, often adversely when the intervention is disruptive. Clearing of forest for agricultural development is particularly disruptive. The native population is often dominated by epigeic species and clearing for agricultural development usually results in loss of litter layer. The result is that native species rapidly die out. Some native species may survive under plantation and orchard

74

crops and sometimes under improved pasture but not usually under arable crops. All these occurrences were observed in this study. The aspect of human intervention that has the most dramatic consequences is the accidental or deliberate introduction of exotic species. Indeed, in most parts of the world, as was the case in this study, earthworm populations in agricultural lands are dominated by introduced peregrine endogeic species.

Indeed, in this study land use had substantial effects on soil organic C, soluble C and microbial biomass C content and on earthworm numbers and biomass. For example, grazed kikuyu pastures supported extremely large soil microbial and earthworm communities while sugarcane under preharvest burning resulted in low organic matter and microbial biomass C levels and small earthworm numbers. Soluble C and microbial biomass C were found to be important indicators of changes in soil management. Both of these small, labile pools of organic matter responded much more markedly to changes in soil management than organic C content. In addition, although microbial biomass C and soluble C were closely correlated with one another, neither were significantly correlated with soil organic C levels. The importance of labile C fractions was further demonstrated by the fact that earthworm numbers were significantly correlated with soluble and microbial biomass C but not with soil organic C.

Earthworms are an important biotic component in agricultural soils and contribute significantly to their physical, chemical and microbiological properties. Because of this, earthworm activity can significantly increase crop growth. Earthworm densities are, however, characteristically low under arable agriculture. Indeed, in this study lowest numbers and biomass were recorded under burnt cane. Even so, there is considerable scope for promoting earthworm activity through changing soil management practices so that constraints to their growth and activity are removed. These changes include liming to increase soil pH, mulching and / or irrigation to overcome unfavourable soil moisture conditions, minimizing the use of conventional tillage and pesticides and increasing food supply by increasing crop residues returns and the use of organic amendments. Certainly,

changing from preharvest burning to trash retention increased numbers appreciably. Because of the importance of earthworms in soil physical, chemical and microbiological processes, the size and composition of earthworm community can be used as biological indicators of soil quality. Since epigeic, endogeic and anecic species have distinctly different effects on soil processes, the relative proportions of these ecological groupings present is an important consideration.

The size and composition of earthworm communities in soils in the study locality are greatly affected by land management practice. Hence, large changes in earthworm numbers were recorded in response to changes in land use. The communities are dominated by exotic species accidentally introduced from India. As is the case in many parts of the humid tropics, *P. corethrurus* is a ubiquitous species present in substantial numbers under all types of land use. *P. corethrurus* was most commonly found in association with *A. rodericensis* and *A. minimus* indicating that these three species can coexist effectively in soils of the region. Studies of the size and composition of earthworm communities in agricultural soils and the relationship between these measurements and land management practices and / or soil properties, have been fruitful areas of soil ecological study in many parts of the world. In South Africa, very little is known regarding the size and composition of earthworm communities in agricultural systems of the different climatic regions of the country. This is therefore, an area worthy of future study. Also in view of the dominant role of *P. corethrurus* in soils, its role in influencing soil properties and fertility in the region deserves further study.

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77

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