EARTHWORMS AND THEIR TUNNELS IN RELATION

TO SOIL PHYSICAL PROPERTIES

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Summary

Physical modification of soil by earthworms has received limited scientific attention. With the use of limited tillage systems in agriculture and the compaction of agricultural soils by machinery, the role of biopores generated by earthworms for root growth and water and air movement is of increasing importance.

This work establishes the pressures exerted by a geophagous (soil ingesting) earthworm Aporrectodea rosea when tunnelling through soil. Axial forces were measured by directing earthworms to tunnel onto discs of soil mounted on an electronic balance. The area over which the force acts was estimated from the size of the hole created. The mean maximum pressure was 72.8kPa which is approximately one-tenth of the maximum axial pressure recorded for plant roots.

Radial pressures generated by the same earthworm species were measured in a study of the fracture of soil discs into which the worms were encouraged to tunnel. The tensile strength of replicate discs was determined by indirect tension tests and by the expansion of rubber membranes in soil discs. Mean values for the radial stress applied by the earthworms to tunnel through the soil discs was 230kPa. Both axial and radial pressures are related to the effectiveness of muscle contractions.

Physical properties of casts of the earthworm A. rosea were examined and compared with the properties of aggregates from the bulk soil. The shape of the earthworm casts and similar-sized soil aggregates were quantified by three ratio methods and two mathematical spectra using data obtained by two dimensional scanning. The tensile strengths of dry casts were measured by the indirect tension method and were approximately 2.5 times greater than those of dry aggregates of similar size. These tensile strengths are used to predict compaction characteristics of beds of dry casts and aggregates. From the relationship between soil water content, matric potential and undrained shear strength of fresh earthworm casts, the mean pressure applied to soil as it is remoulded by passing through the earthworm gut is estimated at 259Pa.

The morphology of tunnels made by earthworms in the field was also investigated. The coordinates of points along tunnels were measured during excavation. Descriptions as a function of depth include length, orientation and frequency of branching points. Mean tunnel length was approximately 400mm with typically 2-3 branching points. Soil carbon content was also determined in relation to depth. Positive correlations between tunnel length and organic matter in the profile were found for the geophagous species investigated. Maximum depth of the excavated tunnels was approximately 25cm, placing them entirely in the soil A horizon. Tunnel numbers per square metre were estimated by examining intercepts on horizontal cleavage faces at different depths.

Published values of soil ingestion rates and physical constraints on activity were used to develop an empirical model of earthworm movement through soil. The model allowed the partitioning of activity between arbitrary soil layers so that comparison of the model predictions was possible with the field studies.

STATEMENT

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university. To the best of the author's knowledge and belief this thesis contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

I consent to this thesis being made available for photocopying and loan.

Blair Malcolm McKenzie

May, 1988

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Chapter 1

Introduction

"In the dry climate of New South Wales I hardly expect that worms would be common"

Charles Darwin (1881)

Stable soil macrostructure is a prime requisite for long term agricultural production. Earthworms have long been cited as an indicator of good soil structure yet the associations between earthworms, their tunnels and soil physical properties are poorly understood.

There are several reasons for this failure in understanding. As earthworms by definition are soil dwelling animals most of their activities occur below the soil surface - beyond easy view. While some attempts have been made to create viewing cages (Evans 1947) these remove the earthworm from its usual environment. So the study of earthworm activity requires the study of the consequences of their actions rather than direct observation.

The creation and modification of cylindrical macropores in soil is one result of the movement of earthworms. To quantify changes in soil macrostructure requires the ability to measure soil structure. The realization (over the last two decades) that soil macroporosity is a major factor for water and air movement through soil and in some cases for root growth has provided an impetus for the development and application of quantitative measures.

The limited range of environments in which earthworms have been studied has contributed to the overall lack of understanding about their activities. Traditionally investigations have been conducted only in the environments most favourable for large earthworms. These are the cool temperate regions of Europe and North America. However Barley (1959 a,b) and more recently Lavelle (1979) have considered earthworms from a wider range of environments.

The division of earthworms into groups on the basis of niche partitioning and resource utilization was first documented by Lee (1959 a), but has only become widely appreciated with the work of Bouché (1971), Phillipson et al (1976) and Perel (1977). For the first time these concepts enable classification of earthworm activity in terms of the sites occupied by different

species. Thus some comparisons between different species occupying similar niches is now practical.

The need to understand earthworm activity away from traditional environments now coincides with the scientific capability to perform appropriate experiments and, using the ecological classifications, to extend results beyond particular species. For these reasons work was undertaken on the project "Earthworms and their tunnels in relation to soil physical properties".

The physical limitations that are placed on root growth by soil structure and strength have been considered by Dexter (1987) and by Misra et al (1986). From this it is known that the growth rate of roots of annual plants becomes reduced significantly when the penetrometer resistance, which is a measure of soil strength, exceeds about 2 MPa. The maximum root growth pressures for annual crops have been reported as 1 MPa. Dexter (1978) reported that the rate of tunnelling into soil by earthworms (*A. caliginosa*) was not limited up to penetrometer resistances of at least 3 MPa. Experiments to determine the axial pressures generated by earthworms are described in this thesis. Earthworm movement includes some radial expansion of the body. It was realized that this may weaken the soil immediately in front of the worm, thus reducing the axial pressures required for movement in strong soils. Experiments were devised to determine whether this was a usual tunnelling mechanism.

Soil material that has been ingested and excreted as casts by earthworms is well documented as differing from the bulk soil, not only in its chemical stability but also in its physical structure. Increases in porosity of this soil material must be the result of shearing as the soil passes through the gut of the earthworm. It was hypothesized that using soil mechanical theory the shearing forces involved in the passage through the earthworm gut could be estimated. An understanding of how ingested soil is moulded will contribute not only to soil structural modification theories but may also reflect on the relative importance of the various muscle layers of earthworms.

The contribution of the excreted material (or cast) to soil structure can be considered only if the structure of the material involved is considered. The manner in which the excreted soil material will pack together, either within the bulk soil or at the soil surface will depend on

both the shape and the strength of the material. Thus in this thesis consideration is also given to physical properties of the cast material.

Investigations were performed to describe the shape and size of earthworm tunnels existing in nature. This permitted an initial assessment of some environmental factors on the tunnelling of earthworms. Earthworm tunnels are a major component of soil macro-porosity and therefore are important in the movement of water and air through the profile. The assumption that they are mainly vertical tubes was tested by the field measurements. Combination with further field work on the density of tunnels opens consideration of the longevity of tunnels and highlights measurements which need refinement for predictive work. Also estimates were made of the length of tunnels per unit volume of soil, facilitating comparison with root density measurements.

Simple computer modelling procedures were applied to combine published earthworm data with the field measurements taken for this thesis as an attempt to understand their relative importance to earthworm movement through the soil profile. This modelling focuses attention on specific areas of earthworm biology which need more elucidation if improvements to the description of macropore space generation are to be made.

The work is summarized and suggestions for further work are made.

Chapter 2

Literature Review

2.1 Biology

Earthworms are soil dwelling animals. While there are some 3000 species documented only a very few, representing a limited number of genera, will be discussed here. These are mainly Lumbricidae (introduced from northern Europe) and some Megascolecidae. However the basic structure varies little (Figures 2.1, 2.2, 2.3). "They are cylindrical animals that consist essentially of two concentric tubes, the body wall and the gut, separated by a fluid filled cavity, the coelom, divided into segments by septa" (Lee 1985).

Figure 2.1 shows the external morphology of a "typical" lumbricid earthworm. The segments, sometimes called metameres are usually visible to the naked eye. When referring to the segments it is conventional to number them from the front of the worm. Around each segment are setae or bristles which which can be extended or retracted , by muscles. The number and arrangement of the setae varies but in the species studied in this work the eight setae on each segment are arranged symmetrically in four pairs.

Earthworms are usually pigmented either red, brown or pink. Additional features visible to the naked eye may include a pale clitellum, typically covering four to ten segments and usually posterior to segment ten. Anterior to the clitellum male pores may be visible.

The cuticle or outer covering of the worm overlies the epidermis as seen in Figure 2.2. Jamieson (1981) notes that the cuticle is about 1-4 µm thick and composed of layers of parallel collagen fibres with alternate layers at right angles. The layers form right and left handed helices along the length of the worm making a fibrous skeleton. The epidermis is composed of three cell types. The columnar or cuboidal cells called the epidermal epithelium which, though a single layer, provide support. Scattered between these cells are the earthworms sensory cells and numbers of basal cells which pack the other cell types together. The epidermis is bound on the inside by a membrane which is attached to the muscle layers.

The two main muscle layers are concentric coats of muscle tissue. The outer fibres
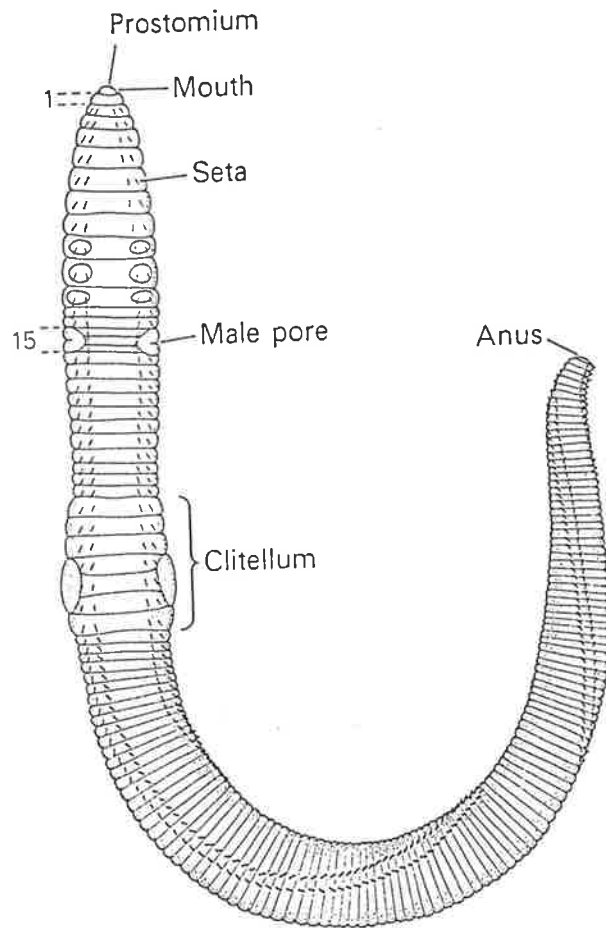
Fig. 2.1 External morphology of a "typical" earthworm. (From Handreck 1986).
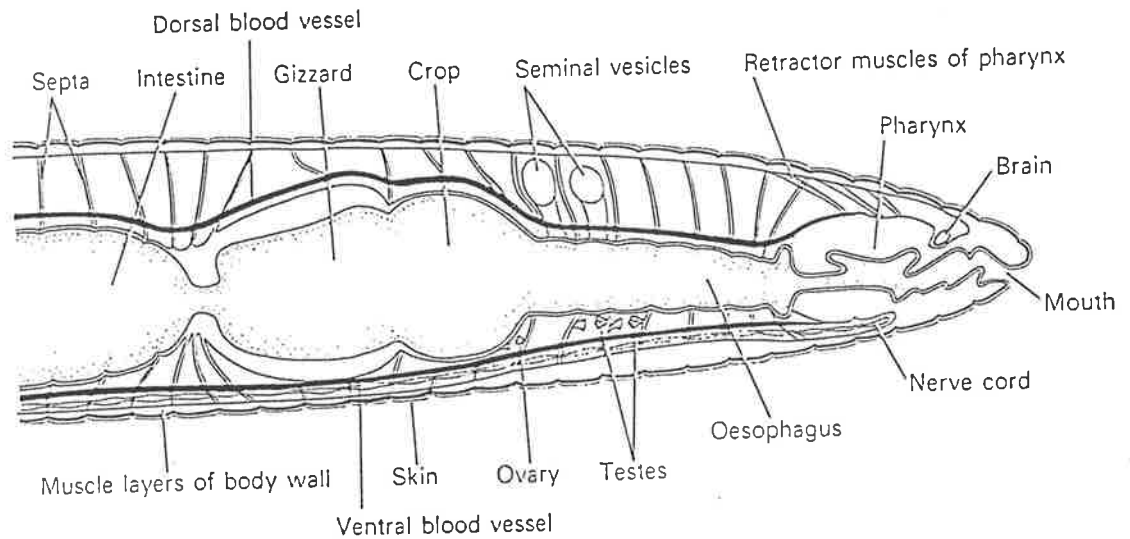
Fig. 2.2 Schematic longitudinal section of the anterior 24 segments of a "typical" lumbricid earthworm, illustrating the disposition of the principal organs of ingestion, digestion, reproduction, blood circulation, locomotion and coordination. (From Handreck 1986).
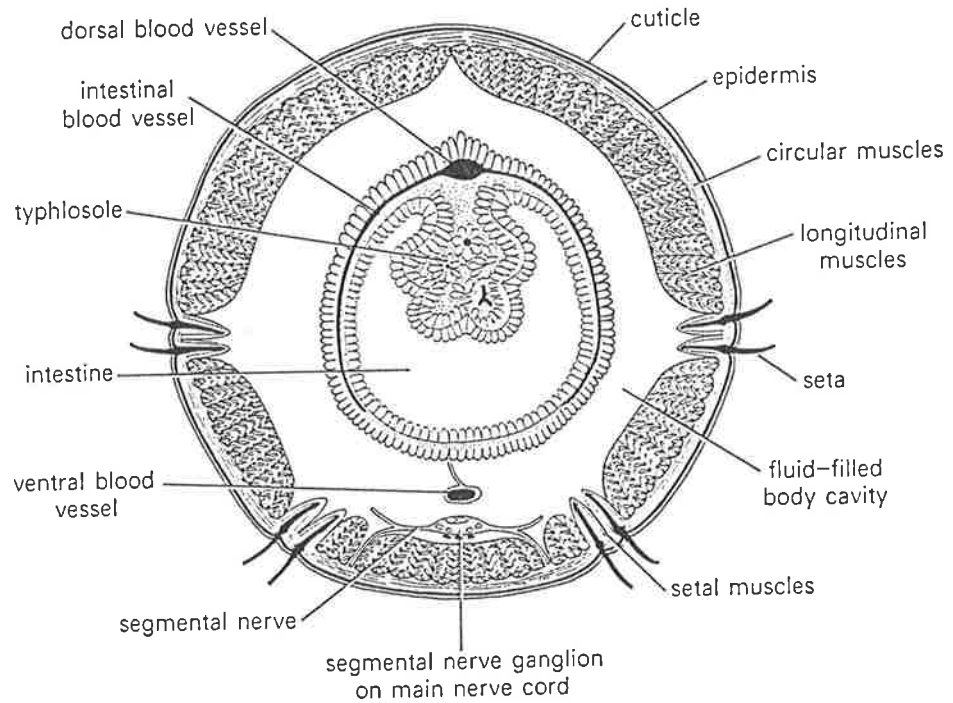
Fig. 2.3 Schematic cross section of the intestinal region of a "typical" lumbricid earthworm, illustrating the structure of the body wall, the intestine and associated organs. (From Handreck 1986).

have their long axes tangential to the long axes of the worm and are referred to as the circular muscles. The circular fibres are irregularly arranged, tend to be aggregated, and are surrounded by connective tissue. The inner or longitudinal muscle layer has its long axes longitudinal with the worm. It is thicker, or at least as thick as the circular layer and is continuous throughout the body length with fibres up to several millimetres long and extending over more than one segment. The ribbon-like fibres of the longitudinal muscle are arranged in U-shaped blocks which are separated from the coelom by epithelial cells. The two muscle layers acting in conjunction with the setae enable the worm to move. Movement is considered in section 2.2.

Inside the muscle layer is the coelom; a fluid filled cavity between the body wall and the gut. The consistency of the fluid varies with the species and the humidity. If conditions around the worm become drier then the fluid thickens and becomes more gelatinous. Coelomic fluid has a range of inorganic particles in suspension, including calcium carbonate and oil droplets. The fluid is confined by the membranous peritoneum which forms the inner boundary of the muscle layers. The coelomic cavity is divided into a longitudinal series of compartments by septa, corresponding to the external intersegmental grooves. Structurally the septa are composed of 2 layers of flattened peritoneal cells with a collagenous layer, muscle fibres and blood vessels between them. The muscle fibres are derived from the longitudinal muscle layer of the parietes (body-wall). In the anterior of the worm, the septa are markedly thicker and more muscular than in the posterior region. The septa are usually vertical partitions but around the oesophagus they may be conical in form with the narrow part of the cone more posterior than the base. This allows eversion (turning inside out) of the pharynx when feeding or tunnelling. The septa are perforated with small pores which are controlled by sphincters which open and close. Thus each septum can behave as a water-tight bulk-head and with the body wall, define a cylinder of constant volume, since under normal circumstances there is no transfer of fluid between segments.

The gut of the earthworm is surrounded by 2 muscle layers; an outer longitudinal and an inner circular layer. This is the reverse of the body wall. Gut muscles are responsible for the movement and grinding of food as it moves from the mouth to the anus. As shown in

Figure 2.3, the alimentary canal (also called the gut) comprises in sequence the mouth and buccal cavity, pharynx, oesophagus,crop, gizzard and intestine.

The buccal cavity, occupying the first one or two segments is overhung by the prostomium. It is eversible and has diverticula or sac like cavities. The pharynx, which may not be obviously differentiated from the buccal cavity, also has diverticula and may in some species also evert to improve suction drawing particles into the mouth. Particles are ingested by contractions of the thick muscles around the pharynx, particularly on the dorsal surface. Thick musculature on the dorsal surface with the whitish lobed mass of pharyngeal glands makes the pharynx one of the thickest portions of the alimentary tract. Digestion of ingested food starts in the pharynx with the secretion of enzyme-containing mucus from glandular cells.

The pharynx is easily distinguishable from the oesophagous which is a narrow tube connecting to the crop. This tube running between approximately segments 5 and 14 often has segmental dilations and inter-segmental constrictions. In epithelial folds in the oesophageal wall of some species are one or more pairs of lateral swellings which form the calciferous glands. These glands, supplied well with blood, produce crystalline calcium carbonate. Many explanations have been proposed for the function of these glands including the absorption of respiratory carbon-dioxide and regulation of pH or ionic or osmotic solutions. The exact reasons are still not known but the glands are known to be more active in litter feeding than in humus or soil feeding species.

Posterior to the pharynx is a thin walled voluminous storage chamber called the crop. In the Lumbricidae this is usually around segments 15-16 but is much further forward in the Megascolecoidae. When empty the crop is partially inverted (invaginated) into the gizzard which is lined with thick cuticle. In the barrel-shaped gizzard, muscle contractions grind the food with the aid of ingested mineral particles. The circular muscles are thickened around the gizzard of Lumbricidae, but the size, form and number of gizzards varies between species in other families. Stephenson (1930) attributed some of the differences to evolutionary changes related to diet.

Posterior to the gizzard is the intestine. Some authors distinguish three zones of the

intestine, the anterior, mid and posterior intestine (Jamieson 1981). The intestine is a straight tube slightly constricted at each septum but the internal surface has many small longitudinal folds. The typhlosole is a large fold from the dorsal wall increasing intestinal surface area, which is important since most digestion and absorption of food occurs in the intestine. Peristalsis is vigorous in the mid portion of the intestine but the posterior undergoes only feeble contractions in peristalsis. (Lee 1985, Jamieson 1981, Handreck 1986, Stephenson 1930, Laverack 1963, Edwards and Lofty 1977).

2.2 Movement

Movement in the earthworm is achieved by coordinated action of the parietal muscles with the setae and the hydrostatic skeleton provided by the coelom and septa. When moving forward in an existing tunnel the longitudinal muscles in a section of the body, eg segments 10-20, will contract and the circular muscles relax. As has been explained, as the segment length reduces the diameter of the segments increases because the volume remains constant. The setae are extended by the protractor muscles, anchoring this group of segments. In the anterior segments the circular muscles contract, longitudinal muscles relax moving the front of the worm forward. The anterior segments are then expanded by the contraction of the longitudinal muscles and protruding the setae to secure the body in the substrate. Posterior segments then release their grip, and are drawn forward. To move backwards the process is simply reversed. Thus there are waves of alternate contraction and relaxation, which are retrograde ie the waves move in the opposite direction to the direction of travel.

When making new tunnels the front segment or segments are pushed into a crack or hole in the soil and this cavity may be expanded by radial expansion of the body. If no suitable cavity is available the earthworm will ingest the soil ahead and move into this space. If the soil ahead is compacted the earthworm can evert (evaginate) its buccal cavity and pharynx and remove small pieces of soil by suction, which are then ingested by retracting the pharynx (Lee 1985, Handreck 1986, Edwards and Lofty 1972).

The importance of the various tunnelling methods either pushing soil aside or ingesting

soil, as they affect soil physical properties in different species is unknown. Only non-specific associations have been made between earthworm species, musculature, tunnelling technique and the pressures generated by the earthworms. Earthworms can apply force to the soil either by using the contraction of the circular muscles to generate an axial pressure or by the contraction of the longitudinal muscles to generate a radial pressure, to expand an existing cavity.

Physiological experiments have been performed to estimate pressures of fluids inside earthworms Newell (1950) measured coelomic pressures of 1.6 kPa in segment 28, and 0.8 kPa near the tail region of active *Lumbricus terrestris* , while for the same species Trueman (1978) estimated pressures of less than 200 Pa for resting worms. The maximum value recorded by Newell was 2.9 kPa in the anterior third of the worm. These worms were not tunnelling in soil, and it was noted that to take the measurements the normal locomotory pattern was completely upset. Direct measurement of the propulsive-tractive forces exerted by earthworms was performed by Gray and Lissmann (1938 a) who had a non-specified earthworm move in the absence of soil from a fixed platform onto an adjoining metal plate which was mounted on knife edges and linked to a displacement recorder. From the forces required to achieve displacement, they concluded that propulsive thrust from the circular muscles and the tractive force of the longitudinal muscles are approximately equal and vary from 2×10^{-2} to 8×10^{-2}N according to the size and activity of the worm. These forces were for locomotion on a flat surface where no penetration through the soil was involved and where the setae would have been unable to grip the substrate.

Newell (1950) compared these forces with data derived from his own work, including estimates of the diameter of the gut and the first septum and the maximum pressure in the anterior third of the worm, to derive the maximum force acting on the septum at 8.5×10^{-2}N. Then by assuming that this force can act through the prostomium which forms the apex of a cone at the front of the worm, and has a diameter of 1.0 mm and hence an area of 0.8 mm2 he obtained a mean pressure of the prostomium against the soil of approximately 100 kPa. Newell maintained that pressures of this order are probably sufficient to allow earthworms to tunnel into and through soil.

When considering the mechanics of root growth Abdalla et al (1969) proposed that when the axial growth of the root tip is restricted by the confining stress of the soil then the root can establish a zone of stress relief ahead of the tip by expanding radially. While earthworms are not limited to pushing soil aside when moving, as they can ingest the soil, or weaken it by the forward excretion of water, the radial expansion mechanism may still be important. Photographic evidence of the radial expansion mechanism is seen in Figure 4 of Roots and Phillips (1960).

Seymour (1978) measured the lifting force of worms by making them crawl under a bridge and recording the internal coelomic pressures, the forces exerted on the bridge and the areas of contact with the bridge. The experiments were not performed in a soil environment. The measured force was always greater than a force value calculated by multiplying the internal pressure by the measured area. This excess lifting force of approximately 1.5 times the mean calculated force was attributed by Seymour to the intrinsic rigidity that can be developed by the contracting and stiffening body wall muscles. The maximum coelomic pressure recorded for *Lumbricus terrestris* was reported by Seymour (1978) as less than 7.5 kPa, while as has already been stated the maximum value reported by Newell (1950) was 1.6 kPa.

2.3 Ecology in soil

The large numbers of different earthworm species occupy a wide range of habitats and use a number of different strategies to survive. These include the occupation of different vertical niches or depths in the soil. Lee (1959 a,1985) distinguished three groups among the megascolecoid earthworms of New Zealand. These were defined mainly in terms of the level in the soil profile where they are usually found. Litter-dwelling species are found in the surface organic horizons, top-soil species found in the A horizon and sub-soil species in the soil B horizon. Further differentiation was based on effects on the soil, food preferences, morphological, behavioural and physiological features. The full scope of the characterization is beyond this work but a number of points are relevant to "Earthworms and their tunnels in

relation to soil physical properties."

The tunnel structures constructed by the different classes vary between no tunnel structures created by the litter dwelling group to extensive systems often deep below the surface and of large diameter. In between these two extremes the top-soil species set up permanent tunnels opening to the surface. The cast material voided by the different megascolecoid species varies with depth in the profile and reflects the food ingested. The litter-dwelling, litter-eating species leave no distinguishable casts, while top-soil species ingesting decomposing litter material void material mainly at the soil surface. The sub-soil species which selectively ingest soil higher in organic matter leave their casts in their tunnels or other spaces in the soil matrix, and only rarely come to the soil surface.

Independently Bouché (1971,1972,1977) developed a similar system for Lumbricidae in France. He defined three ecological groups:

1 Épigées which are detritivorous litter dwellers and are closely allied with the litter dwellers described by Lee (1959 a);

2 Anéciques which construct deep permanent tunnels but feed on leaves collected at the soil surface. This group contains many of the well known lumbricid species but is not compatible with the top-soil group defined for the megascolecoids by Lee; and

3 Endogées which live in the mineral soil horizons and selectively ingest soil rich in organic material. They do not necessarily reside deep in the soil horizons.

In addition to features used by Lee (1959 a), Bouché considered the muscle development of the earthworms, particularly by introducing the term "digging muscles". Bouché (1977) maintains that the digging muscles are apparent as stronger body wall and septa but that they are very weak in epigees, very strongly developed in the aneciques and limited in the endogees. Also the intestinal transit time for food was distinguished by Bouché (1977) who states that this was slow in the epigees, variable in aneciques and rapid in endogees. These two classifying criteria are not entirely rigorous as Lee (1985) notes extensive muscle development in top-soil dwelling megascolecoids to allow them to retract quickly into their tunnels and to secure themselves firmly against predators. Similarly Lee (1985) suggests that the gut transit time for endogees may be considerable as a result of their

long gut and to allow adequate digestion time for their low energy food. This will be considered in more detail below.

Other ecological associations have been proposed (eg Perel 1977) but the examples discussed emphasize that behaviour will be species-dependent. In the practical work considered later in this thesis, 2 main species are considered and these are classified as endogees and thus are mainly geophagous (or soil ingesting) species. They are *Aporrectodea rosea* and *A. caliginosa.*

Burrow formation can be studied by introducing earthworms into large glass sided cages filled with soil as described by Evans (1947). Bolton and Phillipson (1976 a,b) described *A. rosea* tunnelling in an undefined mull type soil as going to the base of the cage, moving along the base until meeting a side wall and then ascending vertically. After this initial construction activity slowed, one or more additional channels to the surface were created as well as several inter-connected side channels. The mean daily tunnel length constructed in the cages ranged from 133 mm g^{-1} fresh wt worm day^{-1} for adults at 10°C to 516 mm g^{-1} fresh wt worm day^{-1} at 14.8°C. These correspond to 877 and 1424 mg of dry soil displaced g^{-1} fresh wt worm day^{-1}. Feeding was described as a grazing process, with soil being removed from the burrow wall, and although it was presumed that feeding took place at the tunnel ends this could not be distinguished from normal tunnelling activity.Feeding was seen to be a selective process and this was supported by cast material having higher loss on ignition than the bulk soil and by the fact that *A. rosea* was found to have smaller maximum mineral particle sizes in the gut (approximately 100 μm) than *A.caliginosa* (200 μm) or *Octolasion cyaneum* (500 μm). (Bolton and Phillipson 1976 a,b).Transit time through the gut of the earthworms have been studied by a number of methods. Crossley et al (1971) using intake and turnover of radioactive caesium found at least 15 hours was required to clear all the non-assimilated isotope material from the body of *O. lacteum* . From measurements of the weight of material voided, the weight of material in the gut and the weight of the earthworm several estimates of transit time through the gut have been made. Barley (1959 a) estimated a transit time of about 20 h through *A. caliginosa* although he noted that if earthworms were transferred from one soil to another of different colour the new soil appeared in the faeces

within 5 h. Satchell (1967) estimated 20-24 h for *L. terrestris* and Piearce (1972) estimated 13-24 h for *L. rubellus* and *A. caliginosa*. However Bolton and Phillipson (1976 a) estimate the turnover time for *A. rosea* as in the range 1-2.5 h, significantly less than the other values. Joannes and Kretzschmar (1983) did field studies on *Nicodrilus* species which are not endogees and found 5 h turnover time. From these values it is apparent that feeding efficiency as indicated by the gut turnover times will vary greatly, not only between species but also as a result of soil nutritional status and whether the earthworm is actively tunnelling.

Bolton and Phillipson (1976 a,b) estimated energy budgets for small immature, large immature and adult *A. rosea* at 10°C.This involved the determination of the amount and energy value of the ingested organic matter and soil using techniques including bomb calorimetry and differential thermal analysis. Of the ingested material the amount assimilated was determined by measuring the amount and energy value of egesta. The energy assimilated was partitioned into production and respiration from measurements of oxygen consumption and the energy required to utilize this oxygen.

These calculations allow comparisons of the efficiency of use of assimilated material between different life stages. Small immatures use approximately 50% of their assimilated food in production whereas large immatures and adults use only 35 and 20% respectively. This reflects a higher demand for tissue growth in the juvenile forms. The ratio of assimilation of food to the food ingested is expressed by Bolton and Phillipson (1976 a,b) as an assimilation efficiency percentage. This assimilation efficiency from the energy content of the ingested food (on a dry weight basis) was found to range from 0.9% for adults to 1.3% for small immatures. While these values are low compared with assimilation values given for other species in Crossley et al (1971), Bolton and Phillipson (1976 a) considered that they reflect the high turnover rates of soil by *A. rosea* .

Lavelle and Meyer (1977,1983) have developed computer simulation models to examine population distribution, vertical migration and soil ingestion by the earthworm *Millsonia anomala*. This is a geophagous endogée which generally resides in the upper 10 cm of the soil profile and is found in the savanna of the Ivory Coast. Meteorological data collected over several years were used to develop sub-models to calculate and up-date soil temperature

and water contents which controlled modeled population activity, and incubation of cocoons. Weight changes of "existing worms" were altered according to empirical information on food quality and intake as well as the environmental sub-models and allowances were made for changes in population density. Further considerations of mortality, migration and reproduction allows simulation of numbers of worms per unit area, their age distributions and their depth in the profile. The simulations may be checked against actual measurements and with some transformations may be usefully generalized to other tropical endogees (Lavelle and Meyer 1983).

2.4 Biopore spaces

Many soil physical properties depend on the number and size distribution of soil pores. Distinctions between classes soil pores is not entirely arbitrary, and may reflect the origins of that classes of pore. Large pores (or macropores) may develop in soil either from major shrinkage of the soil or from the action of soil fauna and plant roots. Macropores are readily visible to the naked eye and may be continuous for up to several metres in both lateral and vertical directions (Beven and Germann 1982). Definitions of macropores used the relationship between the soil water retention curve and the concept of a bundle of capillary tubes to relate capillary potential with equivalent pore diameter (Beven and Germann 1982). To distinguish the shrinkage cracks from the faunal- and root-produced pores the term biopore is used for the biologically produced pore space.

The size, shape and frequency of biopores differentiate them from other soil pore space. Biopores are usually cylindrical and continuous. The shape may vary with the organisms which generate the tunnel. Bryson (1939) in Hole (1981) described the direction and length of simple tunnels made by several insects. These were typically vertical to near vertical and ranged in length from 50 cm for cicada wasps (*Sphecius speciosus*) to 4 cm for dung beetles (*Cathon lecontei*) . These correspond to the removal of in excess of 60 g and less than 2 g of soil respectively. Ehlers (1975) counted the number of earthworm channels per square metre in tilled and untilled loess soil and found numbers increasing with depth from 27

m^{-2} in a tilled plot at 2 cm depth to 363 m^{-2} at 60 cm depth in an untilled site. It was thought that particularly the deeper tunnels were probably made by *Lumbricus terrestris*. Kretzschmar (1978,1982) quantified the volume of earthworm tunnels at 5 litres m^{-2} of soil surface and noted that they were mainly sub-vertical in orientation. However he noted that the quantity of tunnels varied with climatic variables, particularly soil temperature and humidity, and that to consider the spatial variability of the tunnels was impossible because the time to measure the tunnels was so great.

Omoti and Wild (1979) found up to 100 channels per square metre with diameters in the range 2-10 mm using fluorescent dyes to mark solute pathways in the field. Most of these biopores were continuous to 15 cm depth and 10% were continuous to 70 cm. In a study of biologically- developed macropores in soils of Romney Marsh, Green and Askew (1965) found many interconnecting pores, holes and cavities in the subsurface which were considered to be formed by roots, ants and earthworms. Fine pores of approximately 1 mm diameter extending to depths in excess of 1 m were considered to be old root channels, even though observations indicated that they were used by small (about 1 mm diameter) soil animals particularly in the upper horizons. The dominant ant species *Lasius flavus* made extensive systems of galleries with holes of different dimensions forming irregular and often large cavities connecting into complex networks extending to depths in excess of one metre in some cases. *Lumbricus terrestris* was associated with large holes except where the soils were either poorly-drained gleys with high water tables or acidic sandy soils (Green and Askew 1965).

Barley (1959 b) in a study of earthworms under pasture at the Waite Agricultural Research Institute, South Australia found tunnels made by the lumbricid earthworms *Aporrectodea caliginosa* and *A. rosea* to number 300 m^{-2} at 20 cm depth and have a combined cross sectional area of 5 cm2 while at 50 cm depth only 75 tunnels m^{-2} were found with a combined cross sectional area of 0.7 cm^2. Different earthworm species occupying different ecological niches form different sizes and shapes of biopores.

In addition to the insects and oligochaetes tunnelling in soil a range of soil mammals spend time in tunnels to avoid predators or climatic extremes or to find food. Moles, gophers, rabbits and wombats all dig extensive burrow systems. The complexity and range depend on

the species as well as the individual but, as an example, mole burrows may be up to 60 m across.

A number of methods of studying the volume, frequency and continuity of macropores and biopores have been mentioned above. Estimation of the volume and shapes of biopores can be obtained by preparing casts of tunnel systems. This is done by pouring a liquid glue, latex or plaster solution into openings on the soil surface and removing the solid cast from the soil after it has set. Garner (1953) using latex claimed that casts of earthworm tunnels were distinguishable by the mucus lining them, which prevented lateral seepage. In contrast tunnels made by ants had walls roughened by "nibbling". From the cast, the length and (if the density of the hardened material is known) the volume of the tunnel can be estimated. While plaster casts of tunnels provide an introduction to the shape of the soil pore space, quantitative measures of the spatial distribution are required to relate biopores to soil properties.

Techniques to study pore systems were developed by Lafeber (1965) for planar pores but they were extended to describe linear features of soils by Willoughby (1967). These orientation studies concentrate on assigning the pore systems as vector quantities and then plotting the vectors, stating a reference line which is usually horizontal. The two-dimensional case involved photographing a series of parallel cross sections from soil and measuring the length of simplified pore traces as well as the orientation. The cumulative lengths were plotted against the orientation direction in polar coordinates. Three dimensional pore systems can be plotted using similar techniques, calculating the dip and strike of the pores and then plotting these values on an equal area projection. Biopores such as earthworm tunnels were plotted as the two-dimensional case by using best-fitting straight lines to show the longest axis.

In a black soil from a grassland in Queensland, Willoughby (1967) used the same reference planes for equal area projections of root systems and pore distributions. Roots were found to be largely sub-horizontal and matched the orientation of the pore system. While the method does not show that the roots are actually in pre-existing pores it does emphasize the need to understand the relationship between the soil pore system and plant growth in soil.

The continuity of biopores has been estimated by the pouring of various dyes into tunnels and studying either infiltration rates or observing the dye paths on sectioned soil

columns. This method has frequently been used to estimate the significance of tunnels for water movement. The combination of techniques has meant an increased ability to study changes in soil structure. Murphy et al (1977 a) have combined the use of fluorescent dyes with image analysis and photography of thin sections. To separate the void spaces from mineral grains,, which may appear black in microscopic images, fluorescent dyes and high contrast photographs were used to make measurements of void spaces. Basic measurements such as area, number, perimeter, horizontal and vertical projections as well as measurements derived from combinations of the basic measurements were used to describe the void spaces, not only in terms of size and shape but also in terms of orientation and irregularity. Topsoil was found to contain large irregular voids. In soil compaction experiments (Murphy et al 1977 b), morphological changes in the voids favour lateral movement of plant roots in the planar voids. Downward movement is restricted by small void sizes oriented vertically in the platy structure.

Observation of the three-dimensional nature of biopores has been reported by using a soil peel method (Bouma and Hole 1965). This method involves forming "thin blankets" by pouring resin onto exposed soil surfaces. After suitable curing times the blanket is reinforced with cement. The hardened resin is then peeled off with the soil fabric coming apart along natural structural weaknesses. The exposed surface is fixed and is then ready for observation. Biopores are observed either as voids in the fabric or as resin protuberances.Plas and Slager (1964) used pore count numbers obtained by stereomicroscopy of soil peels to gather information about biopore distributions. Smettem and Collis-George (1985) used the soil peel technique with new resins and applied statistical tests to relate the distribution of biopores within peels to calculate sampling frequencies required for meaningful study.

Rogaar and Boswinkel (1978) have studied the size and shape of earthworm tunnels using both conventional microscopy and X-ray stereo-radiography. At least two types of burrows were described. The first and dominant type were not oriented and moved through the A horizon. The site of investigation was a reclaimed polder and the maximum depth of activity of these tunnels corresponded to the maximum depth of tillage during the reclamation. Prominent features of chambers up to 12 mm across with multiple tunnels leading off were

described using the X-ray technique. The tunnels and chambers were attributed to *A. caliginosa* , *A. rosea* and *A. chloritica.*

The other tunnel type described by (Rogaar and Boswinkel 1978) were vertical channels which penetrated to depths in excess of 1 m. While having slightly larger maximum diameters than the unoriented type, these had no branching points below the top few centimetres of soil. The authors attributed these vertical structures to *L. terrestris* , the other main species found at the site. Many of both tunnel types were filled with faecal material. The associations of species with tunnels correlate with the ecological species descriptions of Bouché (1977).

2.5 Casts

Solid material voided by earthworms is referred to as "casts". This material may be deposited at the soil surface, or in tunnels made by the earthworm or other soil voids. Edwards and Lofty (1977) report that only 3 species (*A. longa* , *A. caliginosa* and *L. terrestris*) of all the common species in Britain deposit casts on the soil surface. *A rosea* has been reported as casting material on the surface of soil compacted into pots, particularly at larger densities (Thomson and Davies 1974) . Bolton and Phillipson (1976 a) reported that *A. rosea* produced casts initially at the soil surface but after initial tunnel construction this ceased. It appears that while *A. rosea* may deposit casts on the surface when tunnelling actively through compacted soil it is not usual. *A. caliginosa* deposits large numbers of casts at the soil surface (Sharpley and Syers 1977).

The deposition of cast material at the soil surface leads to a continual cycling of the soil from the region of earthworm activity. This deposition of material at the surface has been reported as ranging from 0.18 mm of casts per year in South Australia (Barley 1959 b) to 15-20 mm of casts per year in Nigeria (Madge 1969) depending on the species, climate and soil type. Barley (1959 b) noted that the 0.18 mm per year corresponds to 250 g oven dry soil m^2 y^{-1} and that this all occurred during the active growing phase of the pasture cover ; ie not in the hot, dry summer.

Irrespective of where in the profile casts are deposited, their resistance to breakdown distinguishes them from the bulk soil. This has usually been measured as the stability of casts in water, either by wet sieving or by measuring the resistance to water drops. Increased water stability of casts over similar-sized non-faecal material from the bulk soil has been well documented (Swaby 1950, Barley 1959 b, Monnier and Jeanson 1964, Rhee 1977).

Swaby (1950) attributed this improved stability to microbial gums and reported that the stability varied with the time after production. Parle (1963) measured the length of fungal hyphae in cast material over time and found that it reached a maximum 15 days after deposition, then declined to initial levels in a further 10 days. These changes in hyphal length paralleled changes in cast stability. Of course in soil where earthworms are active there will be a cycle of cast production and degradation with new material replacing the old.

Lee (1985) described casts that had been excreted at the soil surface as pellets ranging in size from less than 1 mm to greater than 10 mm in diameter though usually between 2-10 mm, or as paste-like slurries. Composite casts were combinations of both of these types. Madge (1969) found composites as fine granular pellets 3-5 cm diameter from the earthworm *Eudrilus eugeniae* while the composite casts from *Hyperiodrilus africanus* in the same area were formed as vertical pipes, sealed at the top and up to 8 cm long. However at Adelaide South Australia Barley (1959 b) estimated that less than 10% of the cast material from *Aporrectodea caliginosa* and *A. rosea* is deposited at the surface.

Barratt (1969) considered the size of faecal pellets and suggested that size classification could be on the same scale as used for particle size of silt and sand: eg 1-2 mm diameter very coarse; 0.5-1.0 mm diameter coarse; etc. Bal (1973) used the term modexi (from moulded and excrement) which have left the animals intestines as shaped three-dimensional individuals. This general term includes the casts of earthworms. He suggests that an ideal size classification system should be directly related to the animals size but notes that this is impractical since often the animals' size is unknown. This is particularly apparent when there is a distribution in the population age structure. Further it was stated that the size of modexi will depend on the quality of food consumed by the animal so that any size classification scheme must be arbitrary. It was concluded that a scheme similar to Barratt's was satisfactory.

A scheme based on Barratt's was given but included more classes and a major division at 3000 μm between macro- and micro-excrements. Bal (1973) considered that uniformity in measurement techniques should be sought since modexi or casts may be wet, moist, or dry and he found that shrinkage on drying may reduce the size of moist samples by up to one third. Since thin section work is confined to dry samples it was recommended that size measurements be performed in that state. As thin sections may be through any orientation of the sample the size should be described taking into account the shape; eg a cylinder should have length described.

The particle (cast) shape is important not only for assessing size in thin sections but will affect packing in the soil and thus influence porosity, aeration, and water movement. Accurate description of the shape of casts may permit distinction between soil influenced by earthworms and that influenced by other soil fauna. Even with earthworms, different cast shapes arising from dietary or excretory differences may permit consideration of species dominance. This could be tested by analysis of casts found in soil samples. Dexter (1985) observed that the shape of soil aggregates influences the relationship between the crushing force and the tensile strength of the aggregate material.

The method of breakdown of aggregates alters their shape. For primary soil particles such as sand grains it is known that abrasion caused by transportation makes the particles less angular (Brewer 1964). Methods of breakdown of aggregates influences the shape of soil particles but with composite systems such as casts the likelihood of fracture is increased. Thus "aged" cast material could be more angular than the new material.

Barratt (1969) in a classification of soil materials which considered organic components in particular, made several divisions according to shape. Of these, two were relevant to faunal-influenced material. These were "pelleted" which were generally discrete faecal pellets and which could be further divided into shape subclasses (eg rugose, cylindrical, or obvate) and "spongy" which were aggregated material with irregular cavitites.

Bal (1973) used his modexi concept to devise a key using five basic shape classes: spherical, elliptical, cylindrical, platy and threadlike. These basic groups were subdivided to improve description and to allow description of modified material. As the classifying criteria

are apparent from the names used in the system only the framework will be shown here.

1   Spherical

      1.1   sphere

      1.2   amoebo-sphere

2   Ellipsoidal

      2.1   ellipsoid

      2.2   spermoid

      2.3   conoid

3   Cylindrical

      3.1   cylinder

      3.2   bacillo-cylinder

      3.3   clono-cylinder

4   Platy

5   Mitoid

      5.1   monomitic

      5.2   helicomitic

This descriptive system is not limited to earthworm casts but is appropriate to describing moulded excrements of any soil fauna. The strength of this system is that it is easily used even to include more general descriptions. For example, Humphreys (1981) described earthworm casts found near Sydney, New South Wales as accumulations of "discrete rod-to-ellipsoidal shaped pellets up to 2.7 mm long but more commonly 1.5 mm long and 1 mm in diameter." Under Bal's system these coarse micro-excrements would be in classes 3.1 to 2.1. Typical shape profiles of compound casts can be seen in sections shown in Barley (1959 b) and Lee (1967).

There have been a number of methods devised to quantify the shape of either individual soil particles or aggregates. Two terms have dominated this discussion - sphericity and roundness. Cox (1927) described a single measure for roundness by comparing the ratio of the particle cross sectional area to the perimeter length with the same ratio for a circle. This measure is of course independent of particle size. Other simple measures to be used to

describe particle shape include several based on aspect ratios.

These techniques use 2 dimensional data normally from photographs or drawings of the samples in their most stable form on a flat surface. Braunack et al (1979) considered the ratio of the principal, intermediate and minor axes of the soil aggregates and found, irrespective of drying treatment or aggregate size that $1 : x : x^2$ was appropriate. This measure unlike the other ratio methods requires 3 dimensional information for the samples. However simple single value quantities can not adequately describe the entire range of particle shapes. This is seen when it becomes necessary to supplement ratio methods with description (Koerner 1970), or combine two measures as in the "standard" particle shapes of Krumbein and Sloss (1963) using a sphericity and roundness cross matrix. Knowing any of these values does not allow prediction of particle shape. To overcome these limitations a number of techniques have been devised to provide unique particle descriptions. These have been possible since the advent of automatic scanning devises and computers.

One of the most common methods is Fourier analysis of a radius vector within a particle. This is done by examining a profile of a particle or aggregate and assigning coordinates to points evenly spaced around the perimeter. The Fourier spectrum of the radius vector is then calculated and this specifies the shape of the two-dimensional profile exactly(Beddow and Meloy 1980, Schwarcz and Shane 1969, Dexter 1985).

Another method is the curvature spectrum of Davis and Dexter (1972). The perimeter of a circle has only one curvature where as irregular shapes will have different curvatures. This method requires the perimeter of the particle profile to be divided into N points equally spaced, and assigned x,y coordinates. The curvature spectrum is very sensitive to particle shape (Dexter 1985).

As with the size of biologically influenced composite particles which depend on the water content so shrinkage with drying may alter particle shape. The changes in size and shape with drying influence the density and strength of modexi. Barley (1959 b) measured the density of incubated then air dried casts from *Aporrectodea caliginosa* at soil dry bulk 1.65 tm^{-3} using the method of McIntyre and Stirk (1954). This value is greater than the density of 1.4 tm^{-3} used in the same work to calculate the depth of soil deposited on the surface by

earthworms. Both these values are less than the density of soil aggregates 1-5 mm diameter which were determined at 1.72 tm^{-3} using the same method.

2.6 Earthworms and soil and crop management

In the consideration of water and air movement it has already been suggested that biopores improve plant growth. I shall briefly discuss the influences on crop productivity of faunal activity. Trends toward reduced cultivation have led to increased interest in interactions between soil fauna, soil structure and tillage. Ehlers (1975) reported an increase in earthworm channel numbers per square metre in untilled plots compared with tilled plots. This work was further developed by Ehlers et al (1983) who looked at root growth of oats in tilled and untilled loess soil. The bulk density and penetrometer resistance were higher in the surface layers of the untilled sites but a tillage compaction layer occurred at around 25-30 cm depth in the tilled plots which gave higher penetrometer resistances than any layer from the untilled site. This traffic pan stopped the penetration of roots as was shown by decreased rooting density below the pan. while rooting density was correlated with soil strength in both tillage treatments. In the untilled sites continuous biopores occupying less than 1% of the soil volume provided pathways of low mechanical impedance for roots.

Edwards and Lofty (1978) used intact soil profiles,which had been transferred to pots to study root growth of cereal crops under direct drilling. The pots were sterilized and then inoculated with earthworms or soil arthropods, before direct drilling cereals, while "conventionally" ploughed pots without invertebrates were used as controls. Root distribution was found to correlate with zones of invertebrate activity and although seedlings in the ploughed pots showed better growth initially final plant heights were nearly equal or slightly in favour of the invertebrate inoculated pots. Recently, Dexter (1986 a) has estimated, from the results of laboratory experiments and computer simulation studies the densities of biopores of various sizes required for a defined proportion of roots of wheat and pea to penetrate through an otherwise impenetrable compaction layer.

Removal of topsoil for mining or urban development in several places has left exposed

poorly-structured clay sub-soils of low nutrient status. Hopp and Slater (1948), McColl (1982) and McColl et al (1982) have used pot studies of the exposed soil inoculated with earthworms to measure plant and root growth. Although McColl used *Aporrectodea caliginosa* whereas Hopp and Slater used a combination of lumbricid species, improved plant growth was noted in both cases. McColl reported increased nutrient uptake and decreased surface bulk density. It is worth noting that Hopp and Slater found by accident that ants also improved the plant growth. Improvement in crop and root growth on very poorly structured soils is not really surprising.

Tisdall (1985) attributed increased infiltration to increased macroporosity and indicated that the number of biopores was related to the numbers of earthworms present. The earthworm numbers were related to management practices and long term stable production required management of soil fauna, organic matter, cropping sequences, tillage and water application.

Increased soil strength in the form of surface crusting can significantly reduce seedling emergence. Improved water stable aggregation and increased infiltrability as a result of the activity of the earthworm *L. rubellus* have been reported by Kladivko et al(1986). This led to improved seedling emergence of soybean and corn.

Improved infiltrability particularly under heavy rainfall or irrigated conditions may depend on the number of earthworm tunnels openings to the soil surface. As was shown by Springett (1983) this varies between species. The mean number of openings to the surface over a twelve day period per earthworm in a laboratory pot study were *A. longa* 14, *L. rubellus* 12, *A. caliginosa* 4, and *O. cyaneum* 0. *O. cyaneum* stayed deep in the soil. The percentage of burrows which remained open for at least twelve days were *A. longa* 89%, *L. rubellus* 58%, and *A. caliginosa* 85% indicating that *L. rubellus* had a less-stable tunnel system than those of the other two species. This is supported from observations that, when the soil surface was disturbed, the percentage of tunnels reopening within 5 mm of the original opening were 67% for *L. rubellus*, 70% for *A. caliginosa* and 83% for *A. longa*. Surface-applied lime was found to be mixed vertically through the profile by *A. longa* but was moved laterally by *A. caliginosa* and *L. rubellus*. Thus the incorporation of fertilizer material is

influenced by the species of earthworm present.

Incorporation of plant material by soil fauna was examined by Jensen (1985) who enclosed straw in bags with mesh sizes of 0.05, 0.5 and 10.0 mm. All but the largest mesh size prevented macro-fauna, particularly the diverse earthworm species present, from ingesting the organic material. Decomposition of the incorporated straw was significantly faster from the larger mesh sized bags.

Enhanced orchard productivity as a result of earthworm action has been reported by Rhee (1977) who introduced earthworms, mainly *A. caliginosa* (70%) and *L. terrestris* (30%) to previously worm free polders, resulting in improved water stable aggregation improved as a result. Over an 8 year period, the numbers of roots produced by apple trees were sampled and compared with control plots. The number of fine roots, less than 0.5 mm diameter in the earthworm-inoculated plots was 2.4 times the number in the controls. Thicker roots, diameter 0.5-1 mm and 1-5 mm also increased significantly but by a lesser factor. The ratios of thin to thick roots after 8 years were 58.5% in the worm plots and 30% in the controls. Fruit production also increased. The importance of knowing which species are involved is highlighted by Tisdall (1978) who suggested that high numbers of *Microscolex dubius*, a litter dwelling species which has little effect on soils, in irrigated orchard plots in Australia showed no correlation between earthworm numbers and porosity.

2.7 Soil as a physical environment for earthworms

For earthworms to be active or even to survive in soil, the soil conditions must be suitable. The factors that determine the suitability of soil as a life supporting medium for earthworms are water, oxygen, temperature and food. If one or more of these factors is at an unsuitable level earthworms must be able to move to find more suitable conditions.

Soil water occupies pore spaces between primary soil particles. This water will be at some defined energy depending on its height above free water (gravitational potential), the amount and species of dissolved salts (osmotic potential), and the suction determined by the capillary action of the soil pores (matric potential). Thus the total water potential is;

$$Y = Yg + Yo + Ym \qquad\qquad (2.1)$$

The relationship between the soil water content and the energy of the soil water is not unique and depends on the shape and size of the pore spaces between particles. The shape of the pore spaces varies greatly not only as a result of the wide range of particle sizes but also with shrinkage and swelling caused by water content changes. Traffic will compact the soil, while soil animals and plant roots may create channels. Thus the pore geometry will be influenced by many factors.

In many cases the entry neck of a pore is smaller than the pore itself. Such a pore can only drain if the air-water interface is able to enter by some neck. ie the bigger the pore neck the more easily the pore will drain.

The capillary height depends on whether the soil is wetting or drying and thus at the same potential two water contents are possible for the same soil. This effect is known as hysteresis and is caused by

1 non uniformity of pore sizes as described above;

2 trapped air pockets which only slowly dissolve into the water;

3 hysteresis in the water-particle angle.

Consequently the soil factors which determine the availability of water for earthworms are

1 texture, determined by the primary soil particles;

2 structure, the arrangement of primary particles into aggregates;

3 ionic strength of the soil solution. (Collis-George 1959)

A typical value for a soil at field capacity is -10 kPa potential, while at the permanent wilting point for most plants it is approximately -1.5 MPa. If earthworms, or other soil animals, are unable to obtain water at high energies, (ie water at large negative potentials), then they must either find water at lower energies or endure desiccation. The cuticle of the earthworm is permeable to water and ions (Lee 1985) and limits its ability to control its water status by osmotic regulation.

The cuticle must be permeable to allow the exchange of oxygen and carbon dioxide between the atmosphere and the blood vessels near its surface. The aeration status of the soil also influences earthworms. Changes in the soil water content and gas diffusion are the two main mechanisms for renewing soil air. Oxygen is about 21% by volume of the free atmosphere while carbon dioxide is only 0.03% by volume. Diffusion of air through the soil is dependent on the soil air filled porosity. If air filled porosity is greater than 10% of the pore volume then diffusion is usually sufficient to supply the soil macro-fauna and plant roots. If the air filled porosity is less than about 10% diffusion is restricted with the tortuosity of the exchange path becoming a limiting factor. Soil structural effects such as crusting severely restrict air movement into soils (Collis-George 1959, Bakker and Hidding 1970, Boone et al 1986). It is worth noting that the respiratory pigment of earthworms, erythrocruorin, has an affinity for oxygen far greater than that of mammalian haemoglobin, and is little affected by carbon dioxide concentrations even in excess of 25% (Lee 1985).

Oxygen consumption and metabolic rate are greatly influenced by temperature. A 10°C rise in temperature leads to an approximate doubling of metabolic activity. It has been proposed (Lee 1985) that oxygen shortage as a result of increased metabolic activity may be the cause of death for earthworms at high temperatures. In the field the upper lethal limit of temperature is 25-30°C although much higher temperatures can be endured by earthworms for short periods.

Soil temperatures depend on the thermal conductivity as well as the absorbed energy (or energy capacity). These are properties of the soil materials and vary with the amounts of air, water and organic matter in the soil (Monteith 1973). The greatest range of soil temperatures occur at the soil surface, both on a diurnal and an annual basis. Thermal conductivity is increased by compaction and irrigation so that a wet soil in the sun will be cooler at the surface and warmer at depth than the same soil when drained (provided the energy can be conducted sufficiently through the profile) (Collis-George 1959, Monteith 1973).

There are of course interactions between these physical properties which influence earthworm activity. Nordström and Rundgren (1974) and Nordström (1975) showed the soil

water potential at which *Allolobophora* spp became inactive depended on the soil temperature. Whenever one or a combination of factors becomes injurious to earthworms, movement to a more suitable environment may be attempted. While the movement of earthworms has already been considered in section 2.2 physical restraints to movement have not yet been discussed.

Soil shear strength is inversely proportional to the soil water content; ie the wetter the soil the lower the shear strength. Thus movement by any soil animal which requires soil deformation will be easier in wetter soil (Collis-George 1959). Conversely soil shear strength is proportional to soil bulk density. In compacted (more dense) soil, movement which requires soil deformation will be more difficult.

In field studies of compaction under very heavy traffic on clay Eriksson (1975) examined worm hole numbers in horizontal sections. At 30 cm depth where the dry bulk density of the soil had increased from 1.51 to 1.61 tm^{-3} the number of tunnels per unit area in a compacted soil was less than 40% of the tunnel density at an uncompacted site. These changes were due to the destruction of existing holes. Aritajat et al (1977) found lumbricid earthworm numbers were decreased at sites which were repeatedly compacted but that in less than one year after compaction numbers had returned to previous levels. While these studies indicate that compaction (which increases shear strength) of the soil is detrimental to earthworms and their tunnels little can be concluded as to the effects of soil strength on earthworms.

Dexter (1978) found that *Aporrectodea caliginosa* (a geophagous species) was not restricted moving into soil blocks which had penetrometer resistances of up to 3.5 MPa. Impregnated sections of soil, 2 mm thick, containing earthworm tunnels, were examined by X-radiography and neither axial nor radial sections showed any soil compaction or cracking, while similar sections around needle probes driven into the soil showed extensive cracking and compaction. However Rushton (1986) found that movement of earthworms *L. terrestris* (a non geophagous species) through moist soil was negatively correlated with dry bulk density over a range from 1.382 - 1.676 tm^{-3}. Since there is a positive correlation between penetrometer resistance and density this implied that soil strength was a limiting factor in the movement of this species as it sought to tunnel through soil.

Chapter 3

Pressures generated by earthworms

3.1 Axial Pressures

3.1.1 Introduction

Physiological experiments have been performed to estimate pressures of fluids inside earthworms. Newell (1950) measured coelomic pressures of 1.6 kPa in segment 28, and 0.8 kPa near the tail region of active *Lumbricus terrestris* , while for the same species Trueman (1978) estimated pressures of less than 200 Pa for resting worms. The maximum value recorded by Newell was 2.9 kPa in the anterior third of the worm. The method used by Newell involved the removal of the earthworms from the soil environment and insertion of a hypodermic needle through the muscle layers into the coelomic fluid. The violent wriggling ensuing completely disturbed the normal locomotory pattern. The needle connected the coelomic fluid to a fluid filled manometer or alternately glass spoon gauges. Pressures recorded by both methods declined with time.

Direct measurement of the propulsive-tractive forces exerted by earthworms was performed by Gray and Lissmann (1938 a,b) who had a non-specified earthworm move in the absence of soil from a fixed platform onto an adjoining metal plate which was mounted on knife edges and linked to a displacement recorder. The metal plate was a horizontal bridge balanced with counter poised weights so that a small movement in the bridge would be mechanically amplified by the lever ratio. A movement of 1 mm was equivalent to 3×10^{-2}N. From the forces required to achieve displacement they concluded that propulsive thrust from the the circular muscles are approximately equal and vary from 2×10^{-2} to 8×10^{-2}N according to the size and activity of the worm. These forces were for worm locomotion on a flat surface where no penetration through soil was involved.

Thus the forward movement of the worm, with the passage of a wave of contraction, was contrived by the frictional force between the worm and the metal plate. The movement of

earthworms up vertical glass plates is well known (Roots 1956). For this to happen with the pharynx securing the worm, muscle contraction drags the worm up the vertical surface. Thus the muscles in the anterior must be able to lift the worm's own weight. If a worm weighs 1 g this corresponds to a lifting force of approximately 1×10^{-2}N.

Newell (1950) gave typical dimensions of the first septum of *L. terrestris* as about 7 mm and a gut diameter at the same site as about 3.5 mm. From this he calculated the area of the first septum to be 2.95×10^{-5} m^2. Using the maximum coelomic pressure that he had recorded in the anterior third of the worm, 2.9 kPa, he estimated the maximum force acting on a septum (and thus transmitting pressure forward) was 8.5×10^{-2}N. By assuming the prostomium formed the apex of a cone, the base of which was segment 4, estimating the prostomium area as 8×10^{-7} m^2 and that the force of 8.5×10^{-2}N acted exclusively through the prostomium then an axial pressure of 100 kPa was calculated. This calculation was claimed to support the statement that "Forces of this order probably suffice to allow earthworms to burrow into and through soil of varying resistance, even quite heavy clays " (Newell 1950). While it is undoubtedly true that earthworms can burrow through soil the mechanisms used in different soils remain unknown.

Three conditions can be defined for the worm when tunnelling through soil; pushing forward, resting and pushing sideways. The pushing forward condition is appropriate to axial pressures. In this section I set out to determine the axial pressures exerted by the earthworm *A. rosea* as it advances through soil by ingestion and by pushing the soil fabric with its body. By comparison of these pressures with those of mechanically driven blunt probes I hoped to establish some of the mechanical constraints on earthworms.

3.1.2 Materials and Methods

Soil

The soil used in all the experiments for this thesis was the Urrbrae fine sandy loam (Litchfield 1951) of the Red-brown Earth group (Oades et al 1981) This soil is a rhodoxeralf in the U.S.D.A. classification and a chromic luvisol in the F.A.O scheme. The soil has 17%

clay (< 2 µm), a plastic limit of 19.5% and a liquid limit of 26.5%. The soil was collected at the Waite Agricultural Research Institute, S. A. (34°58'S 138°38'E). Collection was from the tilled layer which is usually less than 15 cm deep. At an adjacent undisturbed profile, the A1 horizon of this soil extends to a depth of approximately 15 cm and is dark reddish brown with a moderate sub-angular blocky structure and small amounts of gravel (Chittleborough and Oades 1979). Calcium carbonate is not present in the surface layer (by acid treatment) and the pH is 5.7. Collected soil was air dried then sieved < 2 mm and stored ready for use.

Earthworms

The earthworms used in the experiments in this chapter were classified as *Aporrectodea rosea* according to the nomenclature of Sims and Gerard (1985). Identification was from the taxonomic keys of Lee (1959 b) and Martin (1977). This species is common through south eastern Australia and has recently been recorded, for the first time, in the wheat growing regions of Western Australia (Abbot 1981). The other common species at the site were *A. caliginosa* and *Microscolex dubius*.

The earthworms were collected from the A horizon of the Urrbrae fine sandy loam during the winter. The collected worms were stored in bins containing the Urrbrae soil and kept in a growth cabinet at 15°C night and 20°C day until needed for experiments. The main criteria which distinguish *A. rosea* from other worms of the family Lumbricidae and provide the tests for the taxonomic keys are :

1 the prostomium is epilobous;

2 setae are closely paired;

3 the clitellum typically extends over segments 26-30 but always starts posterior to 23 and;

4 the tubercula pubertatis begin on or before segment 30, and are typically on segments 29-31. Other features of the worm are length 25-85 mm, diameter 2-6 mm and the number of segments usually in the range 120-140.

Sims and Gerard (1985) noted that when *A. rosea* is irritated, the anterior region becomes blunt, almost bulbous.

Experimental

To measure the axial pressure generated by the earthworms, discs of soil were formed by moulding the soil at gravimetric water contents approximately 1.1 x plastic limit. Weighed 22 g lots of the moist soil were then placed into brass rings (ID 38 mm, thickness 10 mm) using a spatula. To increase the subsequent strength discs were compressed in a Wykeham Farrance consolidometer (lever ratio 11:1) which had been modified so that a plunger (Diameter 37.95 mm) would fit inside the brass rings. With this method pressures of up to 4.5 MPa could be applied to the flat faces of the disc. The loading time was typically 2 minutes. The discs were air dried and then oven dried after which the soil discs could be removed from the rings. After cooling the discs were stored on ceramic plates, connected to a water source by a hanging column, for 7 days so that the discs could attain a stable matric potential and so that the thixotropic (age hardening) process would approach completion (Utomo and Dexter 1981).

The apparatus used to measure the axial force (Figure 3.1) consisted of two parts. First a digital electronic balance (Mettler type PC4400) on which the soil disc was placed. The balance, which had a negligible pan deflection, indicated the axial worm force. The balance was connected to a micro computer, which enabled the axial worm forces to be recorded automatically and subsequently printed, whenever the balance reading changed by more than 5 x 10^{-3}N in a 1.5 s interval. This change in balance reading was chosen because it is about an order of magnitude less than the propulsive thrust recorded by Gray and Lissmann (1938 a).The time interval was selected, given the limitations of the computer and to limit the amount of printed output.

The second part was a match box with a hole of approximately 6 mm diameter in the base. The hole was made using a standard hole punch. A small plug of soil was smeared across the hole from inside the match box. Inside the match box was approximately 25 g of moist, loose soil and one pre-weighed earthworm. The match box was held in place by a clamp stand which in turn rested on the plastic platform.

The match box was secured approximately 0.5 mm above but not touching the soil disc. Discs were approximately 10 mm thick. The electronic balance measured the force to 1 x
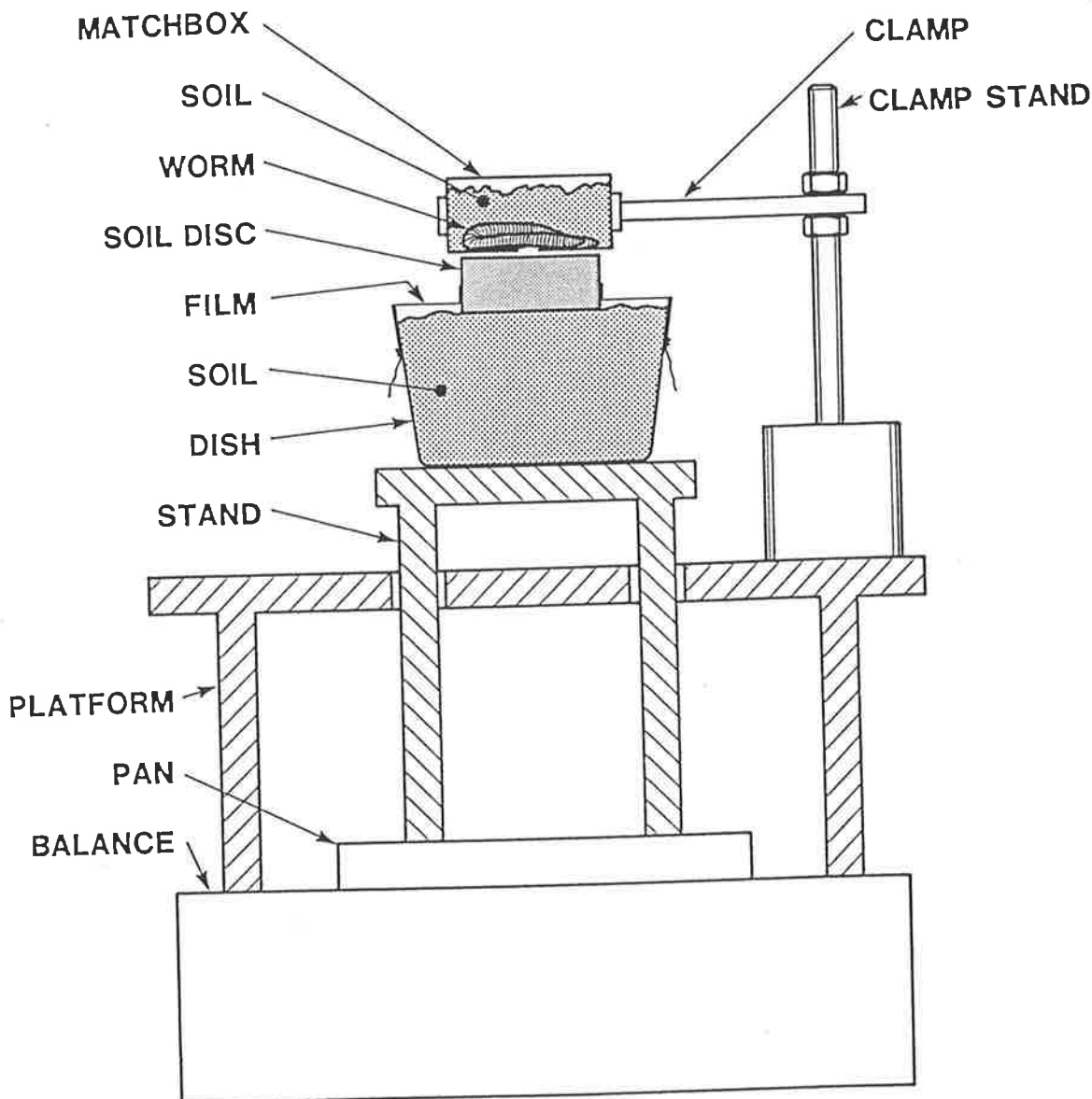
Fig. 3.1 Apparatus for measuring axial forces exerted by earthworms. A worm and approximately 25 g of soil was placed in a matchbox which had a hole approximately 6 mm in diameter in the base. The matchbox was fixed by a clamp to a clamp stand so that is could be freely secured above the disc. The soil disc rested on a dish containing moist soil, which acted as a reservoir and was covered by a plastic film to minimize evaporation. The disc rested on a stand which acted freely on the pan of a non-deflecting balance. The stand separated the soil from the heat of the balance.

$10^{-3}N$ and the pan deflection was negligible. The plastic stand which rested on the pan of the balance supported a small beaker of moist soil, on top of which rested a soil disc. The beaker of moist soil acted as a reservoir to limit the drying of the disc. Temperatures on the platform were approximately 20°C. The apparatus above the platform was covered with black plastic to exclude light and to maintain humidity.

The diameter of any hole made in the disc was measured to within 0.05mm, using vernier calipers and the penetrometer resistance of each disc was measured, through its circular face, prior to the soil water content of the disc being determined. The penetrometer consisted of a steel cone of 1 mm diameter and 60° total angle ahead of a relieved shaft. It was driven downwards at 3 mm min^{-1} and the force for penetration was measured at 4 mm depth (Whiteley et al 1981 a). The final weight of the worm was measured. In some cases the penetrometer resistance of the reservoir soil and the length of the earthworm were also recorded.

Measurements were made of the morphology of the earthworms. Two fine paint marks were made at separations of approximately 20 segments on the bodies of several earthworms selected at random. This separation was chosen as diagrams from cinematographic studies of Gray and Lissmann (1938 b) suggested that this was a common length for longitudinal contractions. The worms were photographed several times as they moved, one at a time, across a flat grid-marked surface. This was done using a single lens reflex camera with electronic flash and mounted on a tripod. The worms were anaesthetized in 10% ethanol (Ljungström 1970) and the number of segments between the markers, and the total number of segments of the worm counted. The diameter, length and weight of the worms were also measured while the worms were anaesthetized. The total volume of each worm was determined by displacement in water. From the photographs, the length and diameters of the segments were measured in lengthened, resting and contracted stages.

3.1.3 Results and Discussion

The distribution of times between the earthworm being placed into the match box and commencing activity is shown on Figure 3.2. If no activity had been recorded within 24 h then the earthworm was removed and a new experiment begun. This happened in 74% of the experiments. The time limit was chosen for convenience and because both the soil in the match box and the disc were drying. The commencement time presumably depends on the amount of soil in the match box and where the worm is placed in relation to the hole but it is worth noting that the median time for commencement was approximately 4 h. While the commencement time might be reduced by having less soil in the match box, a reduced amount would not allow the worm to obtain anchorage using its setae, and thus may limit the axial force. The statistical distribution of durations for worms to complete penetrations of the discs of soil is shown in Figure 3.3.

Once a worm has started to penetrate a soil disc of 8 mm thickness, the median time for penetration is 2 h, although in one instance it took up to 8 h. From the soil density and the tunnel diameter, it can be calculated that the earthworm ingests or pushes aside approximately 0.1 g of soil, in this time. As is shown in Table 3.1 (considered in more detail shortly) the mean weight of the earthworm used was 0.71 g and the mean soil water content was 22%. Thus the weight of dry soil (ingested or pushed aside) per gram fresh weight of worm per day is approximately 1300 mg. This is compatible with the rates of soil displacement during burrowing estimated as 809-1928 mg dry weight of soil g^{-1} fresh weight of worm day^{-1} for *A. rosea* calculated by Bolton and Phillipson (1976 a) from burrowing rates, burrow dimensions and soil density. Thus the compacted soil here does not appear to have influenced the rate of tunnelling.

The distribution of effort for the earthworm to penetrate this compacted layer can be analysed by dividing the total time taken for each worm into ten equal divisions and then studying the the distribution of peak effort within these intervals. For further analysis, peak
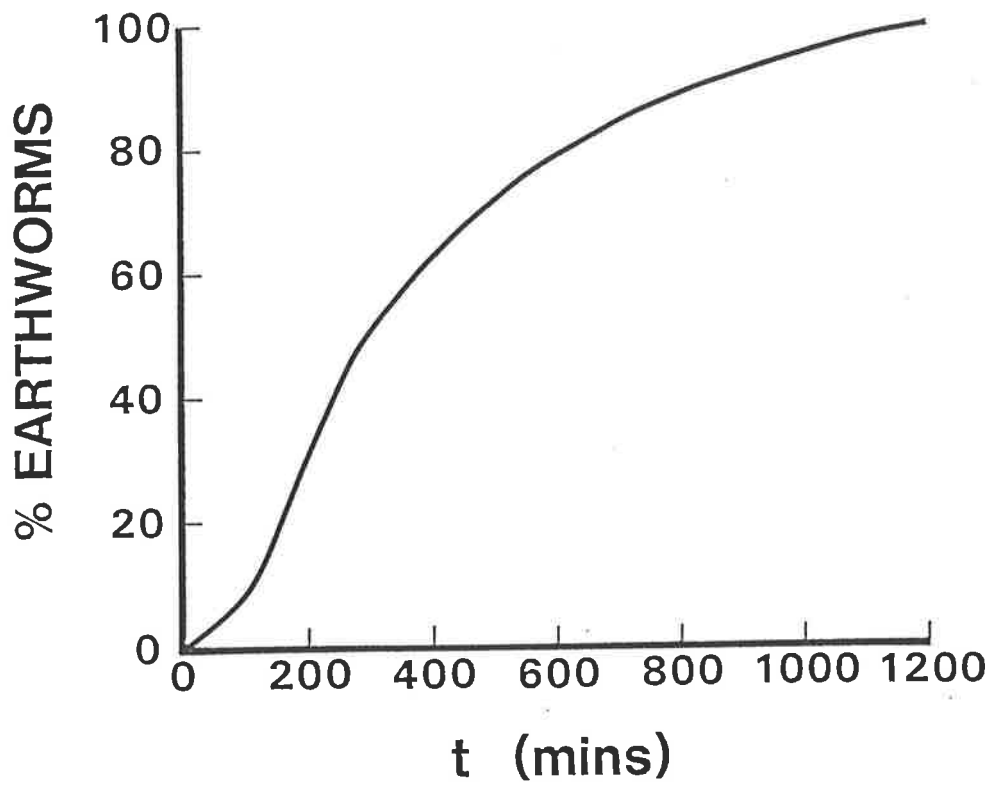
Fig. 3.2 Percentage of earthworms (*Aporrectodea rosea*) that started to tunnel into discs as a function of time.
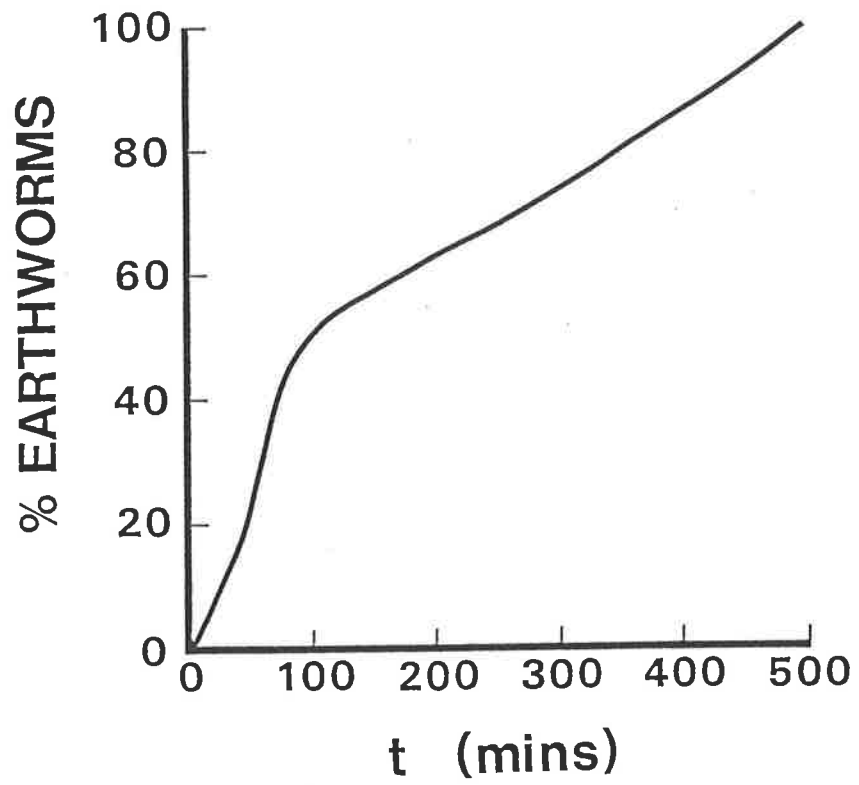
Fig. 3.3 Percentage of earthworms (*Aporrectodea rosea*) that completely tunnelled through soil discs (approximately 10 mm thick) as a function of time.

Table 3.1

Earthworm and soil data from successful experiments

Worm Mass (g)	Max Force (N)	Hole Diam (mm)	Axial Pressure P_{wa} (kPa)	$R = \dfrac{P_p}{P_{wa}}$	Soil Water Content (%)
0.52	0.331	1.90	116.5	19.6	21.9
0.82	0.431	2.75	72.7	19.2	N.D.
0.70	0.286	2.55	55.9	23.3	N.D.
0.74	0.387	2.55	75.7	23.8	23.6
0.73	0.297	2.35	68.5	40.9	20.7
0.56	0.442	2.75	74.5	20.1	21.4
0.46	0.180	2.45	38.1	27.3	22.6
0.62	0.760	3.20	74.7	14.3	22.8
0.77	0.494	4.20	36.0	12.1	22.4
0.95	0.688	3.25	84.1	10.5	21.5
0.80	0.565	3.05	77.3	16.0	22.0
0.79	0.723	3.05	99.0	13.5	21.0
Mean	0.71	0.465	2.84	72.8	20.1	22.0
S.E.	0.04	0.054	0.17	6.5	2.4	0.3

N.D. Not Determined

forces were chosen as being values greater than 5×10^{-2}N and having greater than twice the mean of the positive printed values for any one minute. Only rarely were negative balance readings recorded and these were attributed to the earthworm retreating temporarily toward the match box. The distribution of peak forces was examined for each time segment for each worm, as a proportion of the total peak numbers. The combined histogram is the percentiles for the probability of a peak being less than x N, against the time as a proportion of total penetration time (Figure 3.4). The number of peaks used to compile each class is shown. Maximum activity is apparent in the first and last periods. However the total number of peaks does not correlate with peak intensity.

Twelve worms succeeded in tunnelling through soil discs. Thirty-five worms did not penetrate the discs. In 32 of the unsuccessful experiments no attempt was made to penetrate the disc as indicated by an absence of marks on the disc and by no force values being recorded. Two of the unsuccessful attempts were due to the air gap between the match box and the disc being too great, allowing the worm to move across the disc surface. In the other case the disc was pock-marked indicating an unsuccessful attempt. The equipment could be improved by replacing the match box with an inverted cone or funnel, with a lid made of non-toxic perspex (plexiglass) or plastic. This solid container would be easier to fix in a clamp and would not sag as water from the soil weakened the cardboard match box. Further a funnel-like structure would direct the worm if downward movement were chosen.

The data from the 12 successful experiments is presented as Table 3.1. P_{wa} is the pressure exerted by the worm determined by the maximum force acting over the hole diameter. The use of the hole diameter in these calculations is considered practical since from Sims and Gerard (1985) it is known that A. rosea can alter its anterior segments to become blunt.

Whereas the worm mass and maximum axial force are positively correlated at the 10% significance level, (maximum force = 0.69 x worm mass - 0.22, r = 0.52) as are the hole diameter and the worm mass at the 10% level, (hole diameter = 2.05 x worm mass + 1.39, r = 0.50) the maximum axial pressure is not correlated with either of these worm data. Thus it appears that the axial pressure generated by an earthworm of the species A. rosea is independent of its size.
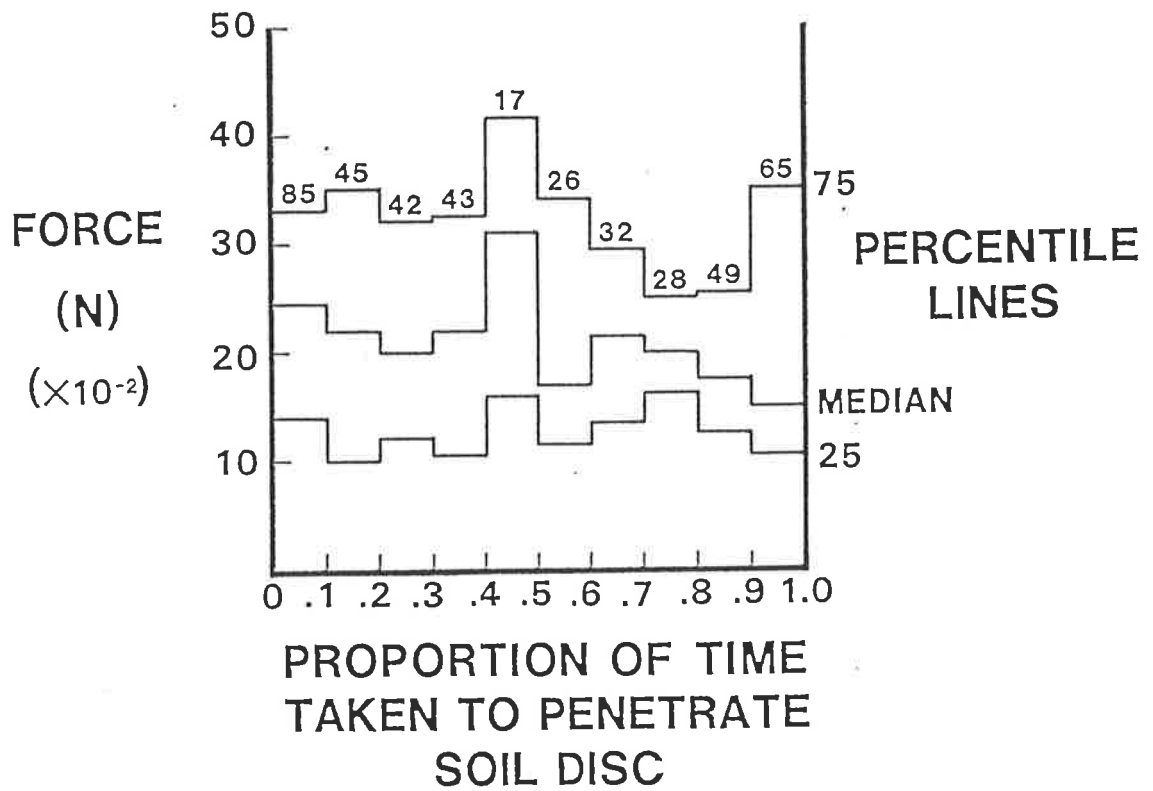
Fig. 3.4 Histogram of percentile axial forces exerted by earthworms (*Aporrectodea rosea*) for each time interval during soil disc penetration. *Number of top of each column* is the total number of peaks in that time interval.

In section 2.3 of the review of literature it was noted that Bouché (1977) considering the muscle development of earthworms thought that endogées would have limited digging muscles. *A. rosea* is classified as an endogée, and although Lee (1985) doubts the use of musculature as a classification feature it may be that earthworms from different ecological classifications may exceed the axial forces and pressures measured here.

The axial forces shown in Table 3.1 are approximately ten times the propulsive tractive forces for worms moving on a flat surface devoid of soil reported by Gray and Lissmann (1938 a). This is not surprising as a metal bridge will not allow the earthworm to anchor its body using its setae. Thus the only grip the earthworm can exert will be the friction between the metal plate and the limited amount of the worm circumference with contact, which must be less than half of the circumference.

Newell (1950) assumed that the prostomium formed the apex of a cone the rest of which is formed by the first four segments of the worm. For *L. terrestris* he estimated the diameter of the prostomium to be 1.0 mm. Using force values similar to those obtained by Gray and Lissmann (1938 a) he estimated the pressure of the prostomium against the soil as approximately 100 kPa. From descriptions of *L. terrestris* (Sims and Gerard 1985) the diameter of the worm ranges from 6-10 mm, the length from 90-350 mm and the number of segments from 140-155. This might for example place the prostomium 5 mm from the 4th segment which could have a diameter of 5 mm. The view of the earthworm tunnelling from Newell's description appears to be a flattened cone, at the front of the worm moving into crevices in the soil like a penetrometer. Figure 3.5

If I use an area of 0.8 mm^2 in the pressure calculations, rather than the hole diameter, then a maximum pressure of approximately 1 MPa is calculated. The prostomium has on its surface a large number of sub-circular buds which act as sense organs (Jamieson 1981). It is these sense organs which enable the prostomium to find a cavity suitable for tunnelling. I believe that it is unlikely that an important sensory site would be subjected to or could withstand pressures as high as 1 MPa particularly as it is soft tissue and not rigidly joined to the peristomium. Thus I consider 1 MPa to be inappropriately large.
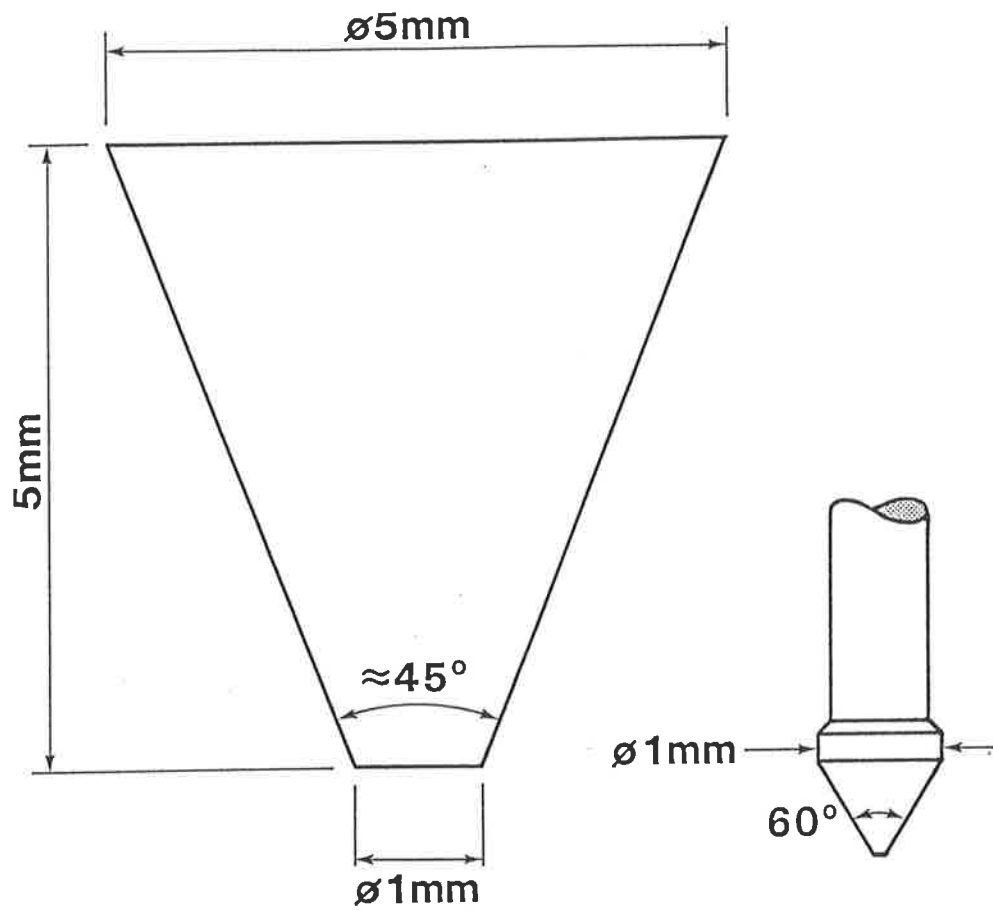
Fig. 3.5 Comparison of the size and shape of the anterior of a schematic earthworm with the size and shape of a 1 mm diameter penetrometer.

The value R given in Table 3.1 is the ratio of the penetrometer pressure to the pressure produced by the earthworm. The ratio,R, is analogous to the ratio used by Whiteley et al (1981 b) to compare the pressures for penetrometer penetration with the pressures for root penetration. The mean value determined by them was approximately 5 :1 while as seen here the penetrometer to the earthworm ratio is 20 : 1. This implies that the earthworms are more efficient in overcoming soil resistance than roots, which is to be expected since the worms can not only move around resistance points but can also ingest soil. The size of the ratio R shows that the analogy of a worm moving into compact soil as a penetrometer is inadequate and further the large area over which tunnelling pressures apply contradict the idea that earthworms can tunnel by compaction caused by axial pressure.

Newell (1950) claimed that pressures of 100 kPa (acting over the small area of the prostomium) would be sufficient for tunnelling by earthworms, even though no support was given for this statement. Pressures recorded here and shown on Table 3.1 show pressures up to 116 kPa acting over the much larger area of the worm cross sectional area.

The three conditions described in the introduction are considered in Table 3.2. Condition 1 is appropriate to the axial pressures dealt with here. For a worm pushing forward, as described in section 3.1.1 each segment will have a number, N_c, of bundles of circular muscles assumed here to be distributed evenly around the perimeter. Each bundle will exert a tension force f_c as the circular muscles contract. The total force

$$F_c = 2 N_c.f_c \qquad (3.1)$$

since each bundle crosses each longitudinal section twice. The force acts over an area, D_1L_1, hence fluid pressure

$$P_1 = \frac{F_c}{D_1 L_1} = P_{wa} \qquad (3.2)$$

where P_{wa} is the pressure that the worm is exerting in the axial direction. If a value of $P_{wa} = 100$ kPa is assumed then from the measurements of the size of the earthworms in lengthened

Table 3.2

Muscle and segment behaviour when the worm is pushing forward,

resting, or pushing sideways

	Condition		
	1	2	3
Action	Pushing forward	Resting	Pushing sideways
Circular Muscles	contracted	relaxed	relaxed
Longitudinal Muscles	relaxed	relaxed	contracted
Segment Length	L_1	L_2	L_3
Segment Diameter	D_1	D_2	D_3
Segment Volume	$\dfrac{\pi.D_1^2.L_1}{4}$	$\dfrac{\pi.D_2^2.L_2}{4}$	$\dfrac{\pi.D_3^2.L_3}{4}$
Fluid Pressure	P_1	P_2	P_3

stages, $D_1 = 3 \times 10^{-3}$ m and $L_1 = 1 \times 10^{-3}$ m. Equation 3.2 may be rearranged to give $F_c = 0.3$ N. If however $P_{wa} = 1$ MPa as was considered in section 3.3. If the force acts over the smaller area of the prostomium $F_c = 3.0$ N. For the reasons given earlier I believe that a maximum tension in the circular muscles of 0.15 N per segment is realistic. It is apparent from the considerations given here that the propulsive tractive forces determined by Gray and Lissmann (1938 a,b) for earthworms on flat surfaces are inappropriate to tunnelling through soil.

3.2 Radial pressures

3.2.1 Introduction

Abdalla et al (1969), considering the mechanics of root growth, proposed that when axial elongation of the root tip was inhibited by confining stress, radial growth of the root became dominant. The resultant radial thickening caused stress relief ahead of the root tip which reduced the stress required for further axial elongation. Maximum radial pressure for two day old pea (*Pisum sativum* cv Greenfeast) seedlings have been reported by Misra et al (1986) as approximately 900 kPa. Elsewhere mean radial pressures have been reported as 509 kPa for *Faba vulgaris* and 659 kPa for *Zea mays* (Gill and Bolt 1955).

Lee (1985) describing earthworms burrowing in soil stated that as the body of the earthworm was dragged forward by contraction of the longitudinal muscles soil particles are simultaneously pushed sideways widening the tunnel. This has been recorded by time lapse photography for *L. terrestris* moving from the soil surface down into very loosely packed soil by Roots and Phillips (1960). Initially the worm pushed its first few segments into a crevice then arched up the succeeding segments to improve its downward thrust. As the thrust was completed the anterior end of the worm was seen to expand forcing soil particles radially aside, prior to the next thrust. Pharynx eversion was not recorded as the worm entered the loose soil but was frequently observed subsequently (Roots and Phillips 1960).

The radial force is generated by the contraction of the longitudinal muscles and the relaxation of the circular muscles. The longitudinal muscle layer , (so called because the muscle fibres have their long axes with the worm,) is thicker than the circular muscle layer in most earthworm species and has fibres which extend over more than one segment (Jamieson 1981). Thus the musculature which generates radial pressures exists in earthworms and is of at least similar power to the circular muscles which generate the axial pressures.

Seymour (1978) measured the unidimensional lifting force by making earthworms crawl under a bridge and recording their internal coelomic pressures, the forces on the bridge and the areas of contact with the bridge. The measured force was always greater than a force value calculated by multiplying the internal pressure with the measured area. This excess lifting force of approximately 1.5 times the mean calculated force was attributed by Seymour to the intrinsic rigidity that can be developed by the contracting and stiffening body wall muscles. However the experiments were not performed in a soil environment, consequently the worms were not confined evenly around their circumference. While the expansion of the earthworms in the unconfined directions will be limited by the elasticity of the body wall, any relief of pressure in the coelomic fluid will alter the lifting force. Maximum coelomic pressure recorded for *L. terrestris* reported by Seymour (1978) was less than 7.5 kPa during this lifting test but this is well in excess of the 1.6 kPa reported by Newell (1950) for the same species not confined in any way.

As has already been noted, Dexter (1978) examined tunnels made into compacted soil blocks by the earthworm *Aporrectodea rosea*. Neither transverse nor axial sections through the tunnels showed any compaction or cracking while similar sections around needle probes driven into the the soil showed extensive cracking and compaction. This indicated that the earthworms were not pushing particles aside. However Rushton (1986) found that movement of *L terrestris* through moist soil was negatively correlated with dry bulk density over a range from 1.382 - 1.676 tm^{-3}. Since there is a positive correlation between penetrometer resistance and density, this implied that soil strength was a limiting factor in the movement of this species as it sought to establish burrows.

Such a finding has important ramifications for the introduction of species to a "new" area whether it is land reclaimed from mining or an agricultural area outside the species' prior distribution. This is the case if introduction is desirable to increase soil porosity and reduce compaction effects, particularly since mechanical methods to increase porosity are detrimental to earthworm populations. It might, however, be desirable to use mechanical methods before introducing earthworms to prepare the environment for them.

Earthworms use radial expansion to burrow through loose soil. However the cuticle allows the body to expand much more lengthways than circumferentially; ie it has anisometric mechanical properties. This may limit the effectiveness of the radial expansion technique. Further, compacted soil may soil also restrict radial body expansion, and unlike a plant root the earthworm has alternative strategies to advance. There is however uncertainty about the ability of earthworms to tunnel in compacted soil and so I now consider the question of the importance of radial expansion as a tunnelling technique.

3.2.2 Materials and Methods

The soil and earthworms used have been described in section 3.1.2. The radial pressures exerted by the earthworms were determined using samples of the Urrbrae soil remoulded at water contents in excess of its plastic limit. A spatula was then used to press the moist soil into plastic rings. Discs of different strength were made by compacting them with different pressures in a consolidometer, as described in section 3.1.2. However in these experiments the batches of discs were prepared by standardizing each procedural step. The loading time was always 2 minutes. The discs were then aged on ceramic plates connected to a water source by a hanging water column, to allow for most of the thixotropic equilibration. Some batches were returned to the consolidometer and compaction repeated to increase disc strength. After ageing, a sub-sample were used to determine the mean gravimetric water content of the soil discs and the tensile strength of the discs. Tensile strength was determined by crushing the discs between two flat parallel metal plates using the method described by Dexter and Kroesbergen (1985) for large and strong aggregates. Briefly this involves resting

discs on their circumference on a flat metal jack of a Wykeham Farrance loading frame and raising them until they just touch the upper plate. The upper plate was connected by a rod to a loading ring (capacity approximately 650 N). Raising the jack loads the disc and deforms the load ring. This deformation is measured on a dial gauge until the disc fractures. Twelve discs were tested from each batch. The tensile strength Yc was calculated from

$$Yc = \frac{2.F}{\pi.D.L} \qquad (3.3)$$

where F is the force required to fail the disc by tensile cracking,

D is the diameter of the disc and,

L is the thickness of the disc (Figure 3.6 A)

An earthworm was placed into soil contained in a match box. Less soil was used in these experiments than those described in section 3.1.2. The matchbox had a hole of approximately 6 mm diameter in the base. The match box was then placed onto the flat face of a disc, with the hole centrally placed (Figure 3.7). The disc remained on the ceramic plate. At 24 hour intervals the disc was inspected and one of four possible outcomes noted. The possibilities were that :

1 No attempt had been made to penetrate the disc;

2 That an unsuccessful attempt had been made to penetrate the disc;

3 That the earthworm had burrowed through the disc cracking it;

4 That the earthworm had burrowed through the disc without cracking it.

Several replicates were set up at any one time. The diameter of any hole made by the worm was measured with vernier calipers, to within 0.05 mm, before I determined the gravimetric water content of the individual disc. Misra et al (1986) measured the maximum radial pressures exerted by plant roots by studying the conditions under which they could crack cylinders of chalk. The pressure required was calculated from the tensile strength of a drilled piece of chalk multiplied by (D/d_i-1) where :
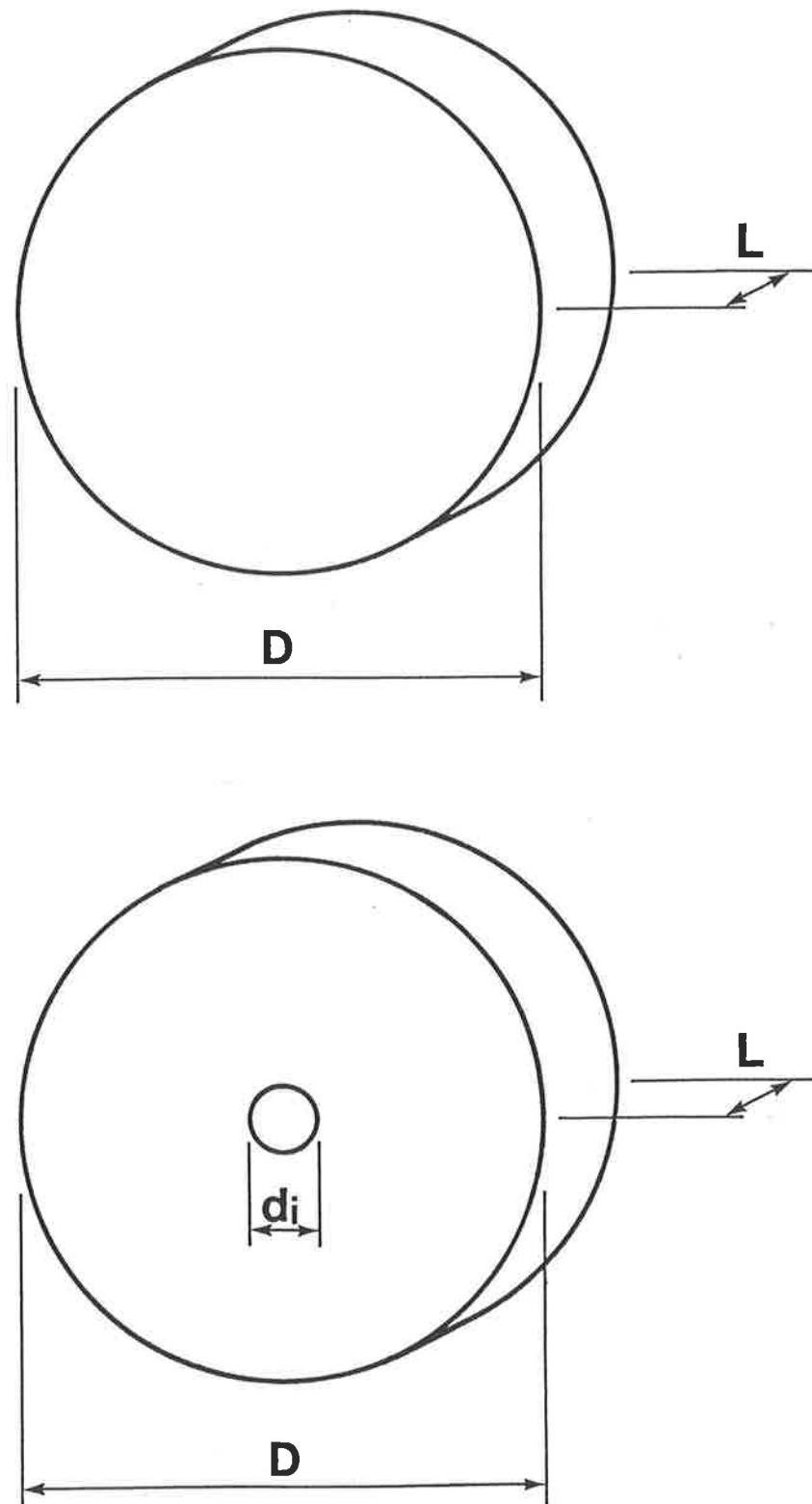
Fig. 3.6 A Soil disc showing diameter D and length L. B Soil disc drilled to become a cylinder with diameter D and hole diameter d_i.

LID

MATCHBOX

SOIL

WORM

SOIL DISC

SOIL

CERAMIC PLATE
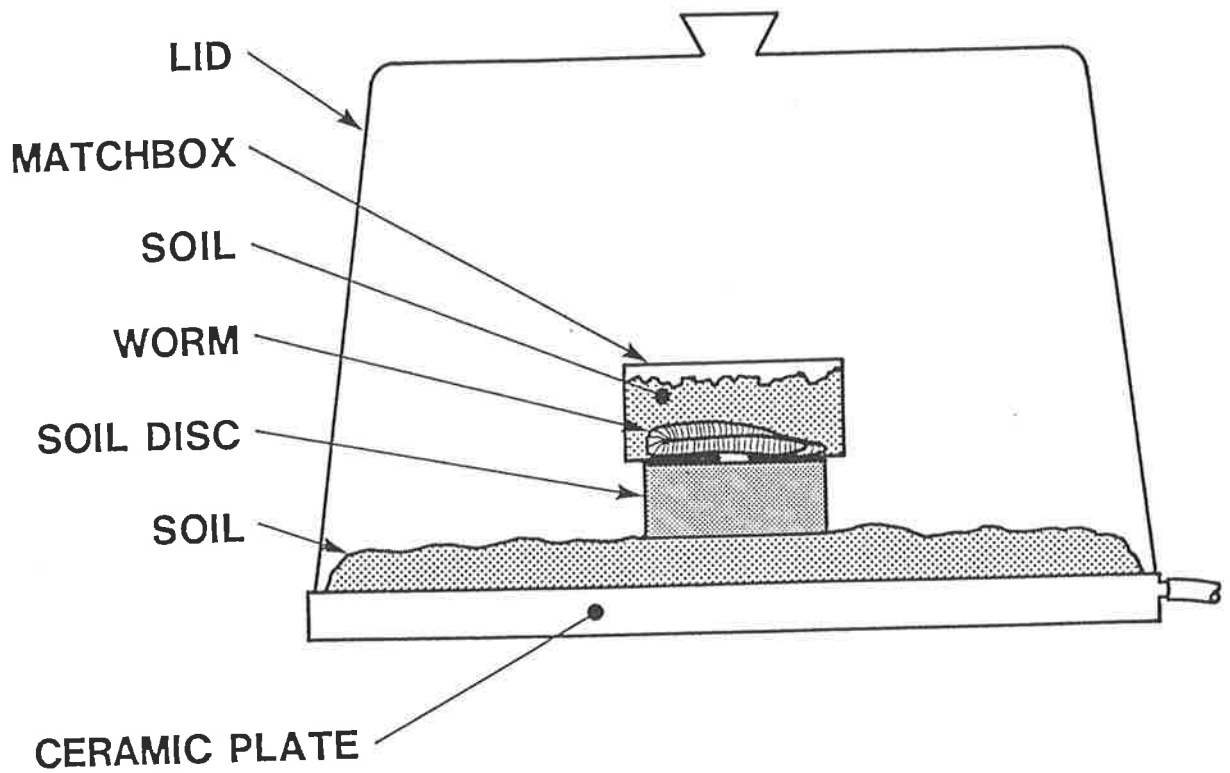
Fig. 3.7 Apparatus for measuring radial earthworm pressures. An earthworm and soil are placed in a matchbox with a hole approximately 6 mm in diameter in the base. The matchbox is placed on the flat surface of a soil disc with the hole in the centre. The disc rests in soil which provides good contact with the ceramic plate, allowing the matric potential of the soil to be maintained. The lid minimizes evaporation.

D is the diameter of the disc (or cylinder) as previously stated;

d_i is the diameter of the hole through the centre of the circular face of the disc (Figure 3.6 B)

To check this estimate I determined the internal pressure required to fracture discs which had been drilled to form thick-walled cylinders. Discs of soil were prepared as previously described and were allowed to age harden on ceramic plates. They were then air and oven dried. A hole was made, with a drill press, through the centre of the circular face of some of the dry discs. The drill diameter was 4.8 mm which is approximately 0.125 of the disc diameter. While drilling, the discs were on a piece of soft wood, so that damage to the discs as the drill emerged were minimized. The discs with drilled holes are henceforth referred to as cylinders to distinguish them from solid discs. After returning the cylinders and discs to the ceramic plate to again standardize their water potential I measured the tensile strength of a sub sample of the cylinders by the indirect (crushing) test as described previously.

The cylinders were then tested by internal pressure (Figure 3.8). This involved fitting the cylinders one at a time over a thin porous tube which had been covered by a latex sheath (similar to that used by Richards and Greacen 1986). The sheaths were produced by dipping 3.75 mm diameter glass rods into a latex solution. After removal from the solution the sheaths were allowed at least 24 h to dry, before being peeled from the rod and fitted over the porous brass tube. The tube was 2.37 mm external diameter, 1.65 mm internal diameter, closed at one end, with several small holes drilled along a 10 mm portion of its length. The latex sheath was fitted over the porous tube and fixed in place by twists of enamelled copper wire.The portion of the sheath which was not covered by the cylinder was contained by a plastic drinking straw. The tube was connected to a N_2 gas line so that pressure could be applied to the inside surface of the cylinder. The gas pressure was measured to within 1 kPa.

The pressure required to cause cylinders to fracture was compared with the pressure required to expand the rubber sheath between spaced straws prior to, and after, being contained by the cylinder. Simple engineering theory allows the stresses through the cylinder
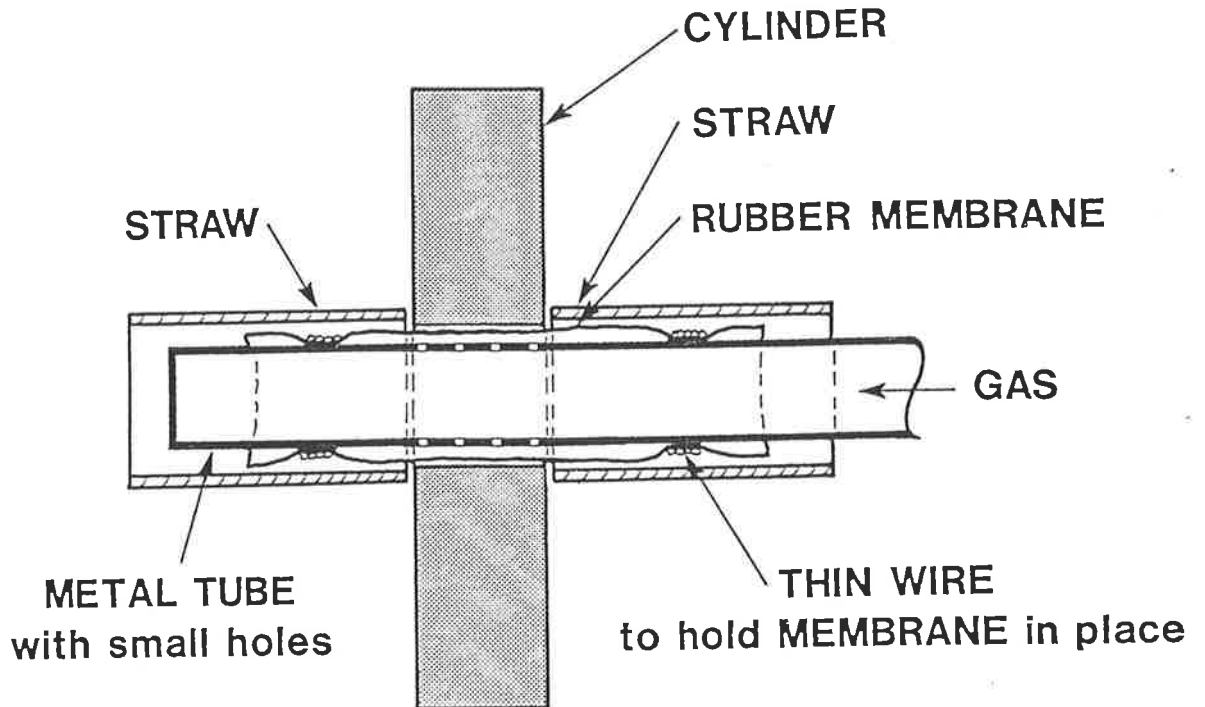
Fig. 3.8 Apparatus for applying known hoop stress to a soil cylinder. A fine tube, approximately 10 mm of which is porous, is connected to a gas pressure line. The porous section is covered by a fine latex membrane sealed to the tube by fine wire. A soil cylinder is positioned over the membrane. To stop expansion of the membrane away from the cylinder plastic drinking straws are used. The pressure required to expand a membrane without a cylinder and the fracture pressures are measured at the gas input.

at failure to be calculated when the internal pressure is being applied. Popov (1952) states that in this case the tangential stress, σ_t , is always tensile and at a diameter, d, is given by :

$$\sigma_t = \frac{p_i(d_i)^2}{D^2-d_i^2} \left[1 + \frac{D^2}{d^2}\right] \qquad (3.4)$$

where p_i is the internal pressure

The maximum tensile stress is stated to occur at $d = d_i$ and is always greater than p_i. The average tangential or hoop stress in the cylinder wall is

$$\sigma_{t.av} = \frac{p_i d_i}{d-d_i} \qquad (3.5)$$

Measurements of the earthworm and the dimensions of the individual segments were given in section 3.1.2.

3.2.3 Results and Discussion.

To calculate the radial pressures exerted by the earthworms in these experiments it is necessary to understand the mechanics of fracture of thick-walled cylinders. The two methods used here to determine the strength were the indirect tensile or Brazilian test (Dexter and Kroesbergen 1985), which was performed on solid soil discs, and the expansion of latex tubes against the interior wall of soil cylinders with nominally identical properties. The tensile strength was considered to be equivalent to the average hoop stress at fracture by Misra et al (1986). The Brazilian test was performed here on a sub-sample of discs for each strength of disc that the earthworms were tested against, as done by Misra et al (1986) for each chalk sample. Comparison of the tensile strength with the maximum tensile stress of cylinders made by drilling was performed on one standard set of discs. Testing was done in this way because the musculature of the earthworm is distributed relatively consistently around its circumference and hence the pressure exerted is assumed to act evenly around the interior wall of the cylindrical hole.

A review of the relevance of the indirect tension test to soils is given in Dexter (1986 b). While much of the discussion is irrelevant to this thesis the relationship between the ratio of the length to the diameter of the sample, (eg see Figure 3.6 A here) with the tensile strength were constant over the range 0.4 < L/D <1.6. The discs used here were outside this range; typically L/D = 0.26. Dexter (pers comm) examined L/D ratios to a minimum of 0.2 and found significant reduction in the measured force. This relationship between L/D and the tensile strength is shown in Figure 3.9. While measurements were not performed at exactly an L/D ratio of 0.26 I estimate that at this value the experimentally determined tensile strength (from indirect tension) is 0.87 of the mean expected.

Table 3.3 presents the experimentally determined dimensions, tensile strengths and internal pressures applied for discs and cylinders. By direct substitution into equation (3.4) it can be seen that the maximum stress required to fracture cylinders by internal pressure is 139 kPa. Cylinders that were fractured by this technique usually broke in half, only a few fractured into three pieces. The average tensile stress across the cylinder at failure can be calculated by substitution into equation (3.5) and is found to be 19.8 kPa. This experimental value is only 1.13 times the predicted tensile strength of 17.5 kPa.

If allowance is made for the reduction in the tensile strength predicted by indirect tension as a result of the small L/D ratio, the value obtained is 0.98 of the 17.5 kPa predicted. I consider that this is sufficiently close to unity to support the implication of Misra et al (1986) that the tensile strength is equivalent to the mean hoop stress at failure. In this work I shall consider the two as the same value in view of the small difference between the experimental and predicted values. Thus the maximum radial pressure exerted by the earthworms can be simply calculated from the tensile strength of the discs and the diameter of the hole created by the worm by assuming

$$\sigma'_{t.av} = Y_c \qquad\qquad (3.6)$$

The radial pressure exerted by a worm, P_{wr}, breaking a soil disc when tunnelling through it is
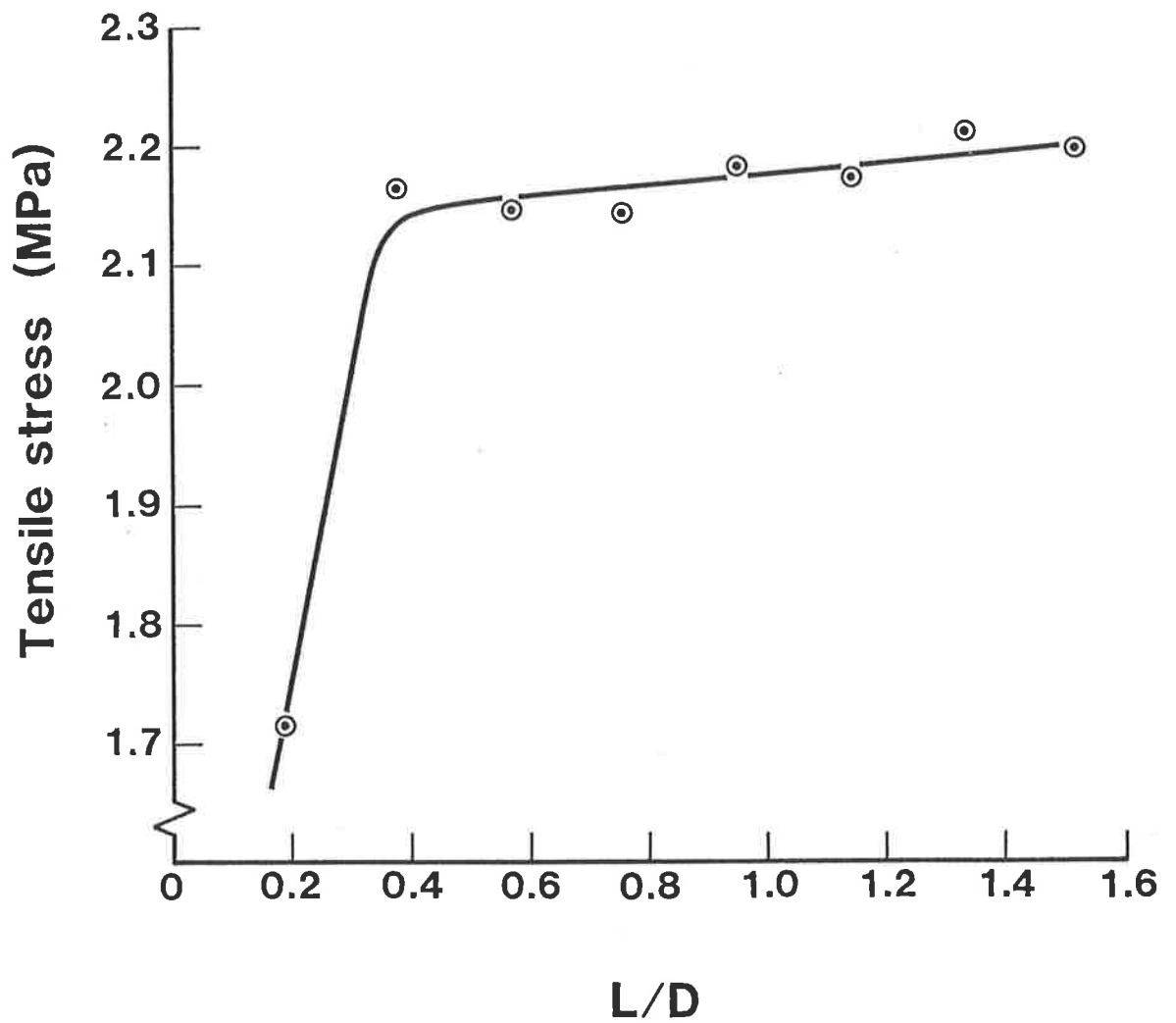
Fig. 3.9 The effect on the tensile strength of soil discs of the relationship between the ratio of their length, L to diameter, D. (From Dexter pers comm).

Table 3.3

Dimensions, tensile strengths and internal pressures applied to control samples.

Figures in brackets are standard errors.

| | DISCS | CYLINDERS | |
	Indirect Tension	Indirect Tension	Direct Tension
D (mm)	37.35 (0.03)	37.35 (0.03)	37.35 (0.03)
d_i (mm)	-	4.70 (0.03)	4.80 (0.03)
Y_c (kPa)	22.00 (0.24)	17.49 (0.29)	-
net p_i	-	-	134.00 (6.0)

$$P_{wr} = p_i' \tag{3.7}$$

The radial pressure exerted by a worm, P_{wr}, if it breaks a disc is from equations (3.6), (3.7) and (3.8)

$$P_{wr} = Y_c \, (D - d_i) \, / \, d_i \tag{3.8}$$

It is also apparent from Table 3.3 that the crushing force of a cylinder is reduced to approximately 80% of the strength of a similar disc as a result of a centrally placed hole of diameter 0.125 the disc diameter. This is compatible with the size of the hole created by the earthworms which had a mean value of approximately 3.1 mm.

The proportions of worms breaking and not breaking discs is shown in Figure 3.10 as a function of the radial pressure, p_i', required to break the disc. The proportion, B, of worms exerting pressure greater than p_i' broke the discs and the proportion, NB, exerting pressure less than p_i' did not break the discs. The broken curve in Figure 3.10 is my estimate of the transition from all worms exerting greater than p_i' to all worms exerting less than p_i'. The cross over point is an estimate of the mean maximum radial pressure exerted immediately adjacent to the worm and is approximately 230 kPa. This is considerably less than the 900 kPa at the cross over point for the maximum radial root growth pressure for peas reported by Misra et al (1986), and also less than the mean radial pressures reported by Gill and Bolt (1955).

The cylinders created by the earthworms tunnelling through discs without fracturing them were tested for tensile strength using the Brazilian test described earlier. These strengths are usually between 50 and 60% of the strength of the solid disc. This proportion did not depend on the initial disc strength over the range used here. Some of the reduction can obviously be attributed to the reduced strength of cylinders compared with discs as mentioned earlier, but some must be as a result of the earthworm presumably producing small radial stresses. It is notable however that none of the discs remaining unbroken after the passage of the worm had less than 45% of its initial strength. Thus the earthworms either fractured the
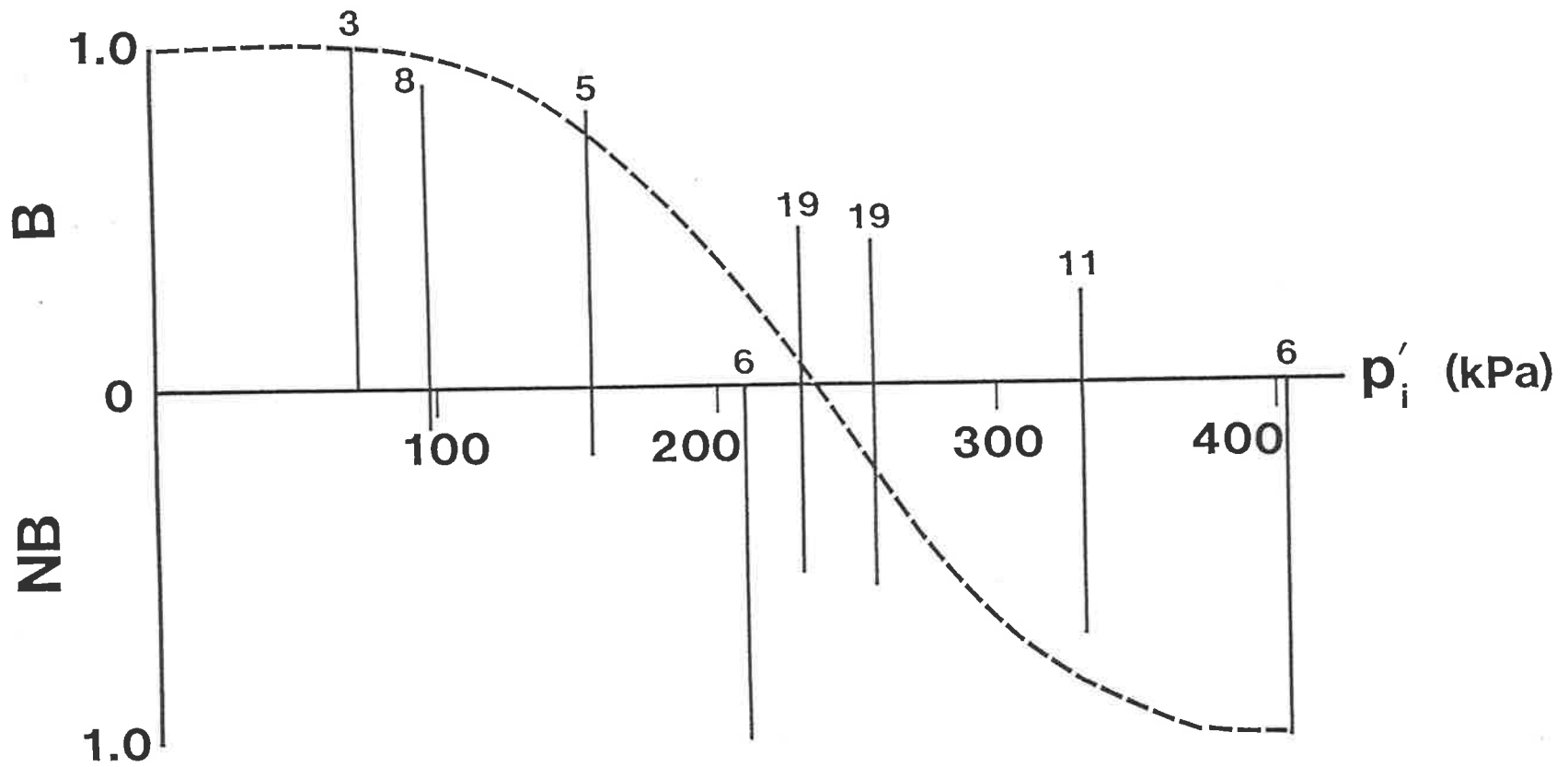
Fig. 3.10 Proportion of worms that broke the disc, B, and proportion that did not break the disc, NB, as a function of pressures required to break the disc, p_i'. *Number on each bar* indicates total number of earthworms used in experiments to attempt to break discs of strength, p_i'. *Broken curve* shows probable transition from all worms exerting sufficient pressure to break the disc, B, to all worms exerting insufficient pressure to break the disc, NB.

disc or caused only limited weakening. This suggests that if the worm was unsuccessful in fracturing the disc then other mechanisms were used for tunnelling.

From soil mechanics theory (Horn 1981) it is known that if a soil has been compacted at a particular water content then subsequent loading at the same water content will not cause further compaction unless the pressure exceeds the initial loading pressure. In many compacted agricultural soils mechanical loads or effective mechanical stresses induced during drying in excess of 230 kPa will have occurred and hence in these cases it is unlikely that compaction can occur around earthworm tunnels. Thus the radial pressures found here are compatible with the absence of cracks around tunnels made by earthworms in compacted soil blocks reported by Dexter (1978).

The mechanisms available to the earthworms to overcome confining stresses which may limit their forward movement include the use of radial pressure, presumably to create zones of stress relief. With the combinations of mechanisms available to earthworms it is reasonable to find that the maximum axial pressure reported in section 3.1.3 is less than the radial pressure reported here. A worm exerting radial pressure with segment length L_3 and segment diameter D_3 will have segment volume $\pi D_3^2 L_3 /4$. A typical maximum worm diameter was $D_3 = 4.2 \times 10^{-3}$ m and the corresponding segment length was $L_3 = 0.5 \times 10^{-3}$ m. Assuming N_1 bundles of longitudinal muscles in each segment to be around the perimeter, and that each bundle exerts a force f_1, then the total force when pushing radially is

$$F_1 = N_1 f_1 \qquad\qquad (3.9)$$

which acts over an area $\pi D_3^2/4$. The fluid pressure inside the worm is

$$F_3 = \frac{4 F_1}{\pi D_3^2} = P_{wr} \qquad\qquad (3.10)$$

where P_{wr} is the pressure the worm is exerting in the radial direction. Rearranging equation (3.10) and substituting values for D3 as above, and the value of P_{wr} used at the cross over point shown in Figure 3.10, gives $F_1 = 3.2N$.

While it is well documented that the longitudinal muscles of earthworms are always at least as thick as, and often significantly thicker than, the circular muscles, the pressure in the coelomic fluid is greater when the circular muscles are contracted (Jamieson 1981). Differences in the physiology of the muscle fibres may be partially correlated with this (Jamieson 1981) but to extrapolate further is impractical.

From this work I propose that the earthworm *A. rosea* uses a combination of mechanisms when tunnelling through soil. For the earthworm to be able to exert radial pressure sufficient to fracture soil aggregates at least some portion of the body must be inside the aggregate. This may be achieved either by ingestion of soil or by pushing the front portion of the body into a crevice in the soil using the axial force described in section 3.1.1. It may be that for different species the ability to apply any or all of these mechanisms will vary. For a geophagous species which are considered to have only ephemeral burrows the tunnelling techniques used may be different from species which establish permanent structures. The species used in this work is of similar behaviour to the *A. caliginosa* used by Dexter (1978) who found no compaction around tunnels using radiography. The finding here that only limited weakening of unbreakable discs occurs and the deduction from this that if one burrowing mechanism is inappropriate, another is used, allows the reconciliation that the worms in Dexter's study, being confined in a dense soil, did not cause further compaction.

L.terrestris is not a familiar species in Australia, however it is known to be a detritivorous species and to establish permanent burrows. The negative correlation between soil density and tunnel length found by Rushton (1986) for *L. terrestris* is consistent with the idea that species from differing ecological niches may have differing strategies to overcome limitations on burrowing. The slowing of burrowing speed implied by the reduction in burrow length may be of less ecological importance to a non-geophagous species than to a geophagous species which relies on soil ingestion for food.

From this chapter it is apparent that the earthworm *A. rosea* can exert pressures of at least 100 kPa in the axial direction and in excess of 230 kPa radially and that this provides an adjunct to the "traditional" tunnelling techniques of soil ingestion, including pharynx eversion and water excretion.

Chapter 4

Physical Properties of Cast Material

4.1 Shape

4.1.1.Introduction

Material voided by earthworms is recognized as differing from aggregates in the bulk soil. Casts exist as discrete entities or bound only to the soil matrix. The range of cast shapes is limited and has been described by Bal (1973), see section 2.5. The shape of soil particles has received some quantitative attention since the advent of micro-computers (Davis and Dexter 1972, Dexter 1985) but these techniques have not been applied specifically to soil particles influenced by soil fauna. Descriptions have placed surface casts in two categories : either ovoidal or sub-spherical to spherical pellets, or paste-like slurries (Lee 1985).

Bal (1973,1982) used the term modexi (from "moulded"and "excrement") for the excrements which have left the animals intestines as shaped three-dimensional individuals. Modexi were classified by Bal according to characteristics of their shape; size; mineral,organo-mineral or organic composition; basic distribution (whether embedded or not) and related distribution. He defined five basic shapes : spherical, ellipsoidal, cylindrical, platy and threadlike (mitoid). More detailed discussion of Bal's classification is given in section 2.5. My intention now is to examine the shape of earthworm casts using quantitative scanning procedures and to compare the results with descriptive techniques.

4.1.2 Materials and Methods

The soil and earthworms used in these experiments have already been described in section 3.1.2. Before the shape of earthworm casts could be determined, fresh casts had to be collected. This was done by placing adult earthworms in soil, on sintered glass funnels. The funnels were connected by hanging columns of water to a reservoir to maintain a constant

matric potential of -5 kPa. After allowing several days for acclimatization, the earthworms were gently removed from the soil and held by hand above a microscope slide until they excreted a cast or until they became agitated.

The slide was transferred to the stage of an Olympus SZ-Tr zoom stereo microscope and the cast illuminated by an optical fibre lamp diffused through a fine frosted glass plate. The cast was photographed at 10 x magnification with an Olympus Tokyo PM-6 microscope camera controlled by an Olympus EMM-7 photomicrographic exposure meter, using black and white film. The excreted material maintained its integrity during the photography. The approximate dimensions and the weight of the cast were determined.

From the photographs, high contrast outline tracings were made of the cast shape. These tracings were then scanned automatically with a television camera which was connected to a digitizer and a micro-computer. Each picture was scanned with a resolution of 256 x 256 pixels. The procedure was " First a quick scan was done along every tenth line and row of the picture so that the approximate centre of the aggregate could be determined. Then a pair of diagonal lines at $+\pi/4$ and $-\pi/4$ were generated through this point as shown in Figure 4.1. Scanning was then done along every line or column within each quadrant, and the coordinates of the edge of the particle were stored. About 500-600 coordinate pairs (x,y) were stored for each particle in this way" (Dexter 1985). The time taken for this procedure was approximately 19 minutes to scan each tracing and a further 26 minutes to perform the spectral analysis.

As a comparison, about 20 air-dried aggregates were collected from gently sieved (> 1 mm and < 2 mm) soil, then similarly photographed and scanned. The aggregate size range was similar to that of the casts but none appeared to be recently biologically influenced material.

From the digitized outlines, three simple ratio methods and two mathematical analyses were performed. The roundness ratio method of Cox (1927) is a single measure of roundness obtained as the ratio of the particle cross sectional area to the area of a circle having the same perimeter.
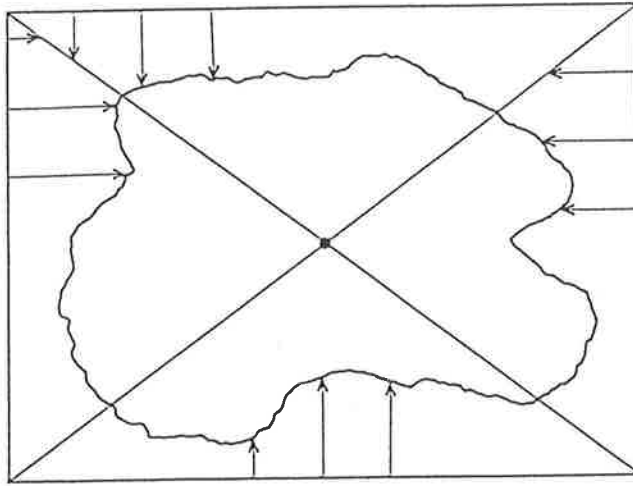
Fig. 4.1 Directions of scanning in four quadrants defined by two diagonal lines through the approximate centre of a photograph of a cast or aggregate.

$$\text{Roundness} = \frac{4 \pi \text{ area}}{(\text{perimeter})^2} \qquad (4.1)$$

Using this measure the ratio for a needle approaches 0 and for a circle is by definition 1. All values of roundness are thus between zero and unity. Two aspect ratios, the right angle aspect AR_r and the shortest aspect AR_s were also employed. Figure 4.2 The right angle aspect ratio is the maximum length of the casts or aggregates, D_{max}, as the denominator to D_r which is the diameter through the centroid at right angles to D_{max}.

$$AR_r = \frac{D_r}{D_{max}} \qquad (4.2)$$

Similarly the shortest aspect ratio AR_s is the ratio of the shortest diameter D_s which passes through the centroid to D_{max}.

From the calculated centroid the (x,y) coordinates can be converted to polar coordinates (r, θ). The radius r can then be plotted as a function of

$$AR_s = \frac{D_s}{D_{max}} \qquad (4.3)$$

From the calculated centroid the (x,y) coordinates can be converted to polar coordinates (r, θ). The radius ,r, can then be plotted as a function of, θ, from $0-2\pi$ radians. Further rotation repeats the sequence. The function, $r(\theta)$ is then described as a Fourier series.

$$r(\theta) = A_0 + \sum_{n=1}^{\infty} [A(m)\cos(n\theta) + B(m)\sin(n\theta)] \qquad (4.4)$$

where n is an integer

    A_0 is equal to the mean radius of the particle

    $A(m), B(m)$ describe the mth harmonic component of the radius spectrum.

Equation 4.4 can be expressed in complex form as
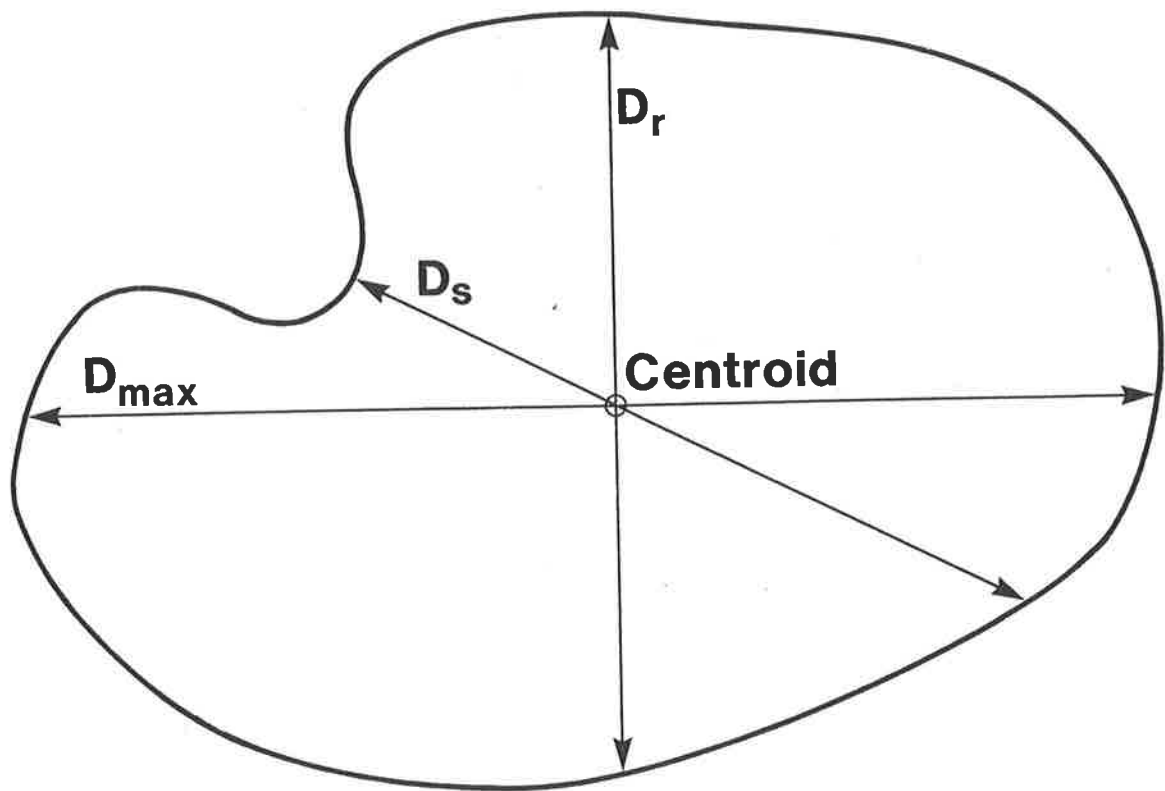
Fig. 4.2 Profile of an aggregate or cast showing the centroid, the maximum length through the centroid, D_{max} the shortest diameter through the centroid D_s, and the right angle diameter to D_{max} through the centroid D_r.

$$r(\theta) = \sum_{m=-n}^{n-1} P(m)^{2\pi i m\theta/N\Delta} \tag{4.5}$$

where P(m) is the complex radius given by

$$P(m) = C(m)^{ei\emptyset m} = A(m) - iB(m) \tag{4.6}$$

where $i = \sqrt{-1}$, N = 2n is the number of sampling points spaced at equal angles, Δ is the sampling interval such that $N\Delta = 2\pi$, C(m) is the amplitude of the mth harmonic and $\emptyset(m)$ is the phase angle of the mth harmonic ($\emptyset(m)$ = arctan (-B (m) / A(m)) relative to the reference angle $\theta = 0$)(Dexter 1985).

The relative magnitudes of A(m) and B(m) for any given value of m depend on the phase angle, $\emptyset(m)$, of the mth harmonic. It can be shown that by multiplying equation 4.6 by its complex conjugate, P(m)*, however that the quantity

$$C(m) = [A(m)^2 + B(m)^2]^{1/2} \tag{4.7}$$

is independent of the phase angle (Dexter 1985). C(m) is the Fourier spectrum value used in Figure 4.3. The Fourier spectrum of the radius vector specifies the shape of the 2-D profile exactly.

The other method used was the curvature spectrum of Davis and Dexter (1972). Unlike the Fourier spectrum of the radius vector the curvature spectrum is not dependant on the radius being a single-valued function of the angle, θ. As was noted in section 2.5, the perimeter of a circle has only curvature whereas irregular shapes will have different curvatures. This method requires the perimeter of the particle profile to be divided into N points which are equally spaced and whose x,y coordinates can be determined. The angle $\emptyset_n$ is the slope of the perimeter between any 2 points n and n+1 where

$$\emptyset_n = \arctan\left(\frac{Y_{n+1} - Y_n}{X_{n+1} - X_n}\right) \tag{4.8}$$
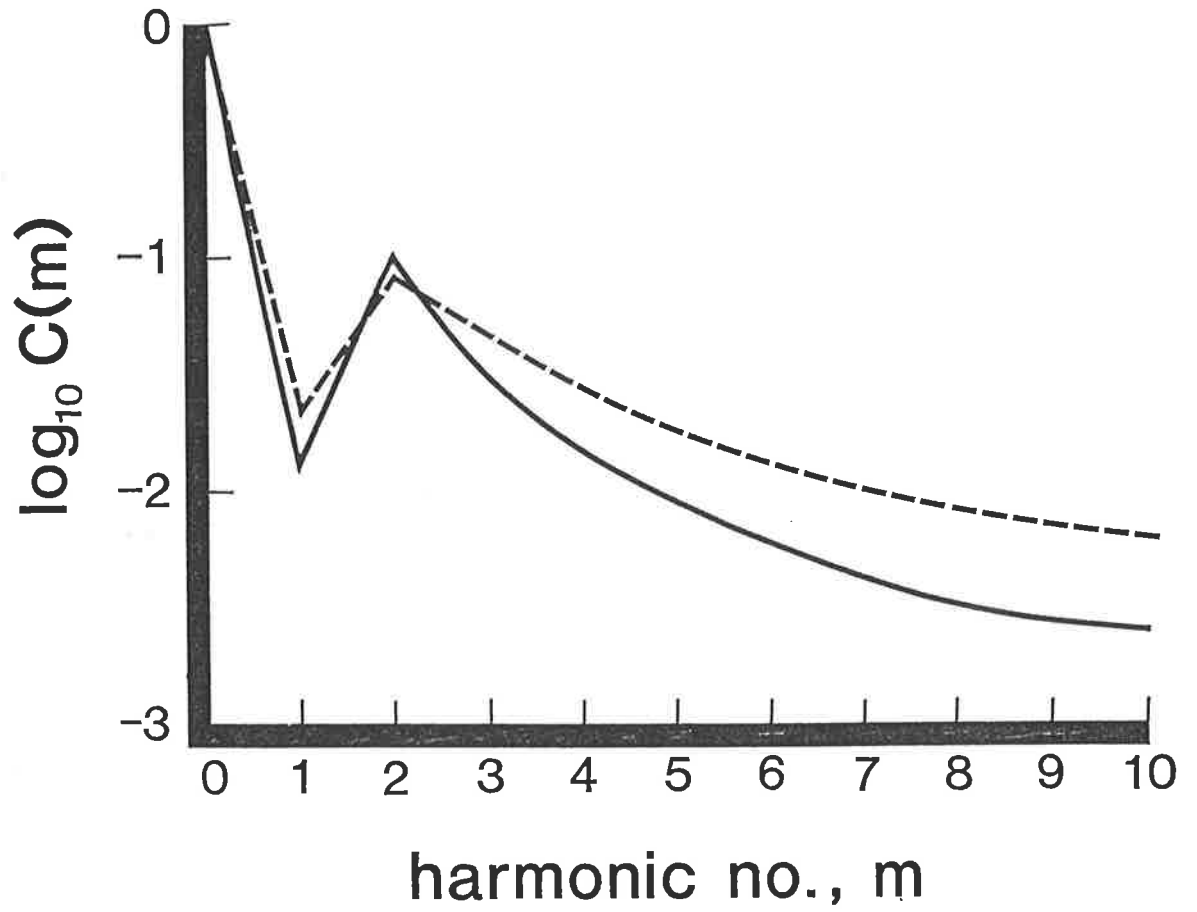
Fig. 4.3 Plots of the normalized radius spectra (C (m)) against the harmonic number (m). Curves are the envelopes of the mean, smooth, discrete values for casts from *A. rosea* (*solid line*) and the similar size aggregates of Urrbrae loam (*broken line*).

A curvature measure in terms of the difference between 2 consecutive segments is

$$fn = e^{i(\emptyset n+1 - \emptyset n)} - 1 \qquad (4.9)$$

The discrete Fourier transform of fn is then calculated from

$$F(k) = \sum_{n=0}^{N-1} fn.e^{-2\pi ikn/N} \qquad (4.10)$$

The discrete curvature spectrum, S(k), as shown in Figure 4.4, is obtained by multiplying equation 4.10 by its complex conjugate :

$$S(k) = F(k) \times F(k)^* \qquad (4.11)$$

(Dexter 1985). For a regular polygon S(k) takes equal finite values at the apexes and is zero for other values of k (Davis and Dexter 1972).The curvature spectrum is very sensitive to particle shape.

4.1.3. Results and Discussion

The three ratios for casts and aggregates are shown in Table 4.1. The values shown are correct and amend a minor typographical error in a previous publication (McKenzie and Dexter 1987 see Appendix 1). The roundness value is the only ratio method to show significant difference between the shape of casts and soil aggregates. The significantly larger roundness value implies that the casts are nearer spherical than aggregates assuming that their two dimensional description can be generalized to the third dimension. While this is believed to be the case for sand sized quartz grains (Tilmann 1973), I have found no consideration for this being appropriate to composite soil particles. It is surprising that the roundness value is the
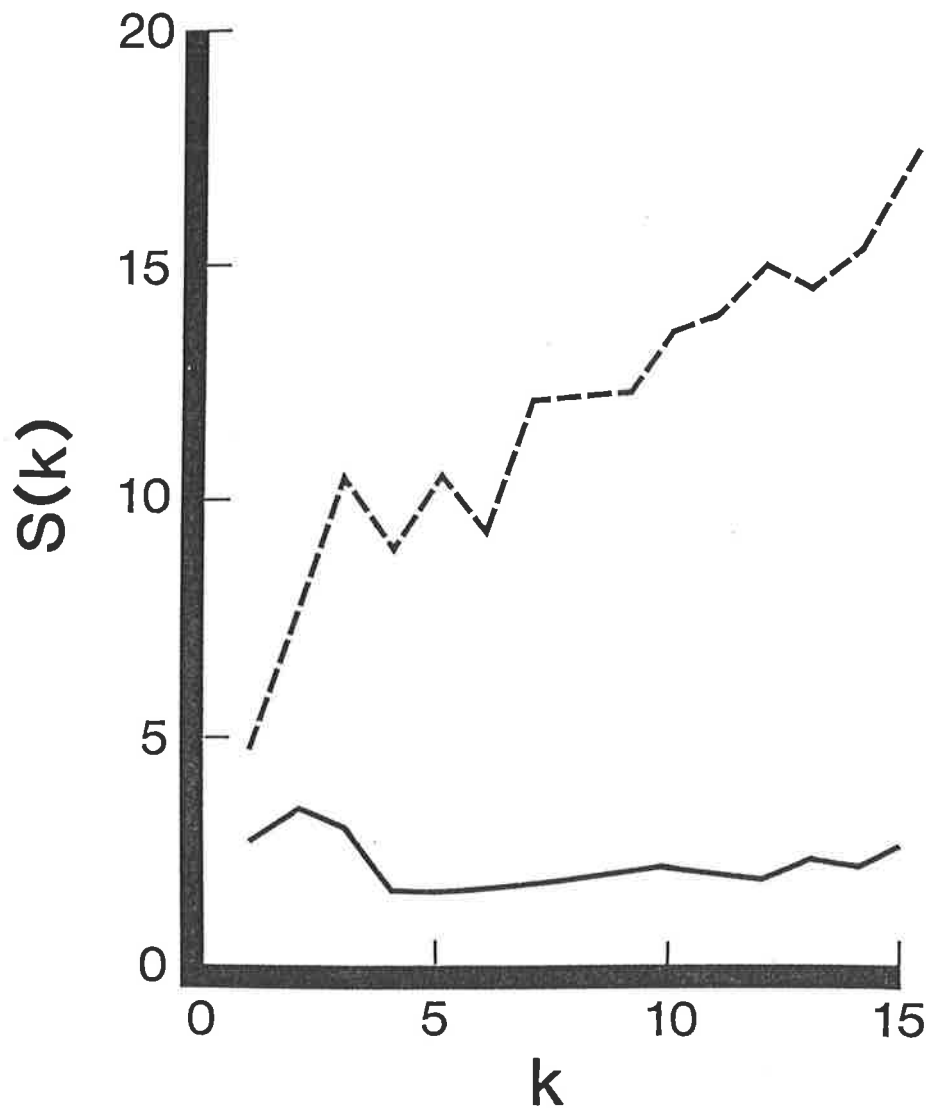
Fig. 4.4 Plots of the curvature spectra (S (k)) for different values of k. *Curves* are the envelopes of the 3-point running mean, discrete values for casts from *A. rosea* (*solid line*) and the similar-sized aggregates of Urrbrae loam (*broken line*).

Table 4.1

Roundness and aspect ratios of casts and similar sized field aggregates.

	Casts	Aggregates
Roundness*	0.795 (.019)	0.650 (.014)
AR_r	0.716 (.039)	0.717 (.028)
AR_s	0.705 (.038)	0.649 (.026)

Figures in parenthesis are SE's.

*Roundness figures are significantly different at the $p < 0.01$ level

only ratio technique to show differences between casts and aggregates in view of the statement by Dexter (1985) that the roundness was the least sensitive ratio for aggregates. The applicability of the roundness method may become less clear with improved resolution of scanning techniques. This is because as the definition of the perimeter increases so will the calculated perimeter length, altering the measurement. As was noted by Dexter (1985) the shortest aspect ratio is the superior aspect technique by virtue of the smaller relative standard errors. By definition the values of the shortest aspect ratios are smaller than those of the right angle aspect ratios.

However these ratio techniques do not account for irregularities on the edges of particles, nor are they a complete definition of the particle shape. The radius spectra, Figure 4.3 and the curvature spectra, Figure 4.4 both show that casts are rounder than aggregates of similar size. For the curvature spectrum regular shapes, eg regular n-gons, appear as evenly spaced peaks separated by $k = n$.

The casts used in this work cover a number of the shape classes described by Bal (1973) including both spheres and amoebo-spheres, ellipsoids and bacillo and clonocylinders. Neither platy nor mitoid forms were observed. Within the size classification scheme of Barratt (1969) as modified by Bal(1973), the wet casts were all greater than 2.5 mm along their longest axis. Bal's size classification scheme used dry casts as this was the state in which thin section work is performed. He suggested that dry excrements were typically two-thirds as long as moist casts, along their major axis. Applying this factor to the casts here places them as either macroexcrements or coarse microexcrements.

When classifying modexi (or casts) Bal (1973) noted that the shape may be transformed as a result of ageing and used the terms weakly, moderately and strongly to describe the amount of breakdown. The spectra measurements described above could be used to obtain quantitative values for the amount of transformation if the initial modexi were known. Thus the techniques described here could be used to study the breakdown of casts in the field and consequently the importance of physical processes leading to their eventual demise could be estimated. Further, the shape of modexi as well as their relative numbers

could lead to an assessment of the activity and numbers of earthworms, or other soil fauna species, involved in soil modification.

The availability of computers with a level of artificial intelligence capable of recognizing shape combined with quantification of shape (as described here) opens the possibility to assess the amount of biologically modified material in thin sections or in electron micrographs. This type of approach could be applied not only to casts, but over a large size range of material. For example : Sullivan and Koppi (1987) noted torus-shaped clay-coated fungal spores or bacterial cells of 1-7 μm in scanning electron micrographs. If shape definition was applied it would be easier to estimate the frequency and distribution of such objects in samples.

4.2 Strength

4.2.1. Introduction

The shape of soil aggregates influences a wide range of soil properties. With time, aggregates will be broken down by natural and man-made forces. Many researchers (Swaby 1950, Jeanson 1960, Rhee and Nathans 1961) have found cast material to be more resistant to breakdown by water than aggregates which have not been recently biologically influenced. This increased stability has been associated with the increased organic matter content, binding the primary particles in the cast with bacterial gums and fungal hyphae. It may also be due to homogenization of the material during cast formation resulting in reduced stresses from fewer incongruities. Increased stability of casts as measured by dispersion in sodium solutions was found to reach a maximum after about 15 days and then decline to reach par with the bulk soil after approximately 1 month. (Emerson 1954).

Soil aggregates in the field may be subjected to physical breakdown as well as dispersion. The physical strength of casts will determine their reactions to treading by animals, compaction by vehicles and raindrop impact. The physical strength of casts has not been examined previously.

4.2.2. Material and Methods

For tensile strength determinations, adult earthworms (*A. rosea*) were placed in soil at known matric potentials. For the range of potentials -1 to -10 kPa this was done by placing the earthworm in soil on a sintered glass funnel as described above. For the more negative potentials (-30 and -50 kPa) the soil was equilibrated using a pressure plate apparatus and then placed in sealed tins along with earthworms. Every 2 to 3 days the tin lid was removed briefly to allow air exchange. After 10 days the earthworms were removed from the funnels and tins and the soil left for a further 5 days. This time was selected to permit all casts adequate time for age hardening. Utomo and Dexter (1981) found after 5 days of ageing that there was little further change in the penetrometer resistance of Urrbrae loam. The soil was then removed onto trays and the casts carefully sorted using a fine brush. The casts obtained were allowed to dry for 24 hours, then oven dried at 105°C for 24 hours.The size of the casts was measured, using vernier calipers, to within 0.05mm.

Tensile strengths of the casts were measured using the indirect tension or crushing test (Rogowski and Kirkham 1976) for small or weak aggregates as described by Dexter and Kroesbergen (1985). Briefly, this involves placing the sample on a top loading balance. The balance was itself mounted on a jack, which could be raised or lowered by turning a handle. In this case the jack was part of a loading frame of the type commonly used for triaxial cell tests. As the jack and balance are raised the sample presses against a flat metal plate, which is parallel to the pan on the balance. The balance scale was watched as the jack was raised and failure of the aggregate is detected by a sudden drop in the balance scale reading. The maximum reading on the balance scale is the crushing force, from which the tensile strength can be calculated using the equation

$$Y_c = \frac{0.576\ F}{D^2} \tag{4.12}$$

where F is the crushing force in Newtons and,

D is the particle diameter in metres.

Thus the tensile strength is measured in Pa. At least 15 casts were crushed from soil at each matric potential. As a comparison 20 aggregates were collected from the bulk soil (in the field) and crushed after air and oven drying. The same aggregates which had been photographed for shape analysis were used for tensile testing.

4.2.3. Results and Discussion

Implicit in equation 4.7 is the assumption that the casts and aggregates are spherical. As was seen in Table 4.1, two-dimensional views show the casts as nearly circular, having roundness values approaching unity. As was noted in section 4.1.3 the values of the third dimension are not determined

Figure 4.5 shows the relationship between the matric potential at which the casts were produced and the tensile strength of the dried casts. Potentials more negative than -50 kPa were tried but the earthworms went into a state of anhydrobiotic quiescence. While this is a less negative potential than reported for some species to become inactive in the field (Lee 1985), laboratory conditions may not favour activity. It is apparent that the tensile strength of casts is greater than the strength of similar sized aggregates irrespective of the potential at which the casts were generated. Swaby (1950) attributed increased stability of casts to microbial gums produced by bacteria or hyphae from the worm gut. Using the method of McIntyre and Stirk (1954) the density of sub-samples of the dry casts and aggregates were determined. The casts had a density of 1.67 t m^{-3}, while the aggregates were found to have a density of 1.51 t m^{-3}. It is known that an important factor determining the tensile strength is the inclusion of inhomogeneities and that fracture surfaces are often formed by linking these inhomogeneities (Braunack et al 1979). Thus it is not surprising that the stronger material, the dry casts, are also more dense.

Over the range -1 to -30 kPa matric potential, the tensile strengths of casts do not differ significantly. At -50 kPa matric potential a significant increase in tensile strength is

Over the range -1 to -30 kPa matric potential, the tensile strengths of casts do not differ significantly. At -50 kPa matric potential a significant increase in tensile strength is observed. The mean mass of the dry casts used for the strength determination was 0.0055 g (SE 0.0002). The mean length along the principal axis of the cast was 2.20 mm (SE 0.025). There was no change in the estimated dry cast density with matric potential at which they were formed, so the increased strength at the most negative potential was not due to density differences. The tensile strength increase may be caused by a modification in water extraction from the soil in the gut at larger negative potentials, however physiological experimentation would be required to test this.

Lee (1959 a) drew attention to management problems when large numbers of surface-casting earthworms were very active in pastures in New Zealand. Treading by grazing animals caused the accumulated surface layer of casts to compact, burying the crowns of pasture grasses and resulting in the death of plants. The model for the compaction of beds of soil aggregates by Braunack and Dexter (1978) can be used to estimate the reduction in height of a bed of aggregates during compression. This model is

$$\frac{H}{H_i} = 0.4 + 0.6 \exp \left[0.017 \left(\frac{U}{Y}\right) - 0.38 \left(\frac{U}{Y}\right)^{0.5} \right] \qquad (4.13)$$

where H is the sample height at pressure P,

H_i is the initial height of the bed of casts,

Y is the tensile strength of the aggregates comprising the bed and,

U is the applied uniaxial pressure.

If the pressure applied by the hooves of sheep is estimated at 80 kPa (Willatt and Pullar 1983) and the tensile strength of dry casts is taken at 10 kPa (Figure 4.5), then equation 4.8 shows the final height of the bed will be 0.63 of the initial height. The same method of calculation can be applied to beds of aggregates with a tensile strength of approximately 4 kPa (Figure 4.5). In this case the final height of the bed will be 0.55 of the initial height. Thus the increased
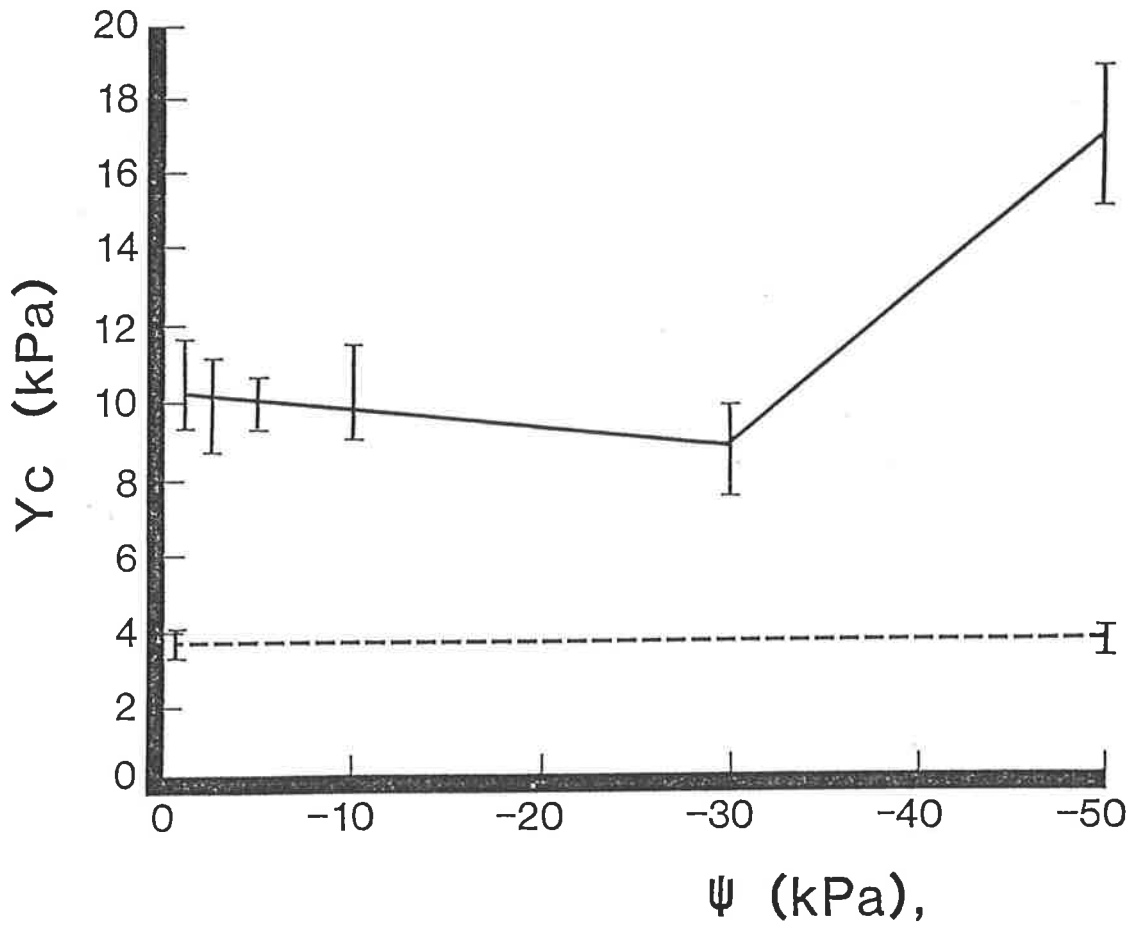
Fig. 4.5 Tensile strength (Y_c (kPa)) of dry casts from *A.rosea* (*solid line*) as a function of the matric potential (Ψ (kPa)) of the bulk soil from which the casts were produced. The tensile strength of aggregates collected from the field and then dried (*broken line*) are shown for comparison. *Error bars* are 2x standard errors.

4.3 Forces in production of casts

4.3.1 Introduction

In the previous sections (4.1 and 4.2) I have demonstrated some differences between soil influenced by earthworms and the bulk soil. Other differences have been reported, including the physical composition of casts. Barley (1959 b) and Lee (1967) have noted that casts had a higher percentage of clay and silt sized particles and lower sand percentages than the bulk soil. This is presumably due to selective grazing by the earthworms. Bolton and Phillipson (1976 a) found that the size of soil mineral particles in the gut of earthworms varied proportionally with the size of the worm. Also increased organic matter percentages in casts are well documented (Graff 1971, Czerwinski et al 1974 and Syers et al 1979).

From the perspective of physical properties of soils these differences seem unlikely to explain major changes observed. It seemed likely that as the soil passed through the gut of the earthworm changes in the physical structure occurred. As was stated in section 2.1, two muscle layers around the gut of the earthworm move the ingested material from the mouth to the anus, grinding the food in the process. These two muscle layers are distinct from the two muscle layers around the circumference of the worm which are responsible for locomotion. Grinding or shearing of the food is part of the digestion process and is aided by the ingested mineral particles. This grinding will presumably expose organic material trapped between or bonded to soil mineral particles. That shearing of soil increases its void ratio (or porosity), is well known and is one reason for tillage.

Croney and Coleman (1954) found a unique relationship between the water content of a continuously disturbed soil and its matric potential. In saturated soil this potential is equivalent to an external pressure on the soil. Critical state soil mechanics (Schofield and Wroth 1968, Leeson and Campbell 1983) shows a unique relationship between the specific volume of a soil which is being sheared and the spherical pressure applied (Figure 4.6). This results from soil being compressed with minimal energy expenditure when it is also being sheared. Whenever soil is sheared it will be somewhere along the critical state line. Thus with
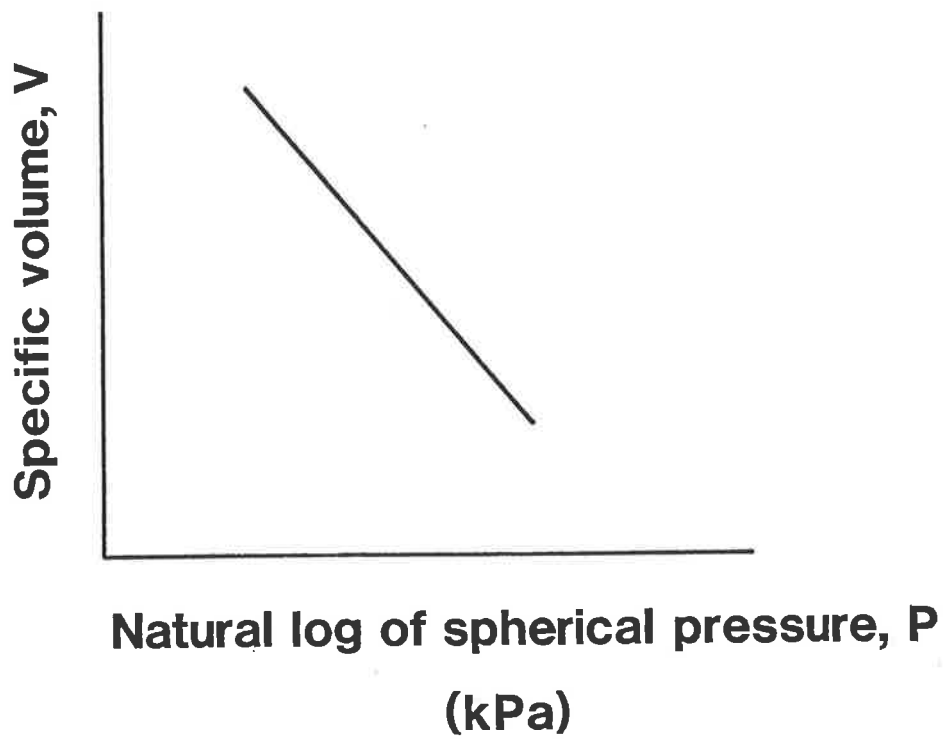
Fig. 4.6 Standard form of the Critical State Line.

the assumption that freshly excreted soil has recently been sheared it is possible to calculate the maximum pressure applied to the cast during shear. The relationship between undrained soil shear strength and the gravimetric water content of saturated soil was also determined to imitate the shear strength of fresh cast material.

4.3.2 Materials and Methods

The soil used in these experiments was the Urrbrae fine sandy loam described in detail in section 3.1.2. A 1.5" (inch) diameter triaxial cell apparatus was used in the initial attempts to determine the critical state line. As the remoulded soil that is cast material was hypothesized to have a high voids ratio, the soil samples used in the triaxial apparatus were remoulded at water contents in excess of the soil plastic limit. To avoid hydrostatic pressure build up which would alter the relationship between axial load and axial strain, and hence the soil properties at failure, drained tests were performed.

The time taken for a drained test to reach failure is defined by Bishop and Henkel (1957) as

$$t_f = \frac{20\ h^2}{h\ c_v} \qquad\qquad (4.14)$$

where t_f is the requisite time to failure in minutes,

   h is one-half the sample height in inches,

   c_v is the coefficient of consolidation and,

   h is a factor depending on the drainage conditions at the sample boundaries.

In the triaxial tests performed for this work h = 0.75 since drainage was from one end only. The coefficient of consolidation was calculated from a plot of the sample volume change against the square root of the time in minutes, using extrapolation of the initial portion of the plot which is a straight line for all drainage conditions (Figure 4.7). Extension of the straight
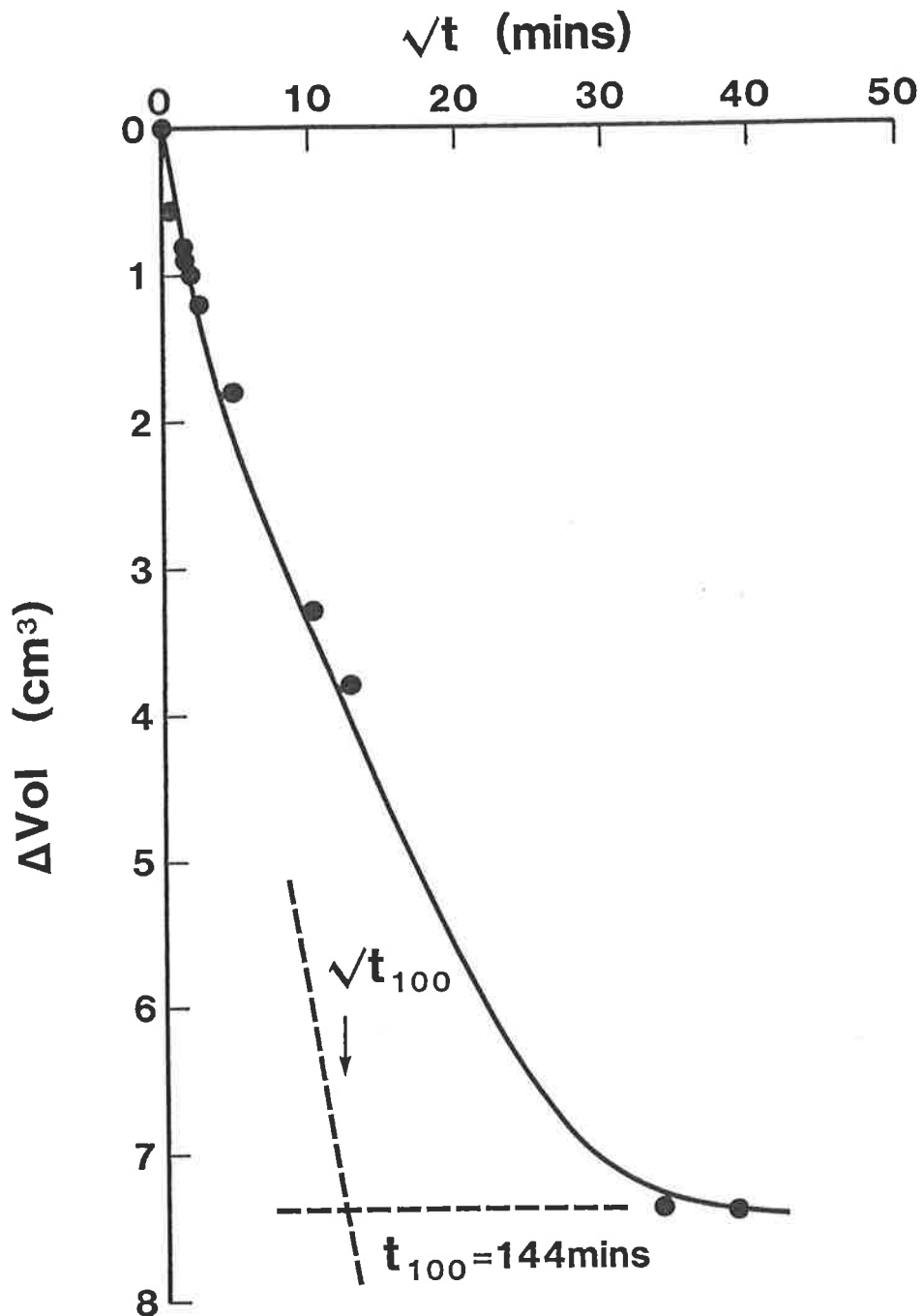
Fig. 4.7 Relationship between the volume change and the √time for a sample of Urrbrae loam during consolidation under an all round pressure. The intercept of the straight line portion produced gives t_{100} = 144 mins, where it cuts the the line representing 100% consolidation.

line portion to cut the line representing 100% consolidation, the time intercept of this point, (t_{100}), is related to c_v for drainage at one end only by

$$c_v = \frac{\pi h^2}{t_{100}} \qquad (4.15)$$

Thus,

$$t_f = \frac{20 t_{100}}{h \pi} = 1222 \text{ mins.} \qquad (4.16)$$

The moulded soil, of known water content, was tested in a 1.5" triaxial cell apparatus mounted on a Wykenham-Farrance, motor driven load frame. The rubber membrane was fitted with filter-paper side-drains, draining to the base. The volume change was measured by connecting the drain to a volumetric burette. Strain rates were approximately 1 mm/day resulting in failure times in excess of 5 days. This is well in excess of the minimum time for failure. In all cases failure was plastic. After failure the gravimetric water content and the bulk density of the sample were determined. Density measurements were performed by weighing and displacement of liquid after coating the sample in a thin film of Saran resin.

From the stress-strain graphs the axial load which is the major principal stress (σ_1)is known. The minor principal stresses (σ_2 and σ_3) were controlled for each test. Fourteen tests were performed using initial water contents ranging from 23 to 38%. Critical state theory relates the spherical pressure, P, and deviatoric stress, R, to specific volume, V. These parameters are defined in Hettiaratchi and O'Callaghan (1980) and in Leeson and Campbell (1983) as

$$P = \frac{\sigma_1 + \sigma_2 + \sigma_3}{\sqrt{3}} \qquad (4.17)$$

$$R = \sqrt{\left[\frac{(\sigma_1 - \sigma_2)^2 + (\sigma_1 - \sigma_3)^2 + (\sigma_2 - \sigma_3)^2}{3} \right]} \qquad (4.18)$$

$$V = \frac{\rho}{D_{bd}} \tag{4.19}$$

where σ_1, σ_2, and σ_3 are the principal stresses,

ρ is the density of the soil particles and,

D_{bd} is the dry bulk density of the soil.

"The critical state line (CSL) plotted in three dimensions with the axes defined as P,V and R is a locus of points and represented as the maximum deviatoric stress, R, which the soil can withstand at various combinations of spherical pressure and specific volume. As the mode of failure is dictated by the path of approach to the CSL the plastic failure experienced in this work indicates that from sub-critical domain or "wet side. Plotting the CSL in two dimensions against V and $\log_e P$ axes results in a straight line (which is parallel to the virgin compression line.)

Croney and Coleman (1954) found a unique relationship between the water content of a continuously disturbed soil and its matric potential. In saturated soil this potential is equivalent to an external load on the soil. This relationship was determined for the Urrbrae soil with a small tensiometer calibrated with a mercury manometer. Wet soil was placed in a small mixer and moulded. As soon as mixing ceased the tensiometer was inserted and a sample of the soil was taken for gravimetric water determination. The tensiometer was a hypodermic needle connected via an oil-filled plastic tube to a transducer and LED read-out. The needle was inserted through a septum (Suba Seal) into a water-filled porous ceramic tube approximately 6 cm long and sealed at the end. The ceramic tube had been de-aired by immersion in water under reduced air pressure. A steady measurement of matric potential was obtained within about 3 minutes of cessation of mixing.

The undrained shear strength of the remoulded bulk soil was determined using a Geonor G-200 fall cone penetrometer apparatus as in the methods of Hansbo (1957) and Towner (1973). (The fall cone penetrometer should not be confused with conventional penetrometers referred to earlier.) The method involves releasing a cone of known weight and dimensions, from a framework, above a soil sample. The depth of penetration into the soil by

the cone is measured after a known time, in this case 5 seconds. The fall cone device relates the undrained shear strength, tf (Pa), to the depth of penetration , h (mm) of a cone into the soil by the equation

$$tf = \frac{KQ}{h^2}$$
(4.20)

where Q (g) is the weight of the cone, which in these cases was 100, 80, 60 or 10 g, and K is the coefficient dependent on the cone angle ß. For the heavier cones, ie 100 and 80 g where the cone angle is 30°, K for a sandy loam takes the value of 1.6×10^4 (Towner 1973). For the lighter cones with cone angle of 60°, tf was taken directly from tables for disturbed soil given in Hansbo (1957) and the cone manufacturer's handbook (Geonor). For each cone penetrometer reading, the soil gravimetric water content was determined enabling the shear strength to be directly related to the water content.

The dry bulk density and the voids ratio of the "wet" casts were determined as follows : Earthworms were kept in soil on sintered glass funnels as previously described. Casts from the hand-held earthworms were excreted onto a pre-weighed slide which was then transferred to a cradle hanging below a balance (Figure 4.8). Kerosene in a beaker was raised by a moveable platform to a set height around the cradle and the change in balance reading noted. The density of kerosene and the displacement of the cradle and slide had been determined previously. Thus the volume of the wet cast was found by subtraction. The cast was then oven-dried and the dry weight taken to establish the gravimetric water content. The wet casts appeared saturated and no air was seen to leave the casts when in the kerosene.

4.3.3. Results and Discussion

Since standard triaxial tests as used here have $\sigma_2 = \sigma_3$ then

$$R = \sqrt{\frac{2(\sigma_1 - \sigma_3)^2}{3}} = 2\sqrt{\frac{2(\tau_s)^2}{3}} = 1.63 \ \tau_s$$
(4.21)
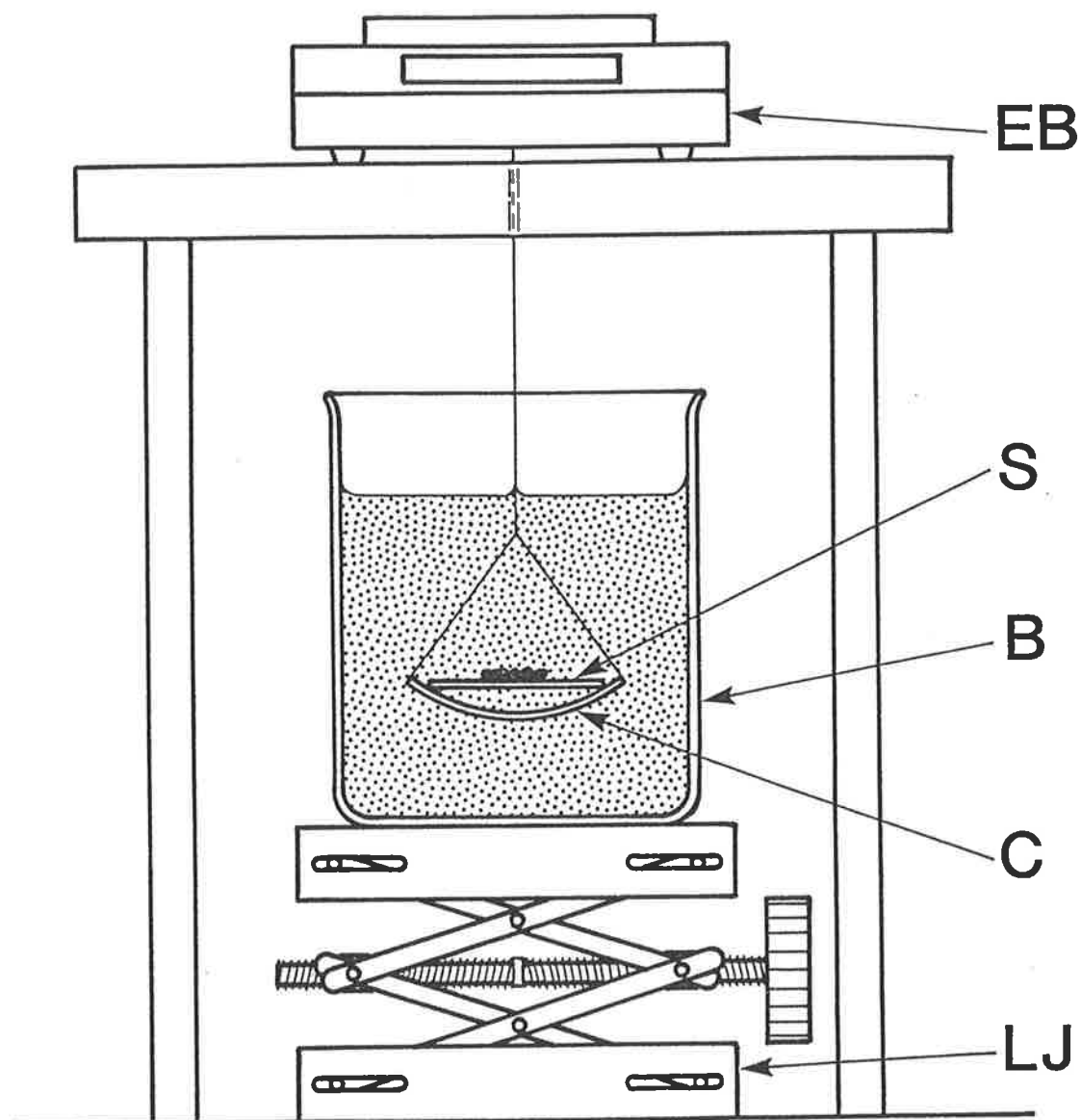
Fig. 4.8 Volume determination for fresh earthworm casts. A pre-weighed slide (S) onto which which an earthworm cast has been excreted rests on the cradle (C), which is attached by a free line to the electronic balance (EB). Kerosene in the beaker (B) is raised around the cradle by means of the laboratory jack (LJ).

where τ_s is the commonly used shear stress. Mohr circles from the triaxial test results of Urrbrae loam are shown in Figure 4.9. The angle of internal friction is estimated on the graph as approximately 35° and the cohesion as approximately 3 kPa for final water contents ranging from 19.6 - 24.6% gravimetric. These values are comparable to those of Farrell and Greacen (1966) who determined friction angles of between 35 and 40° and cohesion values increasing from 9 kPa for the same soil at water contents of 20.9%. The equipment used was similar in both cases but the strain rates I employed were approximately 0.002 times their rate as my samples were saturated and because of the time required for drainage. Table 4.2 presents the the principal stresses, spherical pressures, deviatoric stress and specific volume of the samples. The particle density used to calculate the specific volume is 2.65 tm^{-3} for the Urrbrae loam (Turchenek 1975).

The projection of the CSL onto the P,V plane is shown on Figure 4.10. This should be a straight line with negative slope, which if the sample is saturated will be parallel to the virgin compression line. From the determination of the voids ratios it is apparent that not all the samples were saturated when failure occurred. Lines fitted to relate the specific volume and spherical pressure data are of dubious integrity as the residual variance exceeds the variance of the specific volume. The best fit was

$$V = 1.709 - 0.011 \, \mathrm{Log_e}(P), \qquad\qquad (4.22)$$

where V and P have been previously defined as the specific volume and the spherical pressure, respectively. As reasons could not be established for the failure to determine a satisfactory CSL and because the length of time required to run each test was considerable, the alternative of the Croney-Coleman method was pursued.

The relationship between the gravimetric water content, w%, and the matric potential, Ψ (Pa), of the freshly-moulded soil as determined with the rapid response tensiometer is
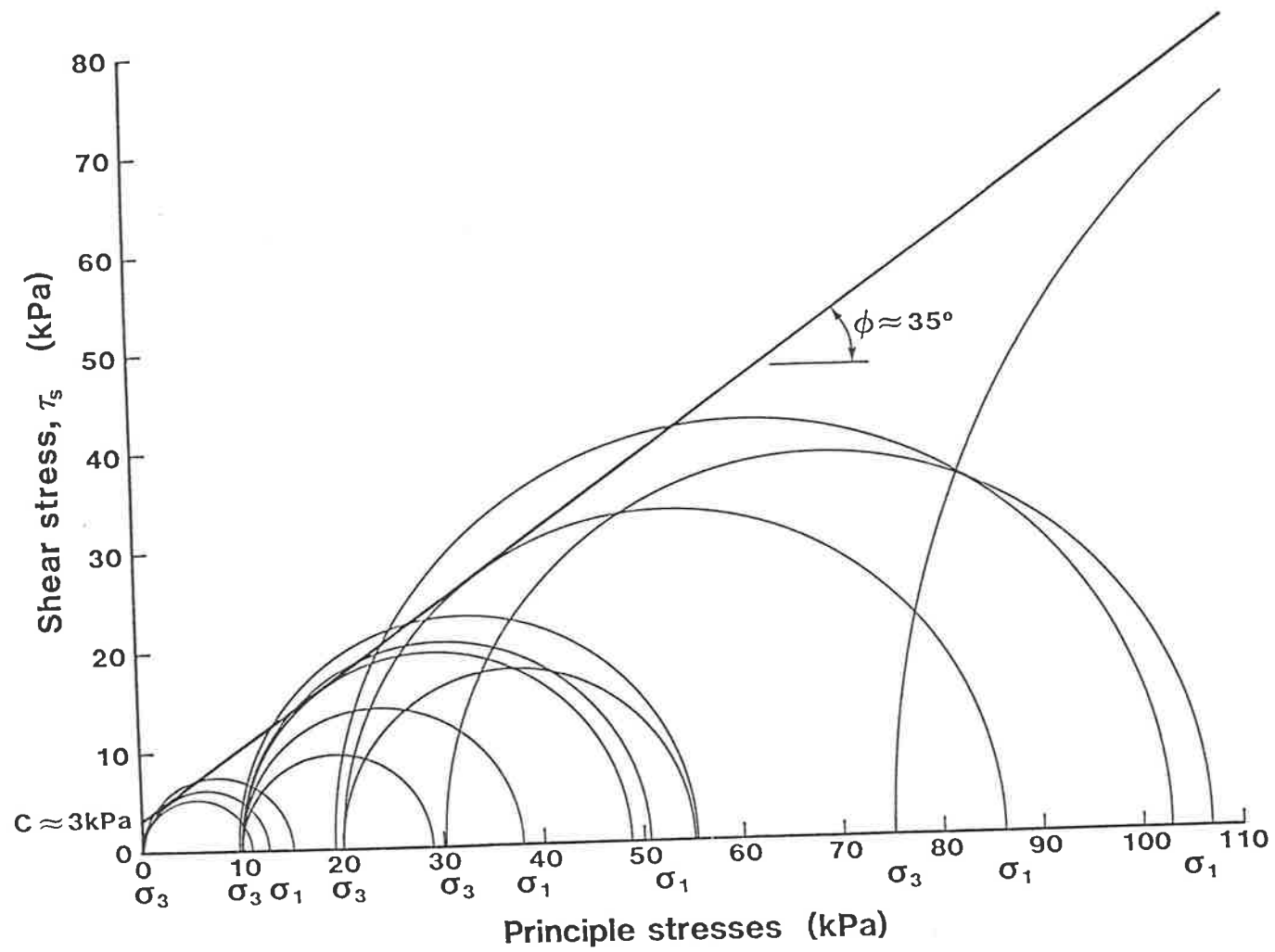
Fig. 4.9 Mohr circles of the Urrbrae loam (cohesion approximately 3 kPa, angle of internal friction 35°).

Table 4.2   Triaxial Cell Results

σ_1 (kPa)	σ_3 (kPa)	P (kPa)	Ln (P)	R (kPa)	D_{bd} (t m^{-3})	V	wc_i (%)	wc_f (%)	wc' (%)
10.7	0.0	6.18	1.82	8.74	1.585	1.65	27.3	24.3	25.8
12.6	0.0	7.27	1.98	10.29	1.583	1.67	27.3	24.3	25.8
14.3	0.0	8.26	2.11	11.68	1.490	1.78	31.0	24.6	29.3
15.0	0.0	8.66	2.16	12.25	1.67	1.59	23.0	19.6	21.3
28.7	10.0	28.12	3.34	15.27	1.607	1.65	27.3	21.4	24.5
37.8	10.0	33.37	3.51	22.70	1.485	1.78	38.4	23.2	29.6
48.4	10.0	39.49	3.68	31.35	1.546	1.71	31.5	22.4	27.0
51.1	10.0	41.05	3.71	33.56	1.586	1.67	23.0	20.7	21.9
55.4	10.0	43.53	3.77	37.07	1.583	1.67	27.0	22.1	25.4
54.8	20.0	54.73	4.00	28.4	1.620	1.64	27.3	21.0	24.0
86.1	20.0	72.80	4.29	53.97	1.55	1.71	31.2	22.4	26.6
103.6	20.0	82.91	4.42	68.26	1.60	1.66	23.0	20.0	21.5
106.8	30.0	96.30	4.57	62.71	1.639	1.62	27.7	20.1	23.3
267.6	75.0	241.10	5.49	157.30	1.648	1.61	27.0	20.0	22.9
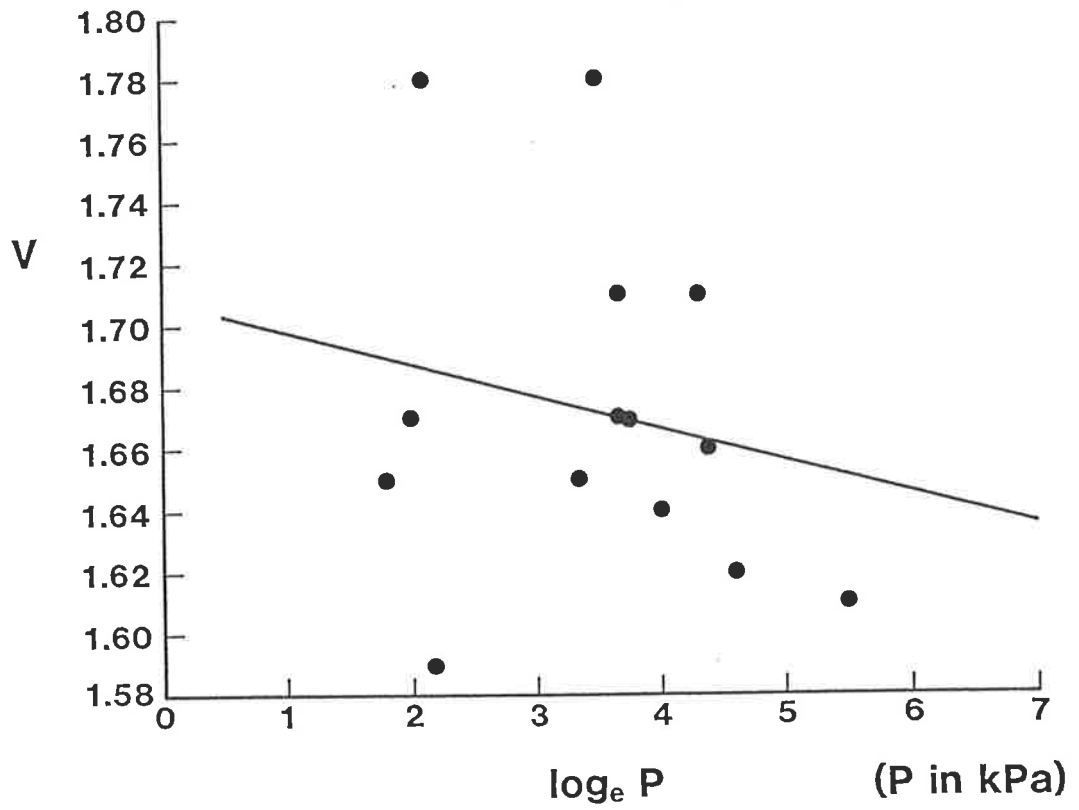
Fig.4.10 Projection of the Critical state Line onto the P-V (Spherical Pressure, Specific Volume) plane.

$$\log_e |\Psi| = 13.58 - 0.300 \text{ w\%} \qquad (4.23)$$

$$(0.37) \quad (0.017)$$

with 96% of the variance accounted for, (Figure 4.11). Similar responses were first reported by Croney and Coleman (1954). Values in parenthesis are standard errors. Similarly the relationship between the undrained soil shear strength, τ (Pa), and the gravimetric water content determined by the drop cone method of Hansbo (1957) is

$$\log_e |\tau| = 19.24 - 0.520 \text{ w\%} \qquad (4.24)$$

$$(1.10) \quad (0.042)$$

with 80.6% of the variance accounted for, (Figure 4.12). Four weights of cone were used to determine shear strength, over the range of water contents. Where possible more than one cone weight was used on each sample. Agreement between cone readings, and between the calculated and tabulated shear strengths was good. Small variations were found at the extreme ranges for particular cones and these are likely to be responsible for some of the unaccounted variation. As the soil used to determine the relationships between the matric potential and the shear strength with water content was in a remoulded state, achieved by a mechanical mixing, inclusion of some air was inevitable. The volume of air as a fraction of the total soil volume, calculated by subtraction of the solid and liquid volumes from the total volume was typically 5%.

Fresh casts collected from earthworms (*A. rosea*) in soil at a matric potential of -5.0 kPa had a mean dry bulk density of the wet casts of 1.15 (SE = 0.06) tm^{-3} and a mean gravimetric water content of 32.0 (SE = 2.9)%.

By substituting each individual water content for each cast into equation (4.17) a mean value of $|\Psi| = 259$ (SE = 93)Pa is obtained. Thus the mean maximum pressure applied to soil as it passes through the gut of the earthworm (*A. rosea*) is 259 Pa. The highest individual pressure achieved was 742 Pa for a cast with 23.2% gravimetric water content. It must be noted that as equation (4.18) is logarithmic, the substitution of the mean water content gives
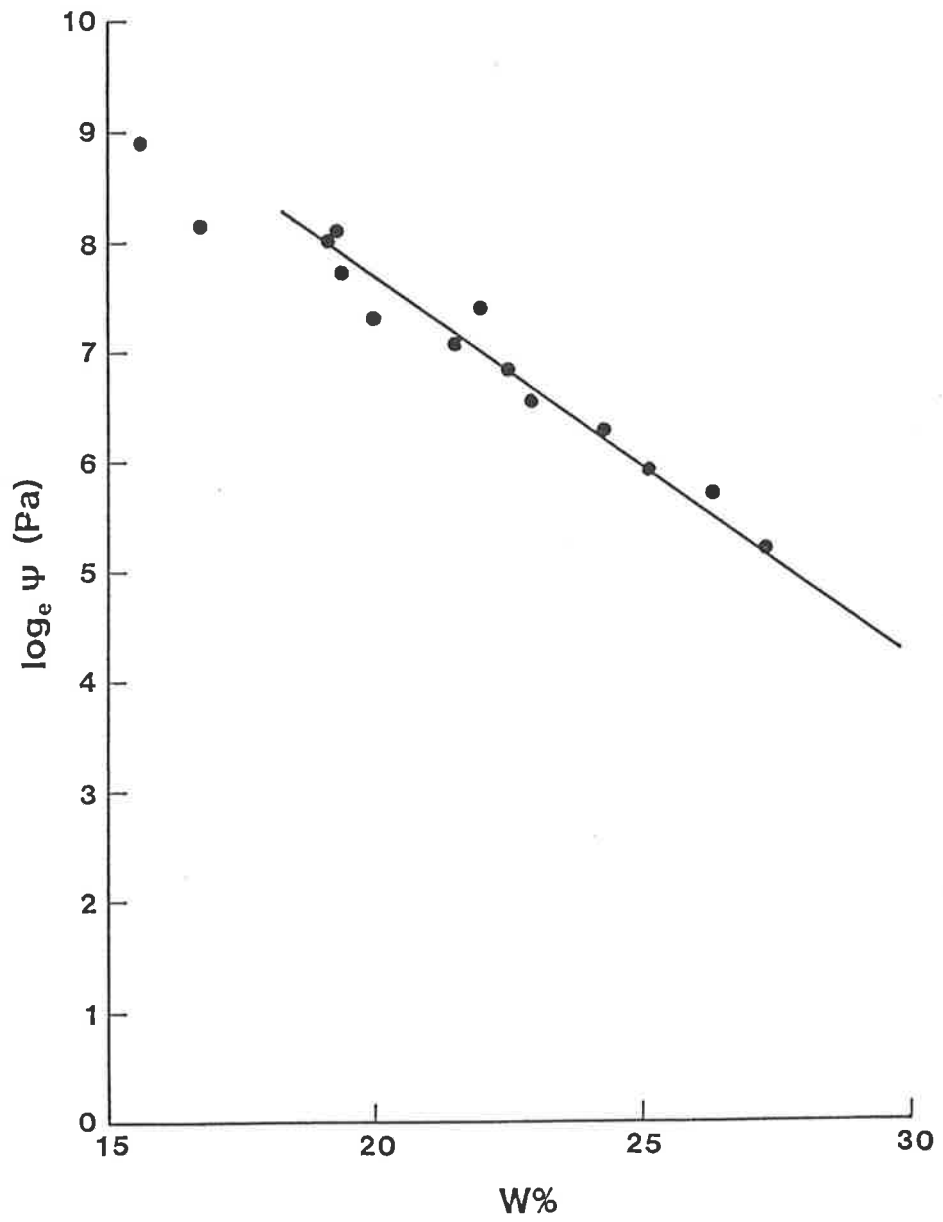
Fig. 4.11 Relationship between the gravimetric water content, w%, and the matric potential, Ψ (Pa) for freshly-moulded Urrbrae loam.
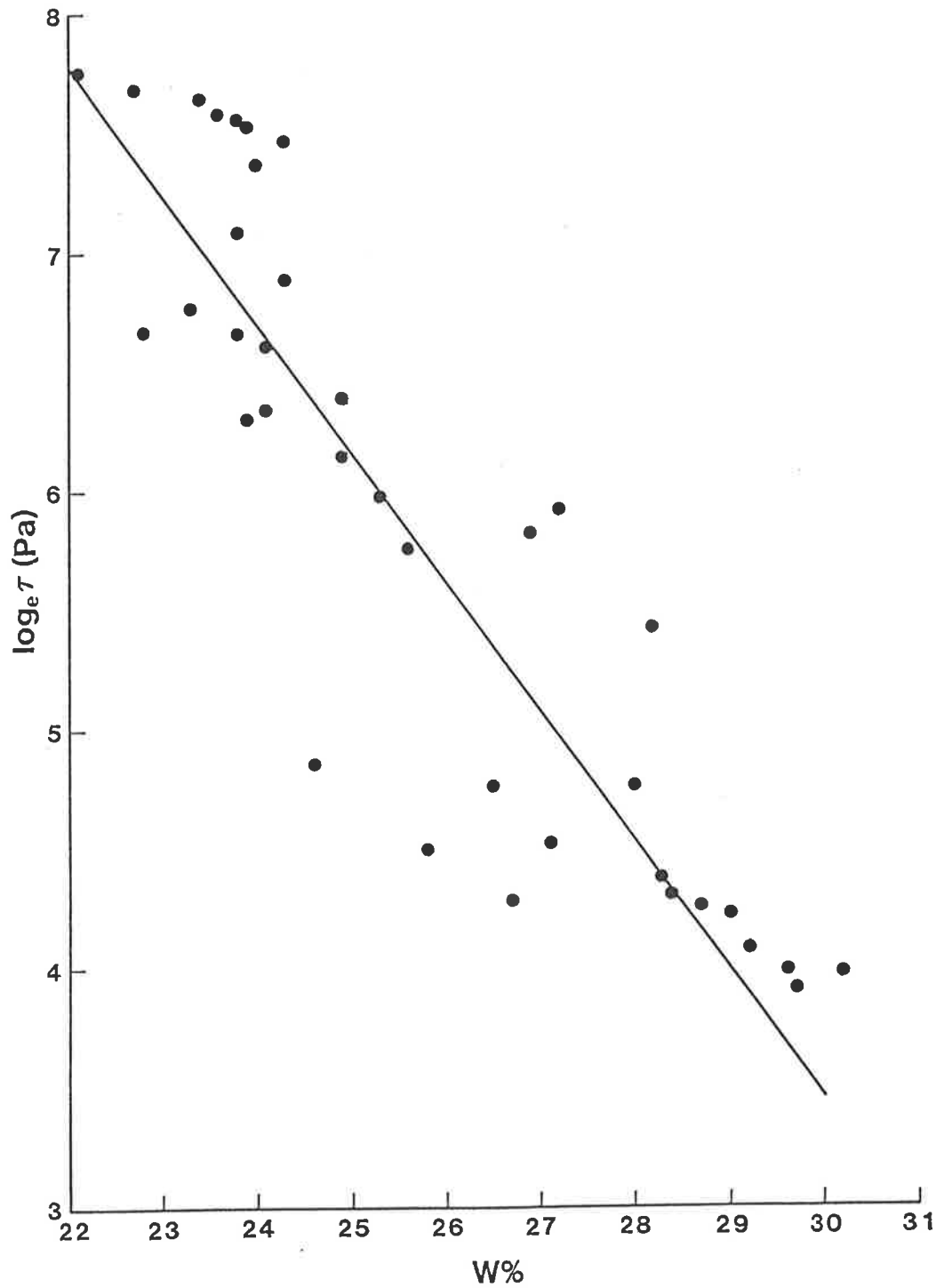
Fig. 4.12 Relationship between the undrained soil shear strength τ (Pa) and the gravimetric water content, w%, determined using the drop cone method.

the geometric mean rather than the arithmetic mean of the pressures. The pressure values achieved in the coelom of earthworms (*L. terrestris*) were estimated at < 200 Pa by Trueman (1978) for resting worms, at 1.6 kPa in segment 28 of active *L.terrestris* and 0.8 kPa near the tail region of *L. terrestris* by Newell (1950). Thus even for different species it appears that the pressure in the coelom is of similar magnitude to the maximum pressure on the ingested soil as it is moulded.

Newly formed casts of *A. rosea* are predicted to have extremely low shear strengths from equation (4.18). Again due to the non-linearity of the equation the predicted value of 364 (SE 163) Pa is the mean for individual casts after substitution into the equation rather than the value obtained by substitution of the mean water content. The maximum shear strength for a fresh individual cast is estimated at 1310 Pa. These pressures exerted by the earthworm on the ingested soil are far lower than the maximum pressures that the earthworm can exert when pushing soil particles out of its path. This difference is almost certainly due to the different musculature acting in each case. The earthworm has a longitudinal muscle layer which is responsible for locomotion by extension and contraction of the segments. Also the gut has two muscle layers, an outer layer of longitudinal fibres and an inner layer of circular fibres. The muscle layers around the gut would be responsible for the movement of food but being weaker would not be able to exert forces as large as the locomotive muscles. Consequently it is not surprising that the pressures exerted on ingested soil as found here are much less than the maximum external pressures exerted by earthworms.

4.4. Miscellaneous Cast Features

4.4.2 Materials and Methods

The total carbon contents of the casts and the bulk soil were determined by dry combustion in a furnace using a Leco CR-12 carbon system. The surface layer of the Urrbrae sandy loam is without carbonate (by acid treatment) and therefore the organic matter content can be estimated by multiplying the carbon content by a factor 1.72.

4.4.3 Results and Discussion

Total carbon measurements of the casts used in this work were 1.65% compared with the bulk soil at 1.54%. As only casts that had been photographed were combined to provide enough material for the carbon test no replication was possible. Since the soil is carbonate free, these values correspond to approximately 2.8% and 2.6% organic matter respectively. These values are markedly different from the 8.3% and 4.8% organic matter reported by Czerwinski et al (1974) from casts and bulk soil in a Polish grazed pasture with the same earthworm species.

Chapter 5

Measurement of Earthworm Tunnels

5.1 Size and Orientation

5.1.1 Introduction

Earthworms move through the soil, creating tunnels. The size and orientation of the tunnels will vary with the type of earthworm and with the soil properties. For example, endogées reliant on frequent soil ingestion to obtain food can be expected to produce tunnels of different form than anéciques which establish deep permanent tunnel systems. Environmental factors such as temperature, water and food availability, may affect the tunnelling strategies of ecological groups (Lee 1985). Tunnels, as with biopores in general, are usually cylindrical and continuous. Because of these features tunnels are important for water and air movement through soil and may provide preferred paths for plant root growth (Dexter 1986 a, Jakobsen and Dexter 1988). The significance of the morphology of tunnels has received minimal consideration.

Descriptions of tunnels have mainly concerned numbers per unit area and their diameters (Barley 1959 b, Ehlers 1975, Omoti and Wild 1979) with only limited consideration of their orientation. Rogaar and Boswinkel (1979) examined tunnels in a polder with a mixed earthworm population and noted two types of tunnels; predominantly vertical burrows up to 8 mm wide continuing to depths approaching 1 m, and twisting burrows of 0-8.5 mm diameter down to a maximum of 27 cm. Vertical tunnels were attributed to *Lumbricus terrestris* (an anécique earthworm) while the less deep tunnels were attributed to several endogée species, including *A. caliginosa*.

Similarly, Kretzschmar (1977,1982) found that different ecological groups of earthworms contribute to the different tunnel forms and that the quantity of tunnels varied through the year and was well correlated with the soil water content and temperature. He

found most tunnels between 20 and 40 cm deep in the soil. To describe their orientation he used the terms sub-horizontal and sub-vertical.

For considerations of the importance of tunnels a satisfactory starting point may be to assume that the tunnel is a vertical pipe, but to better asses the significance of real systems a more detailed understanding of tunnel shape is necessary. For some species it appears that the vertical pipe approximation may be appropriate (Ehlers 1975), but if this idea is generalized misleading conclusions may be drawn. Tunnels of non-vertical orientation are more likely to be encountered in a vertical soil face than are vertical tunnels so that if pore spaces are examined on vertical soil sections, wrong conclusions about the frequency of tunnels may be reached if the tunnels are assumed to be vertical.

No anécique or subsoil earthworms have been reported at the Waite Agricultural Research Institute, where work for this thesis was carried out. Barley (1959 b) found the dominant species at this site to be *A. caliginosa* and *A. rosea*. In a study of biopores, Smettem and Collis-George (1985), found that these species rarely tunnelled below 60 cm into a podzolic soil.

It is not known whether the tunnel length or direction of endogée eco-types is altered by changes in associations with anéciques. It is possible that a vacancy in the niche often occupied by anécique earthworms may lead to a modification of tunnelling behaviour of the endogée earthworms. Until quantitative measurements of tunnel systems are documented such ecological questions can not be answered. This provided added importance to the studies described here.

Techniques for geometrical description of linear and planar features in soil have been reported by Willoughby (1967). I considered this type of technique to be readily applicable to the coordinate records of tunnels created by earthworms. The technique involves the measurement of length and direction of pores. The results are then plotted in two dimensions using a polar coordinate system.

5.1.2. Experimental

The area chosen for investigation was in the arboretum at the Waite Agricultural Research Institute (34°58'S 138°38'E) in a permanent pasture of subterranean clover and grasses growing in the Urrbrae fine sandy loam described in section 3.1.2. There had been no tillage at the site for many years but super-phosphate fertilizer had been broadcast 4 months before the commencement of this study. The area has a Mediterranean type climate with a warm dry summer and a cool wet winter. Most of the mean annual rainfall of 586 mm falls between May and October. The area was not irrigated. Soil temperatures at 15 cm depth range from a mean daily maximum of 30.3°C in January to a mean daily minimum of 9.7°C in July (W.A.R.I. 1987). The mapping was done between August and mid-October of 1986. Barley (1961) found at the same site that earthworm numbers peaked in mid-winter and then declined through the spring.

Tunnels were mapped in the following manner. An aluminium framework 1.2 m x 1 m (Figure 5.1) was placed flat on the soil surface. In tracks along the sides 1 m apart a trolley could be moved (in the x-direction). A wheel-mounted pointer on the trolley could be moved (in the y-direction) at right angles to the direction of trolley movement. The pointer which could be lowered and raised (in the z-direction) could be fixed in place with a screw. To the framework were fixed metal tapes along which were marked 1 mm intervals. Thus moving the trolley and the pointer on the horizontal plane enable the x and y coordinates to be determined, with the vertically moving pointer allowing the z coordinates to be read from a scale. The entire framework weighed approximately 25 kg and could be dismantled for easy transport.

When in use, the framework was first assembled, then penetrometer resistance and volumetric water content measurements were recorded in adjacent soil. These were done with a RIMIK CP02 recording penetrometer (total angle 30° , cone diameter 13 mm) and an IRAMS time domain reflectometer water content meter, respectively. The soil surface was examined for any biopores opening to the surface. Whereas the earthworm species common at this site are not extensive surface casting species (Edwards and Lofty 1977) it is known that material will be deposited at the surface when the worm is commencing a new tunnel or if
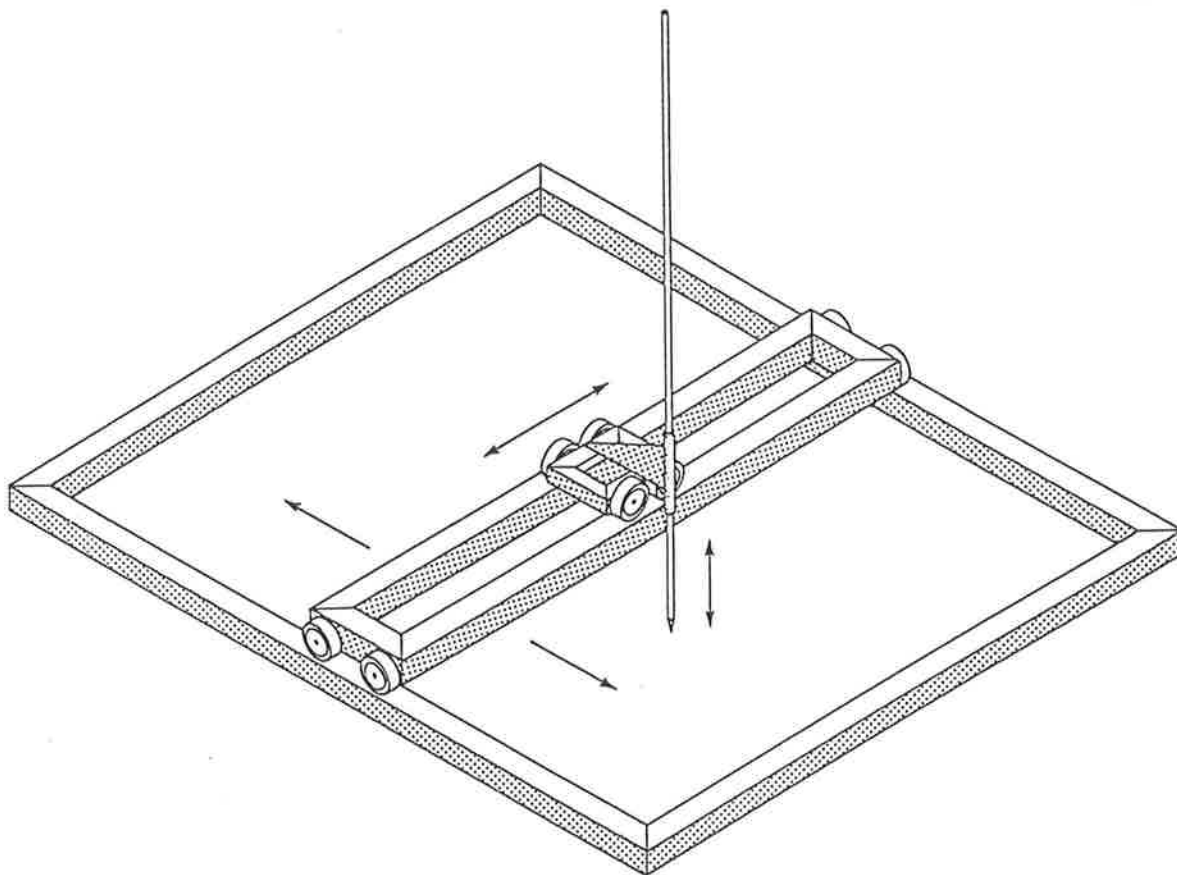
Fig. 5.1 Aluminium framework used for mapping earthworm tunnels showing the trolley for movement in the x-direction, and the wheel mounted pointer for movement in the y- and z-directions . Dimensions are 1.2 m by 1.0 m. Pointer length 1.0 m.

there is no space available within the bulk soil (Thomson and Davies 1974). The presence of cast material on the soil surface was used to locate likely starting points. Once a surface opening of a tunnel had been found, the above ground parts of the vegetation in the immediate vicinity were removed using scissors. Care was taken not to disturb the soil.

After the coordinates of the surface opening had been recorded, mapping of the tunnel proceeded by gently inserting a dissection probe a short distance into the biopore, or until resistance was detected. The soil was then excavated around the probe using spatulas and fine brushes. The coordinates of the newly exposed point were recorded and the procedure repeated. Coordinate readings were taken at approximately 15 mm intervals. Any earthworm found in the tunnel was collected and anaesthetized and returned to the laboratory for identification. The coordinate data were then transferred to computer disc. As there was some skewing of the trolley as it was moved, the x coordinates were measured at each end of the trolley and the mean value calculated to overcome the parallax. From the x,y,z coordinates the length and orientation of tunnels were calculated.

5.1.3. Results and Discussion

Mapping of a total of 80 tunnels was commenced but of these only 16 were considered to have been entirely mapped. These systems met the criteria of having at least one earthworm in residence and that the mapping was not stopped due to an inability to follow the tunnel (eg through plant root masses) or because the excavation process destroyed part of the tunnel system. Rovira et al (1987) observed during sampling of *A. caliginosa* populations that many small worms were associated with plant roots. I believe this type of association to be a major cause of difficulties in the mapping of tunnels found here. The tunnel systems entirely excavated usually contained only a single worm. Of the exceptions to this only one tunnel contained more than one mature adult.

The mean length of occupied tunnels was 392 mm or approximately 370 mm per mature earthworm. All of the tunnels measured were produced by either *A. rosea* or *A. caliginosa.*, ten by the former and six by the latter. The only other species found at the site

was *Microscolex dubius*. No correlations between the worm weight and tunnel length or depth have been found in this study. This may be due to the variability of worm weight with soil water potential. As the study was conducted over a two and one half month period there major changes in the soil water potential would have occurred. Further some of the mapped tunnels may have been in the initial construction stage while others may have been more extensively developed. This uncertainty makes correlations impossible without many more systems being mapped.

The diameter of tunnels varied along their length. This is compatible with the worm selectively grazing along the tunnel length, as was described by Bolton and Phillipson (1976 a). The variability in diameter makes accurate estimation of the tunnel volume impractical. In half of the tunnels cavities were found. The maximum cavity volume was estimated as 1000 mm^3 , which is similar in size to cavities reported by Rogaar and Boswinkel (1978) of up to 12 mm in diameter. They were presumably the result of extensive selective grazing. Unlike the cavities reported by Rogaar and Boswinkel (1978) which had up to 8 tunnels leading from them the cavities found hear had a maximum of 4 passages emerging.

Little cast material was found in the complete tunnel systems. This may be as a result of the method of selection of tunnels for investigation which involved starting at sites which had surface casts, but may also be because tunnels containing cast material were more difficult to map successfully. The cast material that was found often blocked off a small section of tunnel which contained cocoons.

As the mean length of tunnel mapped was approximately 400 mm and the mean fresh weight of the adult worms inhabiting the tunnels was 630 mg the mean length of tunnel per gram fresh weight of worm is estimated at 635 mm. In their study of *A. rosea* in cages Bolton and Phillipson (1976 a) found that burrow construction ranged from 133 to 516 mm per gram fresh weight of worm per day. Immature worms ingested more soil per unit weight than adults. Temperature increases between 4° C and 15° C increased the activity for all maturity levels. The mean fresh weight of adults in their study was approximately one-third of the weight found here. Despite the difficulties involved in accurate estimation of tunnel diameter, a mean value of 3 mm will be used here for calculation purposes. This value is compatible with

measured values. The mean volume of mapped tunnels may then be estimated at 2.8×10^{-6} m^3, or 4.5×10^{-6} m^3 per gram fresh weight of worm. The dry bulk density of the Urrbrae soil in the arboretum is estimated to be 1.6 tm^{-3} which permits the estimation of the mass of dry soil moved in tunnel construction as 4.5 grams or 7.2 grams per gram fresh weight of worm. Up to an additional 1.6 g of soil may be ingested in cavity production.

Bolton and Phillipson (1976 a) estimated the dry weight of soil displaced for adult *A. rosea* as up to 2 grams per gram fresh weight of worm per day in soil in which the worms ingested approximately 5 times their body weight per day, and had gut turnover times of between 1 and 2.5 hours. Barley (1959 a) found rapid gut turnover times of less than 5 hours for *A. caliginosa* when commencing new tunnels. However for worms, (of almost identical mass to those found in this work,) in established tunnels he estimated gut turnover times as 20 hours and the weight of soil in the gut as 0.19 grams. Thus as the loss of soil mass in the ingestion process is minimal the ingestion rates may be estimated at 0.36 grams of soil per gram fresh weight of worm per day.

Because of the large variation between the results of Barley (1959 a ,1961) and those of Bolton and Phillipson (1976 a) it is difficult to estimate the construction times for the tunnel systems reported here, although of the order of 1 week may be an appropriate minimum. Springett (1983) however found that tunnel systems of *A. caliginosa* remained open to the surface for at least 12 days and were usually reopened after disturbance, which together with the information presented here indicates that the traditional view of tunnels made by endogée earthworms being ephemeral and not actively maintained may need to be reassessed.

The number of surface openings per tunnel system is shown on Figure 5.2. The mean number of surface openings per system is 3.2 with the median value being 3. By the Spearman rank non-parametric statistical method, the number of surface openings is positively correlated with tunnel length at the 5% level. In a like manner the number of branching points (ie the number of points from which more than two paths lead away), is shown as a function of depth in Figure 5.3. The mean number of branching points per tunnel system is only 2.7 illustrating their linear format. The majority of the branching points are shown to be in the top 50 mm of soil. Often these provided an alternative, if short, path to the surface. The number
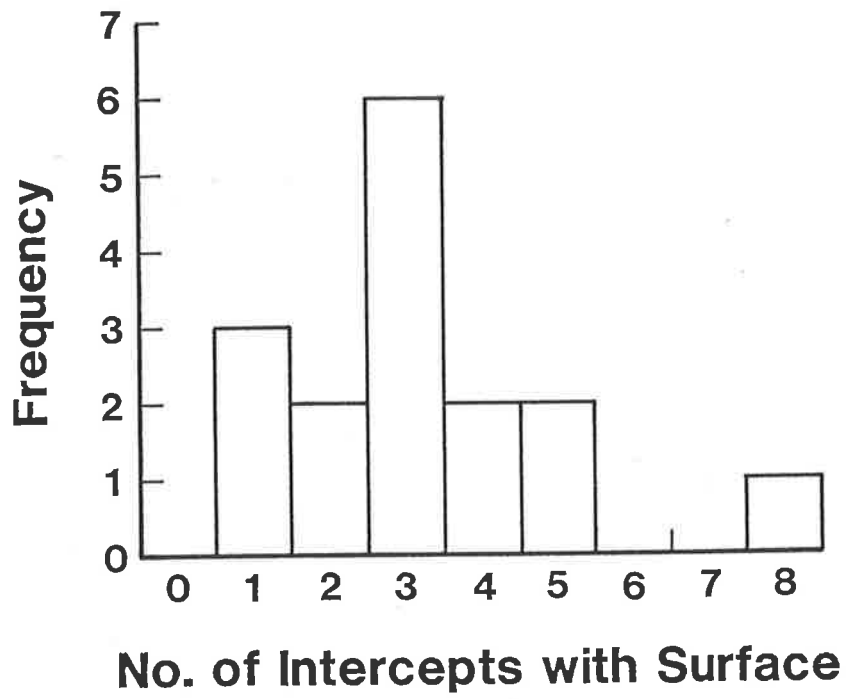
Fig. 5.2 Histogram of the number of surface openings per occupied tunnel system.
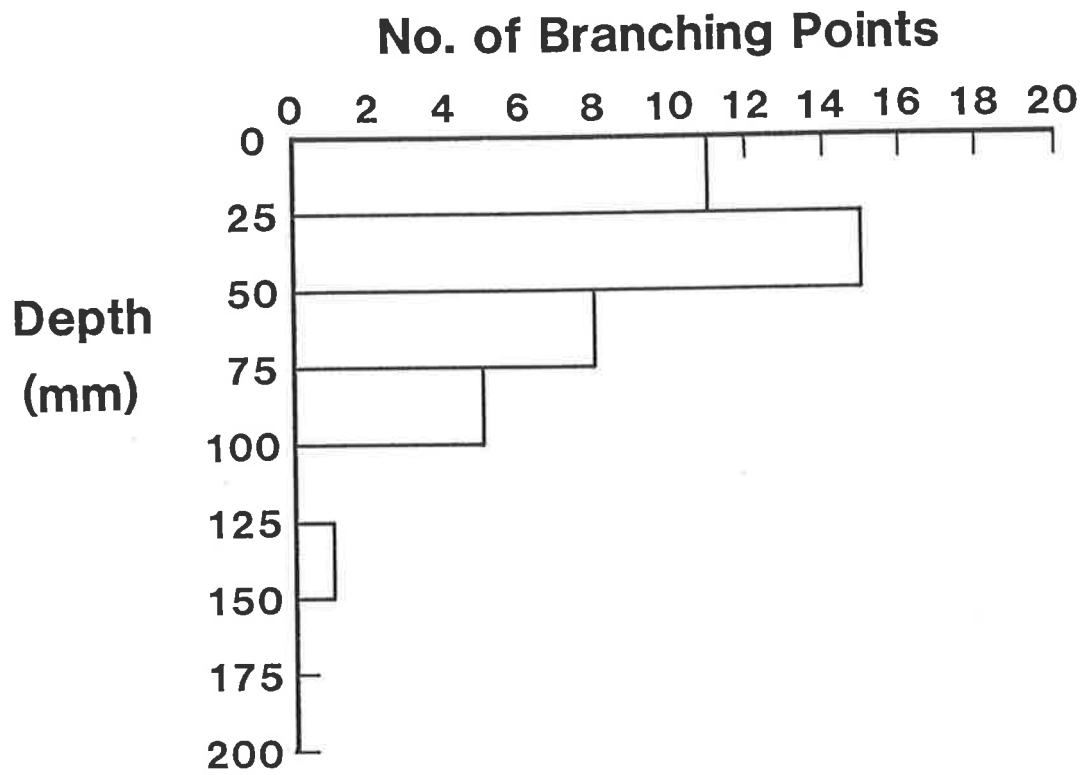
Fig. 5.3 Number of tunnel branching points in 25 mm depth increments for occupied tunnel systems.

of branching points is positively correlated with tunnel length at the 5% level using non-parametric methods. A non-parametric technique was used in both these cases as the distribution of the samples was likely not to be normal.

The distribution of tunnel length as a function of depth in the profile can be seen in Figure 5.4. The greatest depth attained by any tunnel was only 195 mm. A number of environmental factors may be associated with the near surface dominance of the tunnel systems. As is seen in Figure 5.5 the amount of carbon in the profile is greatest near the soil surface. A soil horizon change from an A1 to an A2 occurs at about 150 mm depth (Chittleborough and Oades 1979). The A2 has increased clay and moderate amounts of gravel and stone. These changes, along with water, temperature and aeration gradients, will influence the depth of earthworm activity.

The angle and length of tunnels occurring in 50 mm layers from the soil surface can be seen in Figures 5.6, 5.7 and 5.8. These were plotted using techniques similar to Willoughby (1967). The tunnel sections are divided into $5°$ increments and the total length of tunnel in each increment plotted. As only 53 mm of tunnels were mapped below 150 mm depth these are not shown, but the mean angle of these deepest tunnels was $61.3°$ measured from the horizontal. Barley (1959 b) as a general observation, noted at the same site as used here that the tunnels in the top 15 cm of soil were irregular but that at greater depths they approached vertical.

Figure 5.9 shows the relationship between the mean depth of each layer and the sin of the mean tunnel angle, θ, in each layer. Regression of the four points with d in mm yields

$$\frac{1}{\sin \theta} = 2.108 - 0.185 \ln (d) \qquad\qquad (5.1)$$

with 95.8% of the variance accounted for. The boundary conditions are d > 0 (since tunnels cannot occur above the soil surface), and d < 399 mm (since tunnel angles cannot exceed $90°$ from the horizontal.

Dexter (1986 a) and Jakobsen and Dexter (1988) have illustrated the importance of vertical biopores for root growth, particularly for penetration through compacted soil layers.
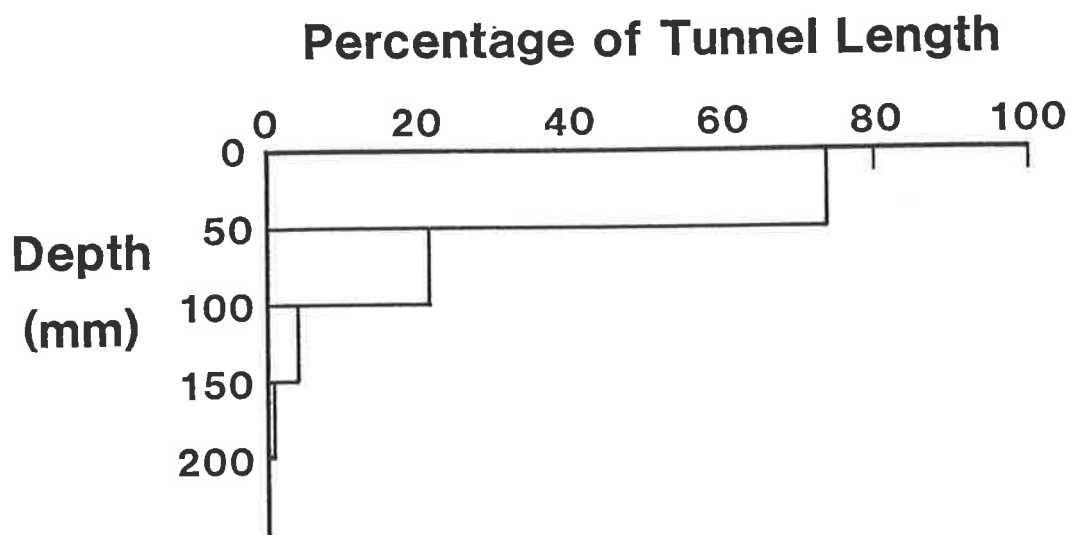
Fig. 5.4 Distribution of total tunnel length as a function of depth, in 50 mm increments.
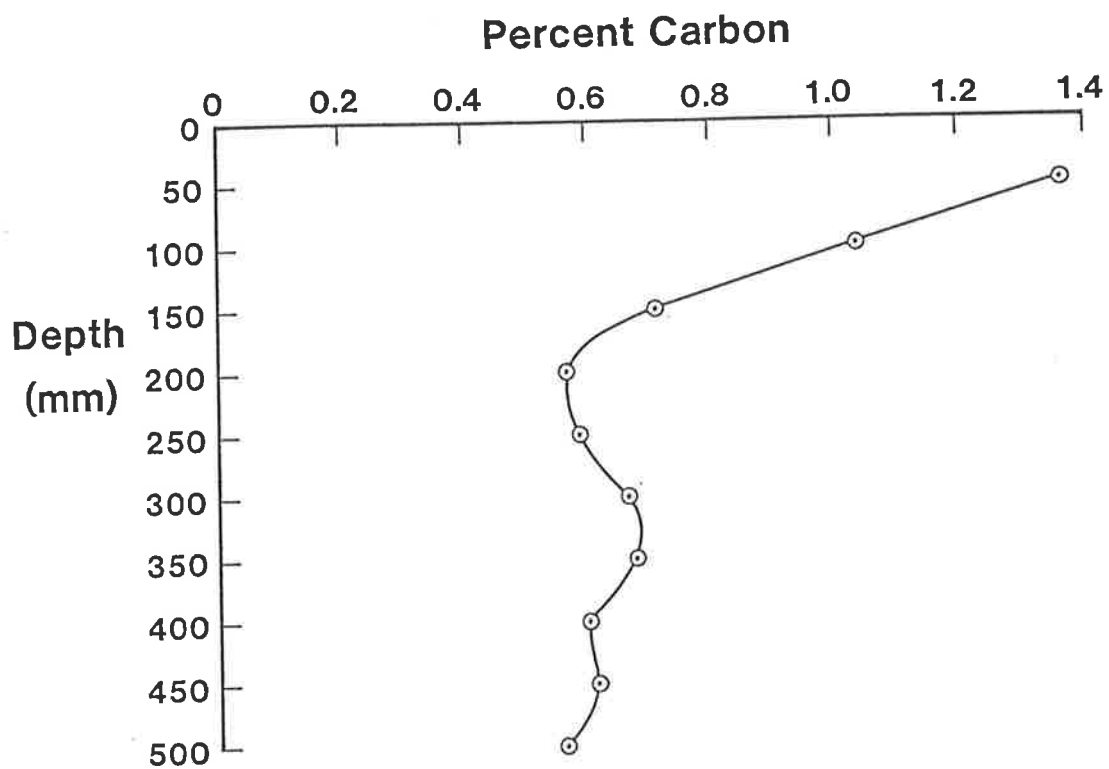
Fig. 5.5 Distribution of total carbon with depth, in a permanent pasture on the Urrbrae loam.

Mean angle
41.9°
from the horizontal

├───┤
50mm
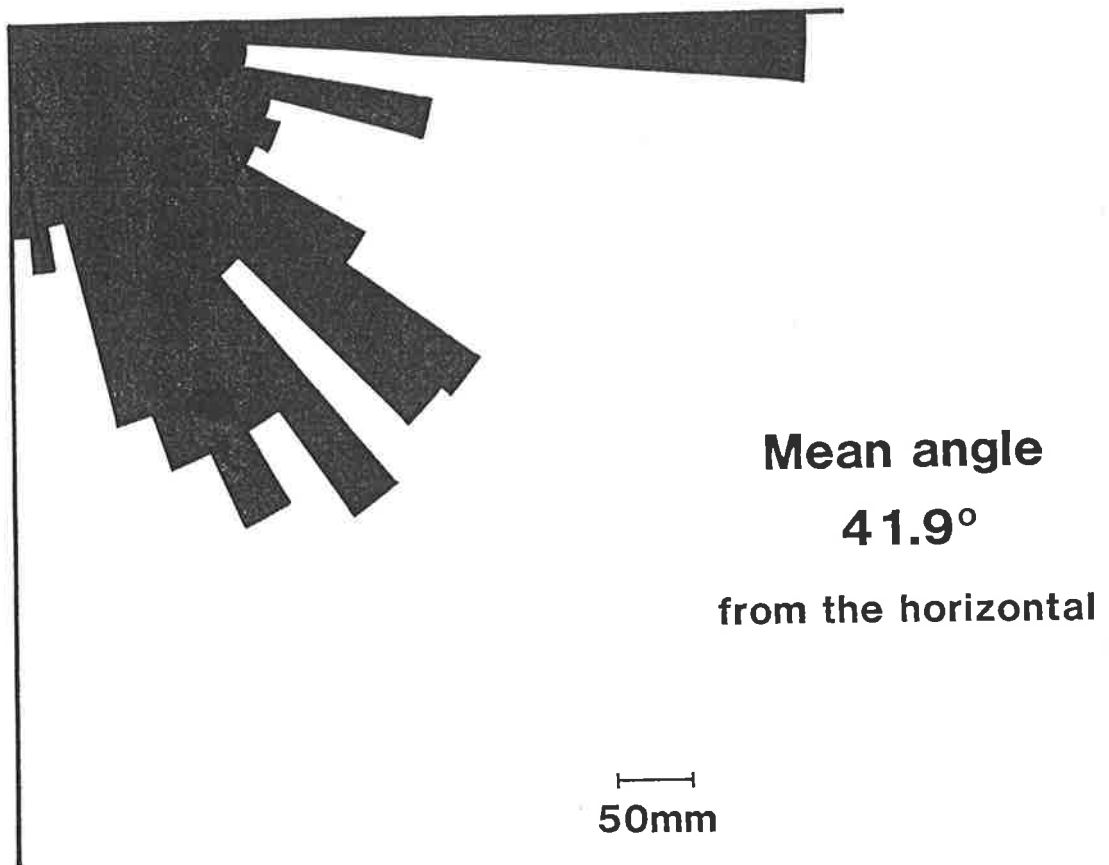
Fig. 5.6 Polar coordinate representation of tunnel length and angle in 5° increments, for 0-50 mm soil depth.

Mean angle
47.9°
from the horizontal
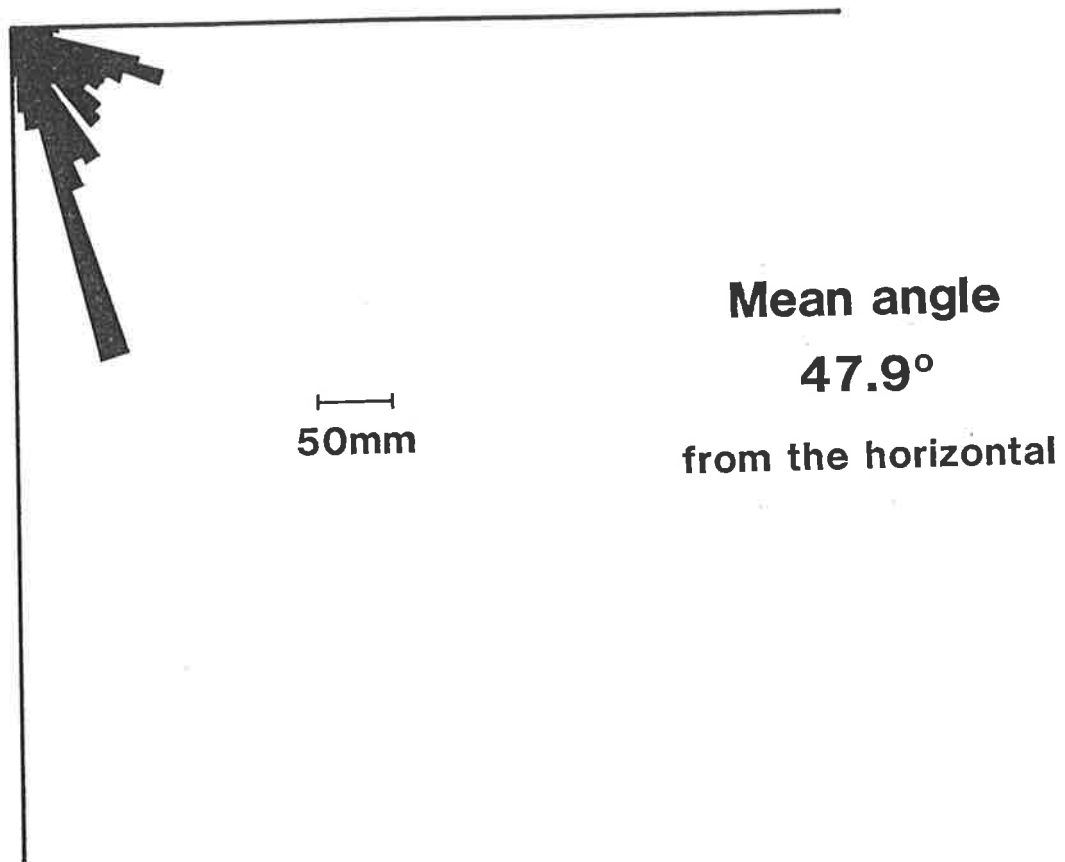
50mm

Fig. 5.7 Polar coordinate representation of tunnel length and angle in 5°
increments, for 50-100 mm soil depth.

Mean angle

56.4°

from the horizontal

⊢——⊣
10mm
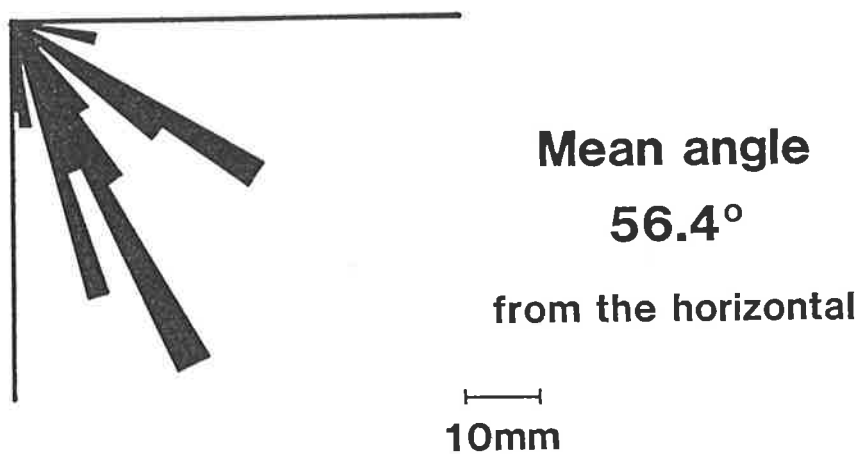
Fig. 5.8 Polar coordinate representation of tunnel length and angle in 5° increments, for 100-150 mm soil depth.
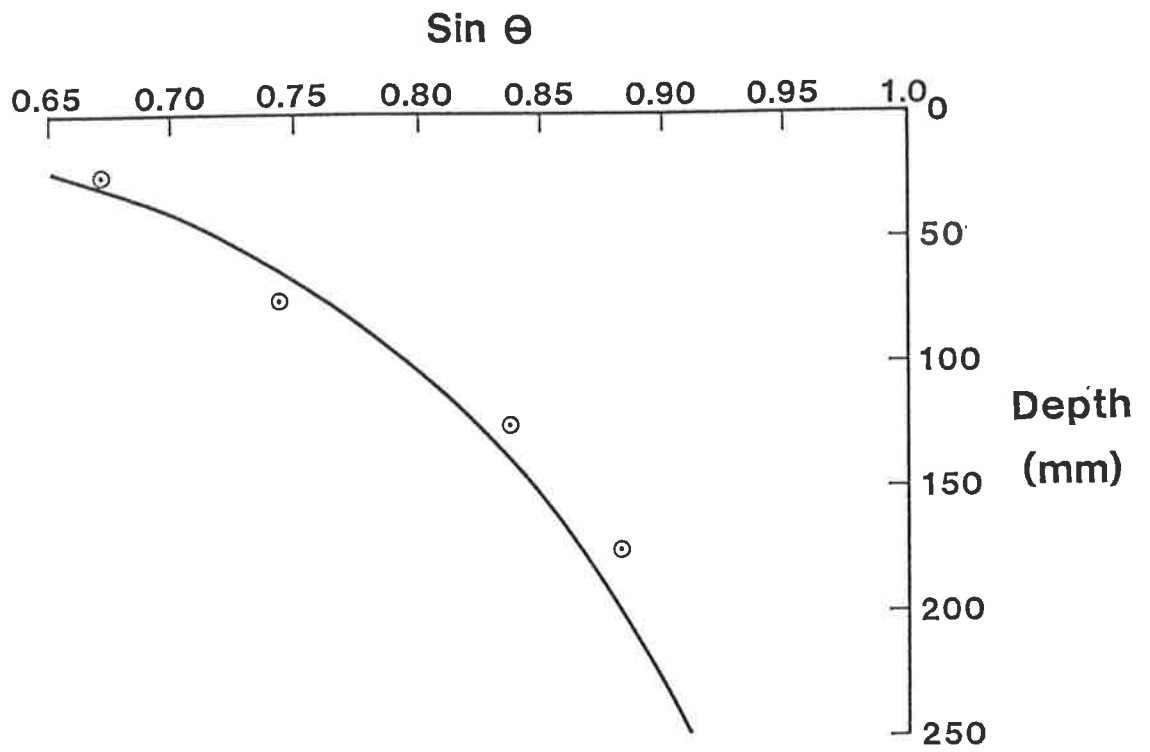
Fig. 5.9 Relationship between the sine of the mean angle made between the tunnel and the horizontal and depth, in mm.

Roots were frequently observed growing along existing biopores during this work. The significance of the relationship between tunnel angle and depth is that the chance of a vertically growing root encountering an earthworm tunnel is greatest near the soil surface. Because earthworm tunnels are continuous, roots following along a tunnel will be drawn deeper into the soil as the tunnel angle increases with depth.

Because of the considerable time involved in mapping each tunnel system and the low success rate in completing the mapping task, the total number of coordinate maps produced was limited to the 16 discussed above. As a result of the limited data obtained, relationships of tunnel morphology with soil and environmental factors, such as temperature, soil strength and water content could not be established.

5.2 Density of tunnels

5.2.1. Introduction

It is important to understand the morphology of "live" tunnel systems. These are not static entities, but are constantly changing form. Decay occurs if the tunnels are not continually maintained by the earthworms. The destruction of the tunnels is expected to be more rapid near the soil surface where treading by animals, litter fall and raindrop impact will be most severe and the washing of material into the tunnel will commence (Trout et al 1987). Tunnel creation and destruction rates are both dependent on depth. In spite of this, creation and destruction exactly balance through the profile. Something close to a steady state must exist in the numbers of earthworms and the depths at which they are found in the profile, though only on a rather short term, seasonal basis.

At the same site as was used in these experiments, Barley (1959 b) measured tunnel numbers and estimated cross sectional areas at 200 and 500 mm depths. From this it is known that tunnel numbers (greater than 0.5 mm) were 4 times more frequent at 200 mm than at 500 mm and total cross sectional area was 7 times larger. Kretzschmar (1982) states that the quantity of burrows is variable at any site and suggests that temperature and humidity affect

the quantity of burrows. Thus the differences may be normal and relate to season and soil water factors.

To improve the definition of the depth of the layer of maximum macro-pore numbers further studies are needed. The techniques necessary to estimate the distribution of pores at various depths are well established. A binomial distribution can be used to examine the likelihood of any quadrant of similar size to tunnels being occupied by a tunnel, as a fraction of the total surface. Smettem and Collis-George (1985) refined this technique, showing that the spatial dispersion of biopores was random and could be characterized using a Poisson distribution. They suggested that a mean of at least 10 biopores should be included in the quadrant area to permit statistical rigidity.

5.2.2.Experimental

Measurements of tunnel numbers and size ranges were done in July and August of the year following the tunnel mapping work. The sites chosen were in close proximity to the sites where tunnel mapping had been done. The procedure was to drive cylinders of mild steel (Figure 5.10) into the soil. The cylinders were 204 mm (8") internal diameter and 152 mm (6") long and bevelled at the cutting end. Thus the area of the enclosed surface was 3.27×10^{-2} m^2. Smettem and Collis-George (1985) estimated quadrant areas necessary for the Poisson distribution to be approximated by a normal distribution. From the data of Barley (1959 b), Smettem and Collis-George suggested that an appropriate sample size for measuring biopore distributions at 200 mm depth was 333 cm^2. However at greater depths where Barley had found fewer tunnels larger sizes were thought to be needed. When the cylinder had been driven into the soil to a depth of 100 mm, the soil around the cylinder was removed. Then the cylinder was levered from the soil, producing by tension a clean, fractured soil face at the bevelled end of the cylinder. This method is similar to that described in Douglas (1986). Biopores in the exposed face were counted and divided into diameter classes using vernier calipers. The three diameter classes were 0.5-1.5 mm, 1.5-2.5 mm and larger than 2.5 mm. Tunnels were recognizable as being cylindrical and sometimes by the presence of cast
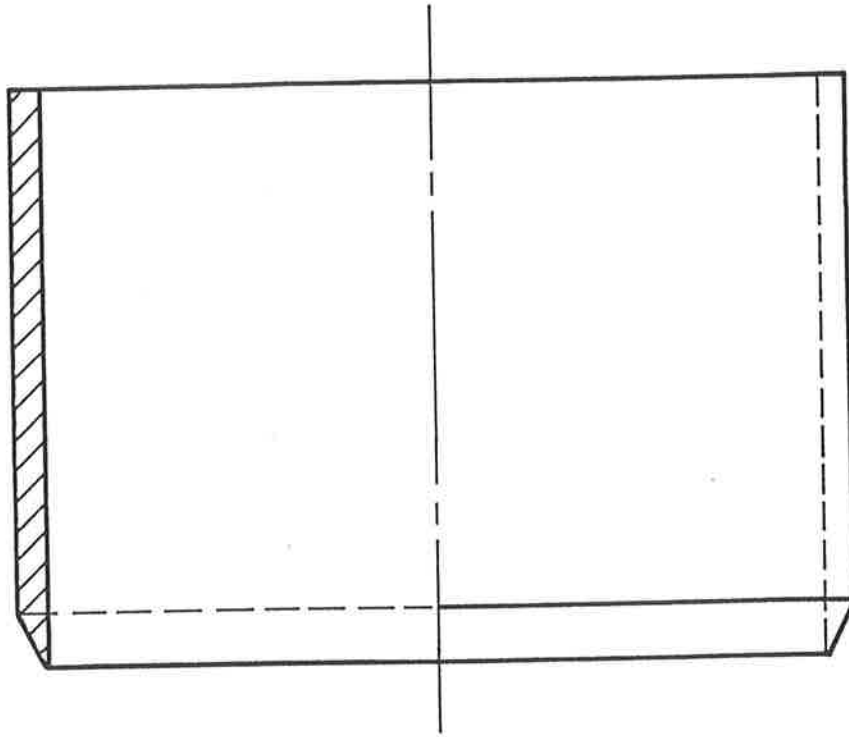
Fig. 5.10 Mild steel cylinder used to provide a fracture surface in the horizontal plane which could then be used to determine biopore numbers. Dimensions : internal diameter 204 mm, external diameter 221 mm and height 152 mm .

material. Occupied root channels were not counted. Each pore was marked with a coloured pin denoting its size class. The fracture surface containing the pins was photographed. The standard single lens reflex camera was mounted on a tripod. After the photograph had been taken, the cylinder was cleaned and driven a further 100 mm into the profile. A standard rule was used to measure depth. The propulsion of the cylinder into the soil was manual.

5.2.3 Results and Discussion

From the study of Rovira et al (1987) involving the effect of rotation and conservation tillage on *A. caliginosa* in a red-brown earth it can be calculated that the number of pores greater than 2 mm diameter per square meter at 100 mm depth ranged from 176 to 237. They found that while tillage and rotation affected earthworm numbers and biomass the number of macropores greater than 2 mm diameter was unaffected. These pore densities are compatible with those found here. Barley (1959 b) found 300 tunnels per square meter at 200 mm depth of the diameter range 0.5 - 3.5 mm. At 500 mm depth he found 75 tunnels per square meter. These figures are despite his recording of up to 740 worms per square meter. Tisdall (1985) measured the number of biopores (> 2 mm diameter) at 50 mm depth in an irrigated red-brown earth soil and found a range from 47 per square metre in a control plot to 207 per square metre in a heavily-manured plot. Other published values have been summarized by Lee (1985). These have usually considered earthworm tunnels as being larger than 1 mm diameter and have included 800 burrows per square meter at the surface of a French pasture (Bouché 1971), 200 per square meter at 250 mm depth in a Dutch orchard (Hoeksema and Jongerius 1959) and a range between 117 and 363 through the profile of a zero-tilled loess in Germany (Ehlers 1975). These results suggest that the numbers of earthworm tunnels per unit area found in this work may be better described by considering only the pores larger than 1.5 mm diameter as they are considerably less than shown in Figure 5.11.

The number of pores greater than 1.5 mm diameter was 350 m^{-2} at 100 mm depth and 450 m^{-2} at 200 mm. The mean length of each mapped tunnel system reported in section 5.1.3 was 392 mm of which (from Figure 5.4) approximately 95% occurs in the top 100 mm and
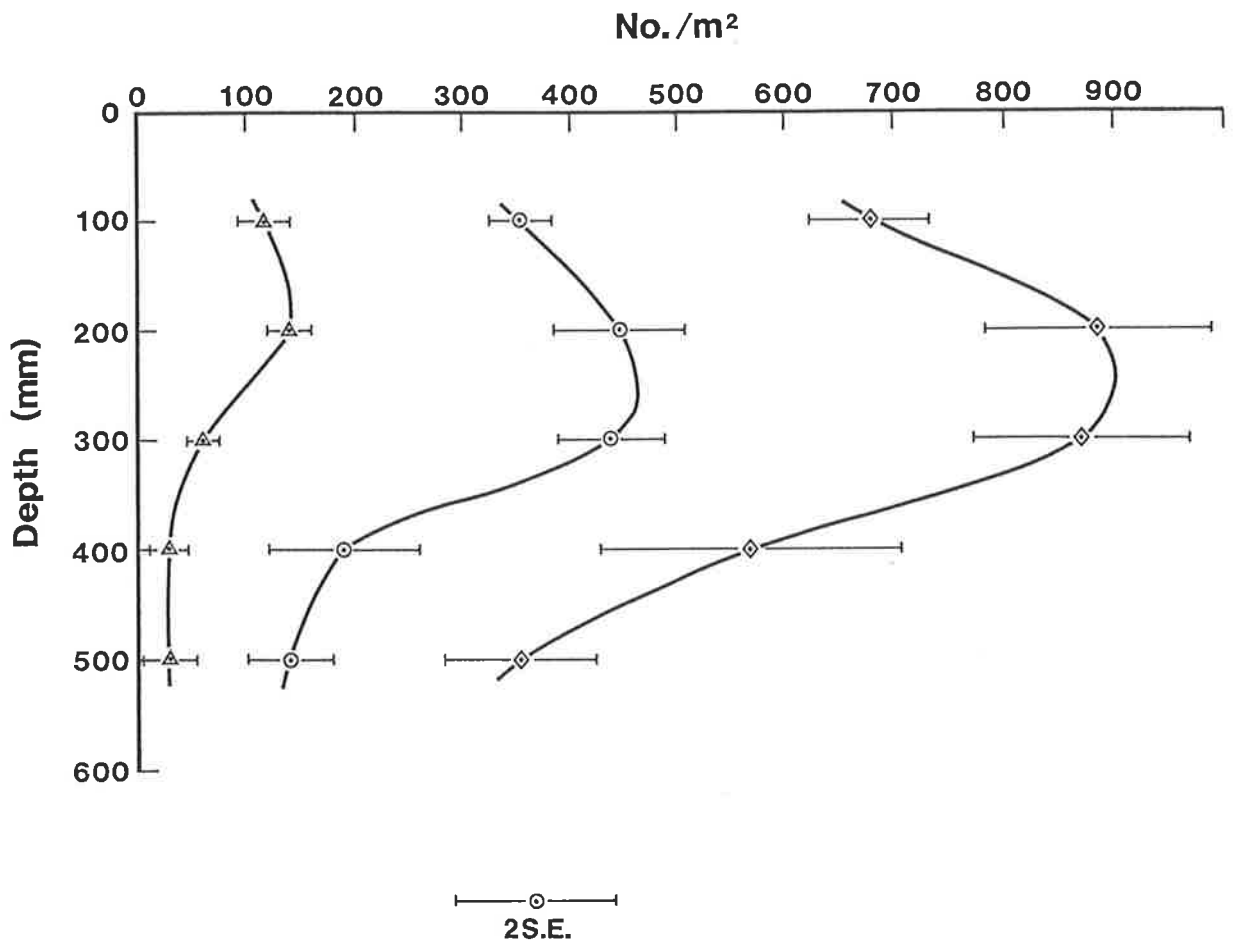
Fig 5.11 Distribution of biopore numbers with depth in a permanent pasture,

    △———△ pores of diameter greater than 2.5 mm,

    ⊙———⊙ pores of diameter greater than 1.5 mm,

    ◇———◇ pores of diameter greater than 0.5 mm.

the remaining 5% occur at 100 - 200 mm depth. By assuming that the numbers of pores at 100 and 200 mm depths shown in Figure 5.11 are typical of the 100 mm soil layers above and recalling from Figure 5.3 that occupied tunnels rarely branch below 100 mm it is possible to calculate, Tv, the tunnel length per unit volume of soil for both the 0 - 100 mm and 100 - 200 mm soil layers. Tv is estimated at 1300 m/m^3 in the 0 - 100 mm layer and 90 m/m^3 in the 100 - 200 mm soil layer. Barley (1970) in a review of root growth reported values of Lv (the root length per unit volume of soil) for crops and pastures as typically being 1×10^5 m/m^3 in top soils, and decreasing with depth. Thus a ratio Tv : Lv of 1 : 100 is estimated.

An assumption that the radius of the earthworm tunnels is 1.5 mm, allows the estimation of the percentage of soil volume, SV, in the top 100 mm that is occupied by earthworms tunnels as

$$SV = Tv \times \pi \times r^2 \times 100 \qquad\qquad (5.2)$$

and is 0.9%. Stöckli (1949) suggested that earthworm tunnels constitute about 5% of the total soil volume. Other European values in excess of this have been reported in Edwards and Lofty (1977) but they maintained that the 5% value was realistic. Clearly the value calculated here from tunnel measurements are considerably less than other reports which were obtained from measurements of soil air filled porosity.

The assumption has been made in this chapter that the radius of tunnels is 1.5 mm. The relative contribution of each pore diameter class, shown in Figure 5.11, to the total cross sectional area of pores can be estimated as follows. Consider the mean diameter of the largest pore class as 3 mm and that the mean size of the two smaller classes was the mid-point of their range. The cross sectional area of tunnels per unit soil area can then be calculated. Table 5.1 presents the estimated cross sectional area of tunnels per square meter of soil. From this it is apparent that the major contribution to the area is from pores larger than 1.5 mm diameter.

Using some simple assumptions and the data given above it is possible to estimate the number of tunnels per unit area,D , and the cross sectional area of tunnels, A, produced by earthworms per square metre per year, between stated depth limits.

Table 5.1

Estimated Cross Sectional Area of Tunnels per Square Metre

Depth (mm)	Pore Size Class			
	0.5 - 1.5 mm $m^2/m^2 \times 10^{-4}$	1.5 - 2.5 mm $m^2/m^2 \times 10^{-4}$	> 2.5 mm $m^2/m^2 \times 10^{-4}$	Σ $m^2/m^2 \times 10^{-4}$
100	2.6	7.5	8.2	18.3
200	3.2	9.6	10.0	23.1
300	3.4	12.0	4.3	19.7
400	3.0	5.2	1.9	10.1
500	1.7	3.5	2.2	7.4

$$D = \frac{l \times a \times N \times P \times \sin \theta}{d} \qquad (5.3)$$

$$A = \frac{l \times a \times N \times P \times \pi \times r^2 \times \sin \theta}{d} \qquad (5.4)$$

where l is the length of tunnel made per worm per week in metres,

a is the number of weeks per year the earthworms are active,

(Thus l x a is the length of tunnel produced by a worm per year),

N is the worm population per square metre,

r is the radius of the earthworm tunnels,

(Thus l x a x N x π x r^2 is the total volume of tunnels made per square metre per year),

d is the thickness of the layer being considered in metres,

P is the fraction of tunnelling that occurs in a soil layer between d_1 and d_2, the upper

and lower boundaries of d and

θ is the mean tunnel angle in that layer.

These parameters will depend on a range of variables including the species of earthworm, the distribution of organic carbon through the soil profile and environmental conditions such as temperature and soil water potential. Also the parameters will not be independent since, for example the population density may be related to the size of the earthworms. The assumptions in equation 5.3 are that within the layer d the tunnels are continuous and extend from the upper boundary to the lower boundary of the soil layer. With these assumptions the cross sectional area produced per square metre per year can be calculated.

From Barley (1959 b) the number of lumbricids averaged 540 per square metre and these were active for approximately 26 weeks per year. Using ingestion rates calculated from Barley (1959 a) together with the mean soil bulk density described in section 5.1.3, the length of tunnel constructed per week is estimated as 0.56 metres per worm. Table 5.2 shows the calculated values from equations 5.3 and 5.4 at two depths, together with the measured data.

Table 5.2

Calculated Values from Equations 5.3 and 5.4 at Two Depths

Parameter	Depth = 100 mm	Depth = 200 mm
d_1	50.0 mm	150.0 mm
d_2	100.0 mm	200.0 mm
l	0.56 m wk^{-1}	0.56 m wk^{-1}
a	26 wk	26 wk
N	540 m^{-2}	540 m^{-2}
P	0.214	0.008
r	0.001 m	0.001 m
$d = d_2 - d_1$	0.05 m	0.05 m
A	7.9×10^{-2} m^2/m^2	3.5×10^{-3} m^2/m^2
D	2.5×10^4 no./m^2	1.1×10^3 no./m^2

The uncertainty of terms in the calculations mean the results presented should be considered only as estimates. Of particular concern is the length of tunnel constructed per week. This is a mean figure and depends on the amount of soil ingested per worm. As has been shown published values of ingestion rates vary greatly. Similarly the number of worms per unit area will not only vary with season but also with their maturity and size. However given these difficulties the values at 200 mm depth, for which the tunnel density values are similar to those measured, a conclusion that tunnels survive for approximately 5 months may be drawn. Nearer the soil surface it appears that tunnels will remain only for weeks. These estimates are of mean values and thus an unknown variance in the life span will occur.

5.3 Influence of tunnels on aggregate strength

5.3.1.Introduction

As has been noted in earlier sections of this chapter biopores, including earthworm channels, decay with time. This decay may result from material falling or being washed into the tunnel. If the tunnel has been created in a "swelling" soil it is possible that expansion of the surrounding soil will close the tunnel. I have found no evidence in the literature relating to tunnel destruction in this manner, but under climatic conditions where soil freezing and thawing occur disruption of tunnels must occur. The problem of soil compaction has been widely reported as restricting root growth (Håkanson et al. 1988, Smith 1987) but what effects this has on existing tunnel structures has not been documented. The bearing capacity of soil with tunnels will determine the resistance to tunnel destruction by compaction.

In this phase of the work, an initial attempt has been made to consider the breakdown of soil aggregates containing tunnels. The surface created by aggregates failing under tension is known to form along existing voids and incongruities in the material (Braunack et al 1979, Dexter 1988). Natural aggregates will be less homogeneous than artificially-prepared samples due to the actions of weather, flora and fauna. So for greater consistency, artificially-prepared aggregates were used in this work.

Finite element analysis computing techniques enable the modelling of stresses in materials. An existing model was used to illustrate the stress distribution through a soil aggregate containing a centrally-placed circular hole.

5.3.2. Experimental

To test the effect of tunnels on the strength of soil aggregates artificial aggregates were prepared by moulding samples of the Urrbrae soil (see section 3.1.2) at water contents in excess of its plastic limit. Artificial aggregates were prepared by taking 50 g samples of the moulded soil and rolling the soil. This formed a ball. Through some of these aggregates holes of different sizes were bored using a cork borer. This was done while the soil was still wet. The cork borer removed a cylinder of soil from the ball. Both the untouched aggregates and the holed aggregates were then air and oven dried. The dried samples were weighed, and the hole diameters were measured where appropriate. Dimensions of the dried samples were taken using vernier calipers. The aggregates with and without holes were then crushed using the indirect tension test for large and strong aggregates as described by Dexter and Kroesbergen (1985) and in section 3.2.2. The cylindrical holes through the aggregates were parallel to the flat metal plates of the crushing apparatus. This is analogous to a horizontal tunnel through an aggregate.

As a comparison artificial aggregates were produced in a similar manner to that just described, but were left entire. Before drying, the aggregates were sealed in tins containing earthworms. The prepared aggregates provided the only soil for the earthworms to tunnel into. After five days the aggregates were removed from the tins and allowed to dry. The earthworms were encouraged to leave the aggregates by placing the aggregates on moist soil during the initial drying stages. The aggregates were then air and oven dried. Measurements of the lengths of tunnels through the aggregates were taken using cotton thread. Diameters of the tunnels were initially estimated from the diameters of the hole openings. The air and oven dried worm-affected aggregates were then crushed as described above. Improved estimates of

the tunnel length and diameter inside the aggregates were obtained from the broken samples. This was because the fracture usually passed through the tunnels.

The finite element analysis method was used to simulate the principal stresses through a centrally holed aggregate under load. The model was adapted for use by Professor J.L. Nieber of the University of Minnesota, while he was at the Waite Agricultural Research Institute as a Distinguished Visiting Scholar.

The method is a numerical procedure for solving physical problems which can be expressed by differential equations. The two main features of the method are that it uses integrals to obtain systems of algebraic equations and that continuous stepwise smooth functions are used to approximate unknowns. While these features separate the finite element method from other methods the numbers of equations involved necessitates the use of a computer. To prepare the method, a grid of nodal points at known coordinates is created and numbered. This is referred to as the discretized region. The nodes are joined by elements. Approximation equations are then established for each element. These must be written to cover unknown nodal values. Development and solving of these equations allows the calculation of quantities required. (Segerlind 1984). In the two-dimensional case used here, these quantities were the two principal stresses.

5.3.3 Results and Discussion

Experimental results for the strength of artificial aggregates is shown as a function of the dimensionless hole radius in Figure 5.12. Making a hole radius of greater than 0.3 times the aggregate radius weakened the wet aggregates so that they either collapsed or fractured during drying. As

$$\frac{\text{Volume hole}}{\text{Volume aggregate}} = \frac{3}{2} \left(\frac{\text{radius hole}}{\text{radius aggregate}} \right)^2 \qquad (5.5)$$
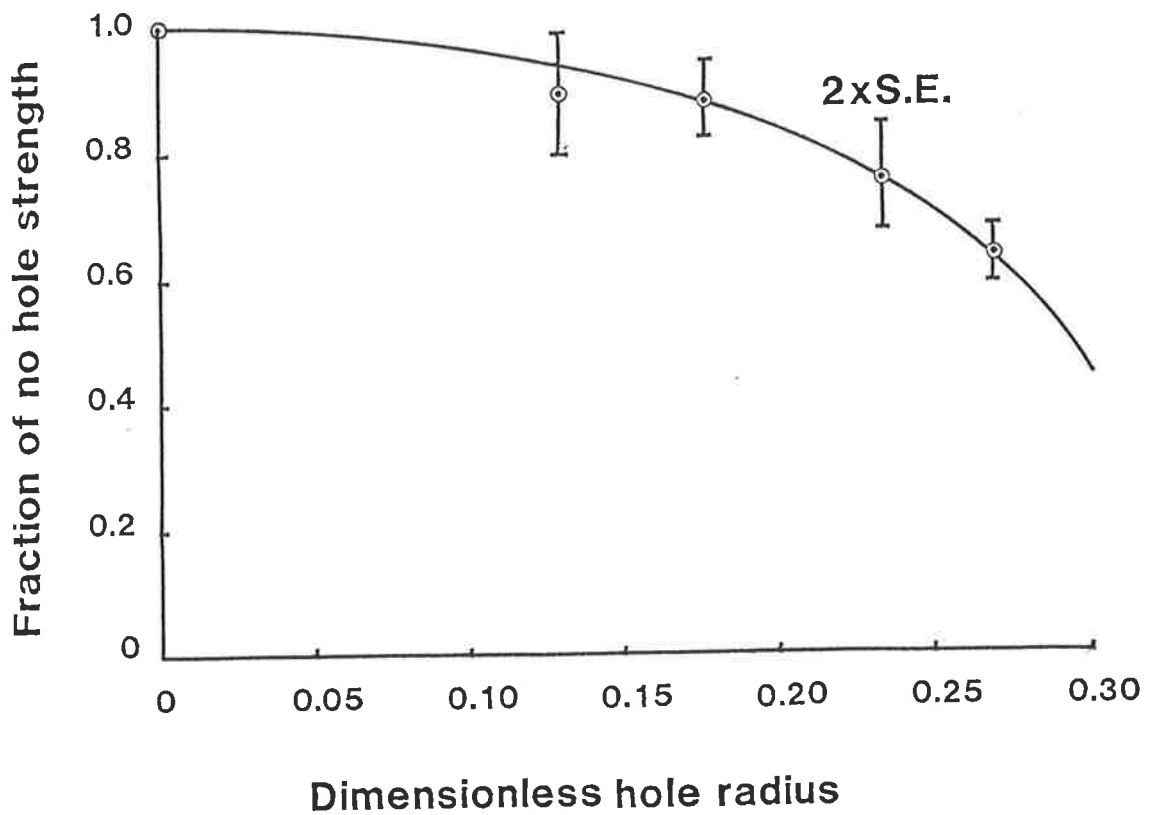
Fig. 5.12 Relationship between the strength of artificial aggregates containing holes and the dimensionless hole radius.

extrapolation of the curve in Figure 5.12 to show decreasing strength at increasing hole radius is soundly based. The volume of earthworm tunnels in aggregates never exceeded 0.04 of the aggregate volume. Consequently no significant strength reduction occurred. Attempts to decrease the ratio of aggregate to earthworm size were unsuccessful because the handling of the smaller aggregates became impractical.

For the finite element model the circumference of a natural soil aggregate in its maximum area projection was assigned coordinate points. The finite-element model used here was only 2-dimensional. The aggregate is assumed to be a prism with a cross-section as shown in Figure 5.13. However, the effects of holes on real aggregates may be expected to be of similar magnitude to that predicted by the model. The simulated load is applied in the Y direction through 3 contact points (Figure 5.13). All hole sizes are centred on the centroid of the aggregate. Having arbitrarily set Young's modulus and Poisson's ratio, the principal stresses were computed.

Figure 5.14 shows the distribution of principal stresses as a function of the hole diameter expressed as a fraction of the sample height. The compressive stress σ_1 shows a rapid increase with hole size until the hole is in excess of 10% of the aggregate diameter. Increasing hole size above this value results in a less rapid stress increase. The tensile stress (which in this case is the minor principal stress, σ_3) relationship with hole diameter is of similar form to that found experimentally for the strength of aggregates found by the indirect tension test. Since it is indirect tension which results in aggregate failure this is to be expected.

The much larger values of hole diameter required for a rapid change in simulated tensile values as compared with those found experimentally can be attributed to inclusions of inhomogeneities in the artificially made aggregates, and to the fact that the simulation was done in 2-dimensions while the experimental aggregates were 3-dimensional. Thus direct comparison of the experimental and calculated strength reductions is not possible. The inhomogeneities will provide paths for rapid fracture development around the central hole. Further the simulated aggregates had three contact points for load application in the model. The additional contact point divides the load thus reducing the concentration of tensile stress.
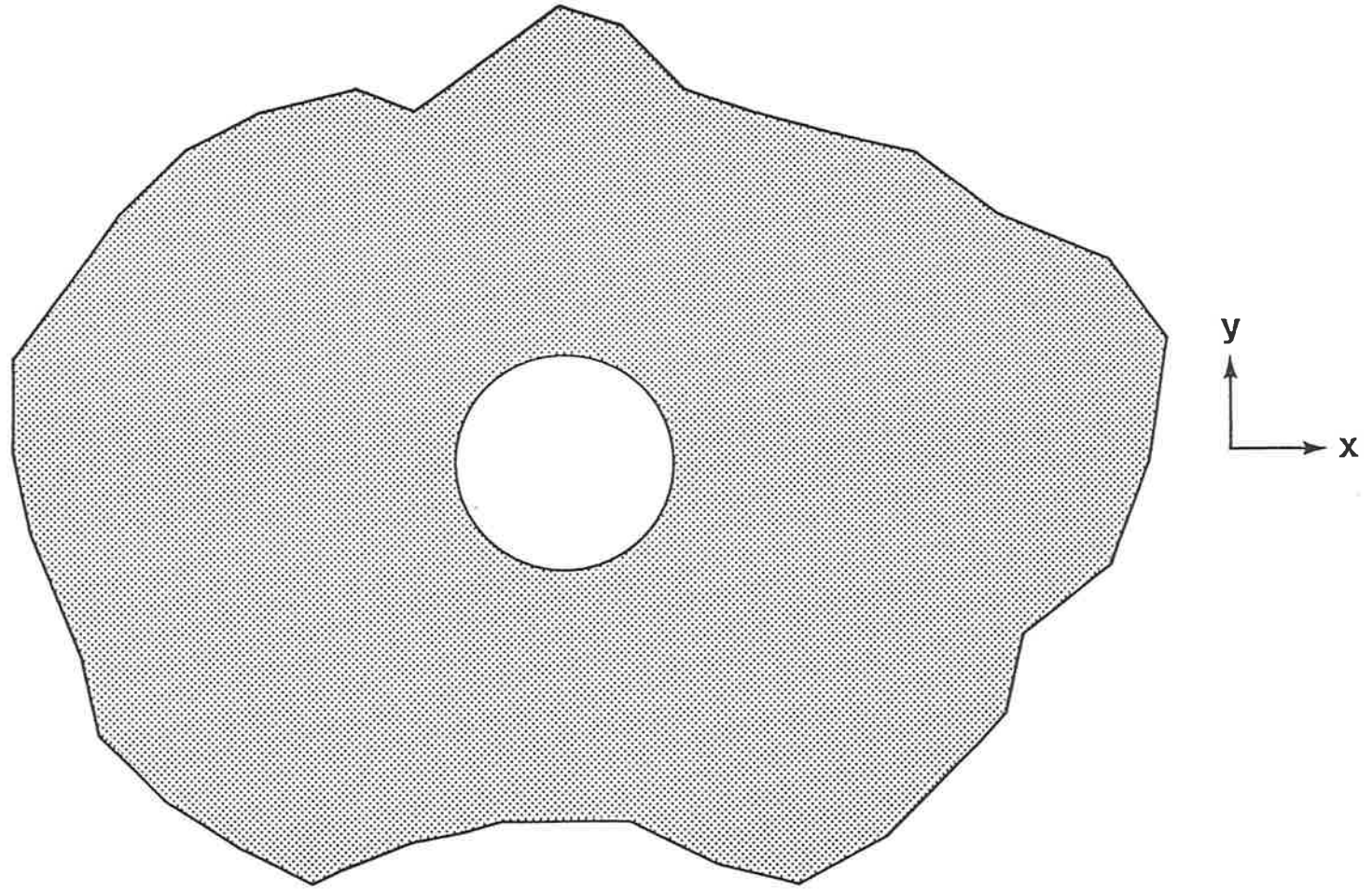
Fig. 5.13 The cross-sectional shape of the aggregate used for finite element modelling, showing a simulated tunnel.
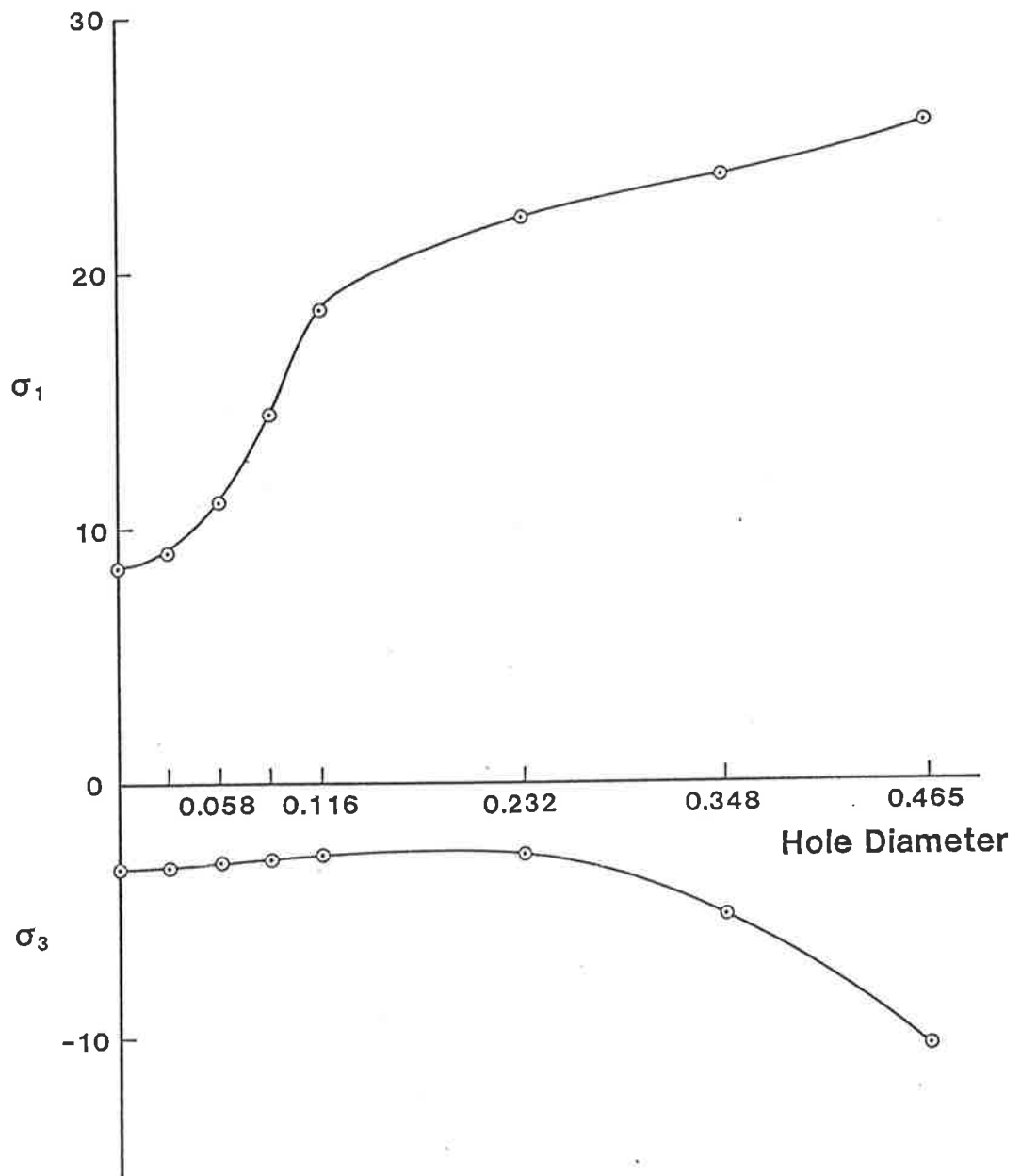
Fig. 5.14 Relationship between the principal stresses, σ_1 and σ_3, and the dimensionless hole diameter through an aggregate, as calculated using finite element analysis.

From this work it can be anticipated that in the field, holes made by earthworms through soil aggregates will reduce the loads which the aggregates can support, however the degree of weakening will depend on the size of the hole relative to the size of the aggregate. As natural aggregates will be less homogeneous than simulated or artificially prepared aggregates it is estimated that if the hole to aggregate radius ratio is greater than 0.1 significant weakening will occur. Of course this assumes that in producing the hole the earthworm did not fracture or weaken the aggregate as was discussed in section 3.2.3.

Chapter 6

Computer Simulations of Earthworm Activity

6.1 Introduction

The activity of earthworms is determined by a range of environmental and biological factors. For example, a reduction in soil water content may result in earthworms moving deeper into the soil seeking more favourable water status or it may result in the earthworms becoming quiescent. Of course such scenarios may not only provoke a response from earthworms but may also alter soil physical properties and plant growth. A reduction in earthworm activity may by itself adversely modify plant root growth by reducing the amount of biopores in the soil and thus the access of plant roots to deeper soil layers. This simple example illustrates the complex nature of the soil- faunal-environment interactions and suggests that computer simulation may be useful in the study of such systems.

The application of computer modelling to earthworms in ecosystems is still relatively undeveloped. Lavelle and Meyer (1977, 1983) have developed a model (ALLEZ-LES-VERS) of the population dynamics of the earthworm *Millsonia anomala*. This has resulted in good correlations between simulated and observed values of the depth and frequency of earthworms in the African savanna. Despite some difficulties with the simulation of the quantities of soil ingested, their model provides some prediction of population density.

The other documented model of ecological and environmental earthworm data is the R.E.A.L. (Rôle Écologique et Agronomique des Lombriciens) model of Bouché and Kretzschmar (1977) and Bouché (1980,1982). This is a large scale project designed to consider and integrate the entire range of earthworm activities and energetics up to a global scale. Lee (1985) suggests that while long term development of this model may enable its practical use, it is useful only at the conceptual level at the present stage of development .

As there has been only limited application of computer modelling techniques to earthworms and as none has dealt with tunnel production an attempt was made to create such a model.

6.2 Soil properties and earthworm activity

The model used in this study is a modification of a model for simulation of root growth and water uptake by wheat (Jakobsen and Dexter 1987). The model here, considers the growth of earthworms by ingestion of soil organic matter and the length and depth of tunnels created by such ingestion. Soil and earthworm parameters used in this model are described by functions.

The soil water characteristic between field capacity and wilting point is described by

$$|\Psi| = \exp(a - b \ln(\theta + c)) \qquad \text{(kPa)} \qquad (6.1)$$

where Ψ is the soil water potential, θ is the gravimetric water content and a,b and c are constants for a particular soil. Hydraulic conductivity is described by the function

$$K = A\rho^2 |\Psi|^{-(2+2/b)} \qquad \text{(mm day}^{-1}) \qquad (6.2)$$

where b is the constant from the water characteristic, ρ is the soil bulk density (tm^{-3}) and A is a constant determined by use of a measured value of conductivity (Jakobsen 1988).

As a response to the influence of soil water on the suitability of the soil for earthworms a (water) activity function was defined as

$$
\begin{aligned}
act(\Psi_{z,t}) &= 0 & &\text{for } |\Psi| < |\Psi|_{min} \\
&= \frac{(|\Psi| - |\Psi|_{min})}{(|\Psi|_a - |\Psi|_{min})} & &\text{for } |\Psi|_{min} < |\Psi| < |\Psi|_a \\
&= 1 & &\text{for } |\Psi|_a < |\Psi| < |\Psi|_b \\
&= \frac{(|\Psi|_{max} - |\Psi|)}{(|\Psi|_{max} - |_b)} & &\text{for } |\Psi|_b < |\Psi| < |\Psi|_{max} \\
&= 0 & &\text{for } |\Psi|_{max} > |\Psi| \qquad (6.3)
\end{aligned}
$$

where act($\Psi_{z,t}$) is the earthworm activity at soil depth z and time t. This is represented graphically in Figure 6.1. $|\Psi|_a$, $|\Psi|_b$, $|\Psi|_{max}$ and $|\Psi|_{min}$ are constants for each earthworm species acclimatized to a particular site.

Soil temperatures fluctuate due to the approximately cyclic surface temperature variations. These variations are both annual and diurnal and both can be approximated by sine functions.

$$T_{(z,t)} = T_{av} + C_0.exp(-z/D).sin(\omega T - z/D) \quad (^\circ C) \tag{6.4}$$

where $T_{(z,t)}$ is the temperature at depth z and time t, T_{av} is the constant "average" soil temperature, C_0 is the amplitude of the sinusoidal temperature variation at the soil surface, w is the angular frequency of the temperature variation and D is the damping depth (Koorevaar et al 1983). The angular frequency is

$$\omega = \frac{2\pi}{t_c} \tag{6.5}$$

where t_c is the time needed to complete one cycle of the wave.

As a response to the influence of soil temperature of the suitability of the soil for earthworms a (temperature) activity was devised

$$
\begin{aligned}
act(T_{z,t}) &= 0 & &\text{for } T < T_{min} \\
&= \frac{(T - T_{min})}{(T_a - T_{min})} & &\text{for } T_{min} < T < T_a \\
&= 1 & &\text{for } T_a < T < T_b \\
&= \frac{(T_{max} - T)}{(T_{max} - T_b)} & &\text{for } T_b < T < T_{max} \\
&= 0 & &\text{for } T > T_{max}
\end{aligned}
\tag{6.6}
$$

where act($T_{z,t}$) is the earthworm activity at depth z and time t. This is represented graphically
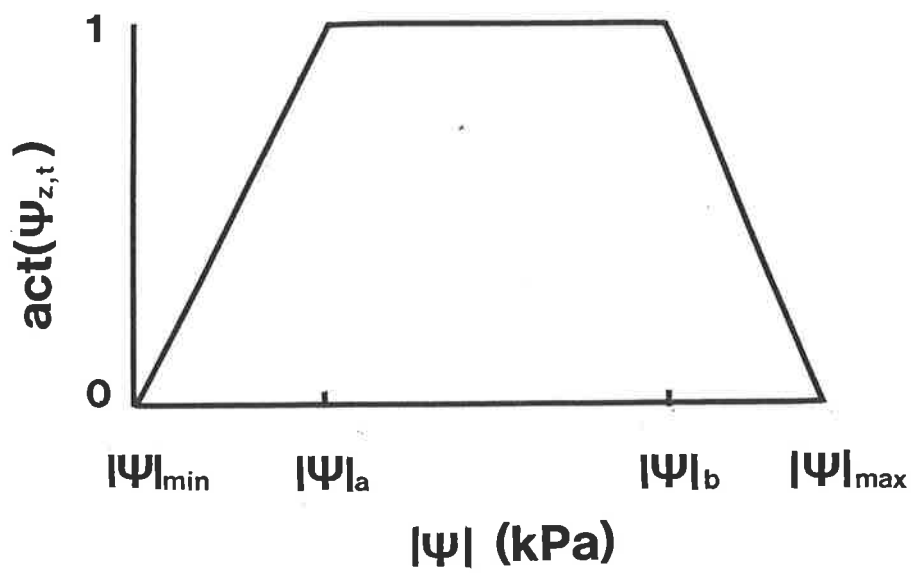
Fig. 6.1 The water activity function, act($\Psi_{z,t}$) for earthworms at soil depth, z and time, t as a function of soil water potential.

in Figure 6.2. T_a, T_b, T_{max} and T_{min} are constants for each earthworm species acclimatized to a particular environment.

An overall activity function appropriate to any water potential and temperature can be calculated by multiplication of equations 6.3 and 6.6. This yields the formulae

$$Act(\Psi, T) = act(\Psi_{z,t}).act(T_{z,t}) \qquad (6.7)$$

The energy budget of earthworms can be expressed as a simple function

$$I = P + R + E \qquad \text{(mg OM)} \qquad (6.8)$$

where I is the energy contained in the ingested food, P is the energy assimilated and retained in tissue production and storage materials for growth, R is the energy assimilated but lost in respiration to maintain the earthworm and E is the unused energy voided as excreta (Lee 1985). The units are mg of dry organic matter.

The basal respiration of earthworms can be expressed as a function

$$R_{bas} = k.W.T_{(z,t)} \qquad \text{(mg OM)} \qquad (6.9)$$

where W is the mass of the worm in grams, $T_{(z,t)}$ is the temperature of the soil around the worm and k is a constant depending on the earthworm species. Values of R greater than the basal rate are considered in equation 6.20. The maximum amount of organic matter that can be used by an earthworm for production is limited and so the maximum growth potential is expressed as

$$P_{max} = \frac{p}{W} \qquad \text{(mg OM)} \qquad (6.10)$$

where p is a constant.

Organic matter provides the energy source for earthworms. The variability of the
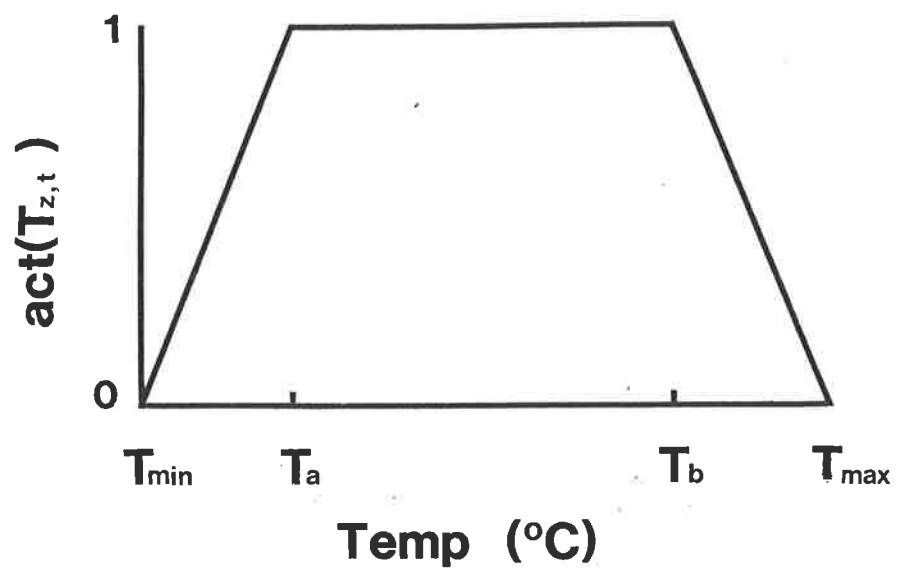
Fig. 6.2 The temperature activity function, act($T_{z,t}$) for earthworms at soil depth, z and time, t as a function of soil temperature.

horizontal distribution of organic matter is unknown but it is apparent from the increased carbon content of cast material over the bulk soil (McKenzie and Dexter 1987) that earthworms can select soil with increased organic matter. The variance of organic matter through the bulk soil, OM_v is expressed using random numbers, $0 < RN < 1$, such that

$$OM_p = OM_i + RN.OM_v \qquad (\text{mg mg}^{-1}) \qquad (6.11)$$

where OM_p is the organic matter at any point expressed as milligrams of organic matter per milligram of soil and OM_i is a constant for any soil depth. (OM_i was usually equal to OM_v, in which case the mean value of OM_p is 1.5 times OM_i.)

Since description of earthworms usually includes the maximum and minimum length and diameter of the species (eg Sims and Gerard 1985) the relative dimension and weight of the earthworms are considered here to be constant for any species. They were expressed as functions

$$d = g(m.W)^q \qquad (\text{mm}) \qquad (6.12)$$

where d is the diameter of the worm, W is the mass of the worm as described in equation 6.9 and g,m, and q are constants for a particular worm species. The length of the worm, L, is linearly related to its diameter

$$L = r.d \qquad (\text{mm}) \qquad (6.13)$$

where r is a constant aspect ratio for a given species.

Note that the volume of a cylindrical worm

$$V_w = \frac{\pi d^2 L}{4} \qquad (\text{mm}^3) \qquad (6.14)$$

and since

$$\rho_w = \frac{W_w}{V_w} \qquad (\text{g mm}^{-3}) \qquad (6.15)$$

(where the suffix refers to worms), then

$$\frac{W_w}{\rho_w} = \frac{\pi\, d^2\, L}{4} \qquad (6.16)$$

and combination with equation 6.13 yields

$$d = \left(\frac{4\, W_w}{r.\rho_w.\pi}\right)^{0.333} \qquad (6.17)$$

where r is the aspect ratio in equation 6.13. Therefore

$$d = \left(\frac{4}{\pi}\right)^{0.333} \left(\frac{W_w}{\rho_w.r}\right)^{0.333} \qquad (6.18)$$

where the coefficient is equal to g from equation 6.12 and equals 1.0839 for all sizes and aspect ratios of cylindrical worms. The power is equivalent to q in equation 6.12 and is also constant for all sizes and aspect ratios of cylindrical worms. $1/\rho_w r$ is equivalent to the constant m in equation 6.12. The density ρ_w of any worms will be approximately 1000 kg m^{-3}. Therefore, for idealized cylindrical worms, the only variables are the mass, W, and the aspect ratio, r.

If the worm is active, food ingestion occurs when food reserves are below a constant value. The uptake of food by earthworms is described by the formula

$$F_{upt} = \frac{OM_p\, \rho\, \pi\, d^2\, l}{4000} \qquad (\text{g OM}) \qquad (6.19)$$

where l is the maximum distance an earthworm can tunnel per unit time. During active tunnelling, by ingesting soil, work is being done. This work is additional to the basal respiration described in equation 6.10. The additional work, R_{work}, is expressed as

$$R_{work} = f.W \qquad (mg\ OM) \qquad (6.20)$$

where f is a constant for the worm species.

If there is no food uptake, movement up or down is based solely on the comparison of layer activity functions with those of adjoining layers. Vertical movement is limited to one layer per time period. No tunnel length is created by this since no food is ingested. This is analogous to the worm moving through an existing tunnel. When food uptake is required, a comparison of the organic matter and the activity in the soil layer currently occupied is made with the adjacent layer or layers. Vertical movement, if any, is then determined by comparison of a calculated layer preference function, for each layer.

$$Pref = Act(\Psi,T)\ .\ OM_p\ .\ RN \qquad (6.21)$$

where $Act(\Psi,T)$ and OM_p have previously been defined and RN is a random number ,$0<RN<1$, but which is weighted by selection of the largest of four such numbers for no vertical movement, while only one such choice is made for each direction of vertical movement. This is because horizontal movement may be in any one of four directions. (see lines 208 to 211 of Appendix 2)

6.3 The Model

A flow chart of the model is shown in Figure 6.3. The layers were numbered (1 to I), from the soil surface with the top six layers each being 25 mm thick, the next three layers 50 mm thick and then three 200 mm layers giving a total profile depth of 900 mm. The soil data input to the model, which can be chosen for each layer, was the layer thickness, the bulk
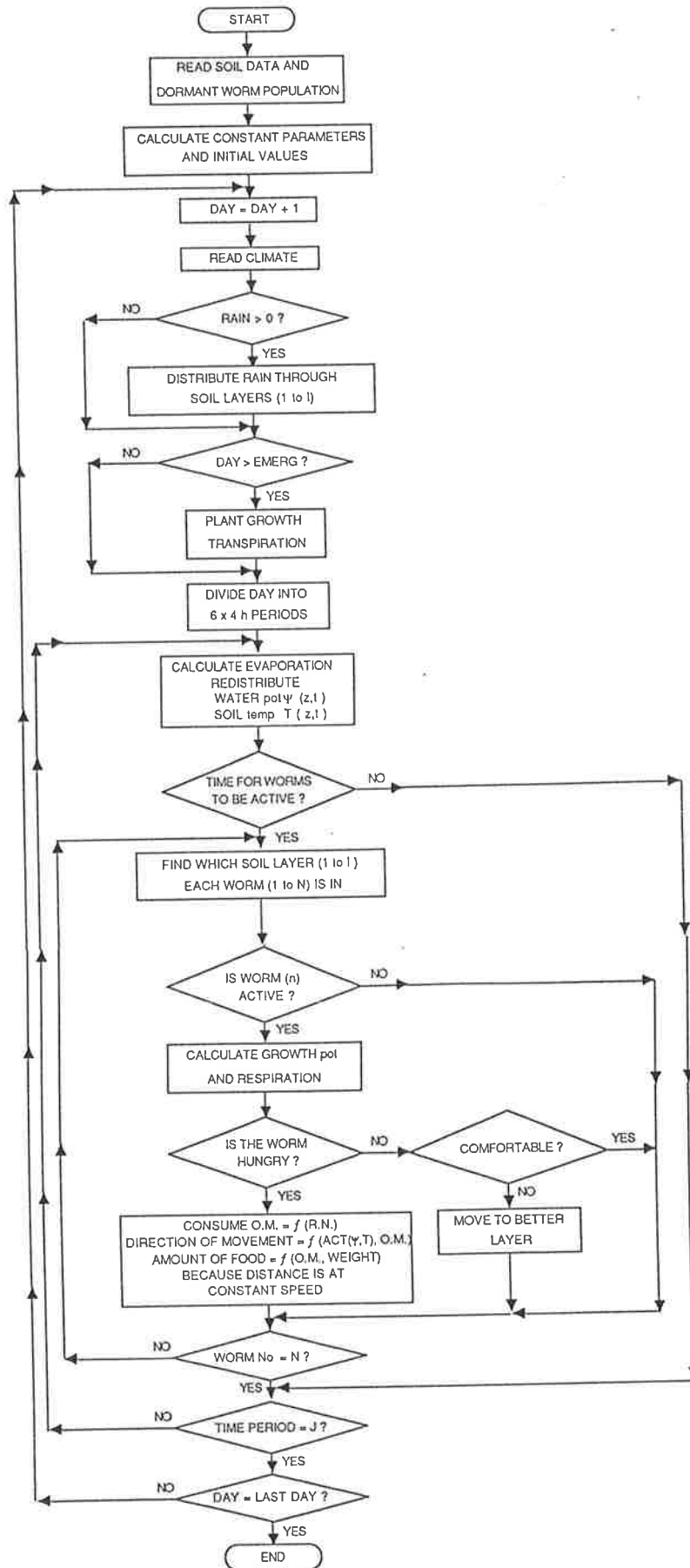
Fig. 6.3 Flow chart of the model.

density, (r), of each layer and organic matter and organic matter variance for each layer.

Climate data inputs were daily values of rainfall, pan evaporation, soil temperature at 25 and 675 mm and air humidity. The distribution of rain through the profile and the soil temperature changes were calculated in 4 hour time steps. The climate data was from the Waite Agricultural Research Institute, South Australia (lat. 34° 58'S, long. 138° 38'E). The climate at this site is Mediterranean, with a mean annual rainfall of 625 mm (W.A.R.I. 1987), of which 465 mm falls during the growing season from May to November. Parameters used in equations are shown in Table 6.1.

The temperature functions used in the model are described in equation 6.4. (See lines 91 to 99 of Appendix 2). The procedure was to first determine the values of the annual temperature cycle at 600 mm depth. From published values (W.A.R.I. 1987) the average temperature at this depth was 16.4° C and the amplitude of the variation was 5.86° C. These correspond to the annual values of Tav and $C_0\exp(-z/D)$ for 600 mm depth respectively. At 600 mm depth the temperature is considered to follow only an annual cycle. Daily maximum and minimum temperature values from 25 mm were read into the model. The arithmetic mean of these was considered the average and the amplitude was half the difference. Here the damping depth D is 90 mm. The mean temperature is thus linear with depth and the amplitude of the daily variation declines with depth.

Earthworm data inputs were taken where possible from information on the species *Aporrectodea rosea*. Twelve worms with a mean fresh weight of 0.326 g and a standard deviation of 0.200 were used in the simulations. The number of worms can be varied. The range of initial weights was from 0.15 g to 0.75 g. This is in excess of the weights published by Bolton and Phillipson (1976 a) when describing the energy profile of the species, but was consistent with the weights found in the previous chapters of this thesis. The energy profile determined by Bolton and Phillipson (1976 a), presented in tabular form in Lee (1985), is adapted and given in Table 6.2. The time step, (t), for all earthworm calculations including the activity functions was 4 hours. The units of mg of dry organic matter are used by Bolton and Phillipson (1976 a) and from combustion in bomb calorimeters were found to be equivalent to 24.7 Joules. Similar results were obtained by Lavelle (1974). Note that worm weight is a

Table 6.1

Standard values of parameters used in the simulations, from equations 6.1 to 6.21

Equation	Parameter	Value
6.1	a	4.0
	b	34.8
	c	1.0
6.2	A	5.2×10^5
6.3	$|\Psi|_{min}$	0.1
	$|\Psi|_a$	1.0
	$|\Psi|_b$	50.0
	$|\Psi|_{max}$	500.0
6.6	T_{min}	0.0
	T_a	15.0
	T_b	25.0
	T_{max}	30.0
6.9	k	2.68×10^{-4}
6.10	p	0.0013
6.19	l	3.0
6.20	f	0.003

Table 6.2

Daily energy budgets per gram fresh weight per day of *Aporrectodea rosea*

(at 10° C) after data of Bolton and Phillipson (1976 a)

Life Stage	Small immature	Adult
Fresh Weight (mg/individual)	60.0	225.0
Consumption (I)		
mg (dry wt.) organic mater $g^{-1} d^{-1}$	232.0	194.0
Assimilation (A = P+R)		
mg (dry) organic matter ingested	6.6	2.6
Production (P)		
mg (dry) organic matter ingested	3.3	0.4
Respiration (R)		
mg (dry) organic matter ingested	3.3	2.2
Egestion (E)		
mg (dry wt.) organic matter $g^{-1} d^{-1}$	227.0	191.0

fresh weight while food intake is dry organic matter.

Two earthworms are initially assigned to each of layers 1 to 5 and one in each of layer 6 and 7. Daily respiration is approximately 0.25% of the worm weight, and the food required for work is approximately one-half that of the worm weight.

Meteorological data from three years; 1977,1979 and 1986, has been applied to the model. The year 1979 received a total rainfall of 733 mm and was the wettest year for which data was available on computer file. The year 1977 was the driest year for which records were accessible receiving only 443 mm. The year 1986 had a total rainfall of 683 mm and was used in the simulations as it was the year in which tunnels had been studied in the field (Chapter 5).

A simulated wheat crop grown during the year modified water use through the profile. Earthworms were assumed to become active only after the date of emergence of the crop. Prior to this ingestion, respiration and egestion are all assumed to be zero. The day of simulated crop maturity was 327 in 1979, 318 in 1977, and 319 in 1986.

6.3 Simulations and Discussion

Typical input and output files are shown in Appendix 2, on lines 305 to 330 and lines 333 to 341 respectively. The output file shows the cumulative tunnel length in mm of each layer, the day of the year, (in this case day 240), the weight of each worm in grams, the layer occupied by each worm at that time, whether the worm was active or not (as shown by 0 or 1) and the activity of each layer.

The mean simulated tunnel length per earthworm produced during the active period (approximately day 145 to day 320) was 7.65 metres. This is equivalent to approximately 300 mm of new tunnel created per earthworm per week during the active period of the year. In Chapter 5 it was suggested that 560 mm wk^{-1} was a realistic value from tunnel lengths measured and published values of gut turnover time.

The mean simulated distribution of tunnels per worm for each layer of the profile is shown in Figure 6.4. As can be seen in excess of 90% of the simulated tunnels are in the the top two soil layers, ie in the top 50 mm of the profile. This is similar in form to the measured
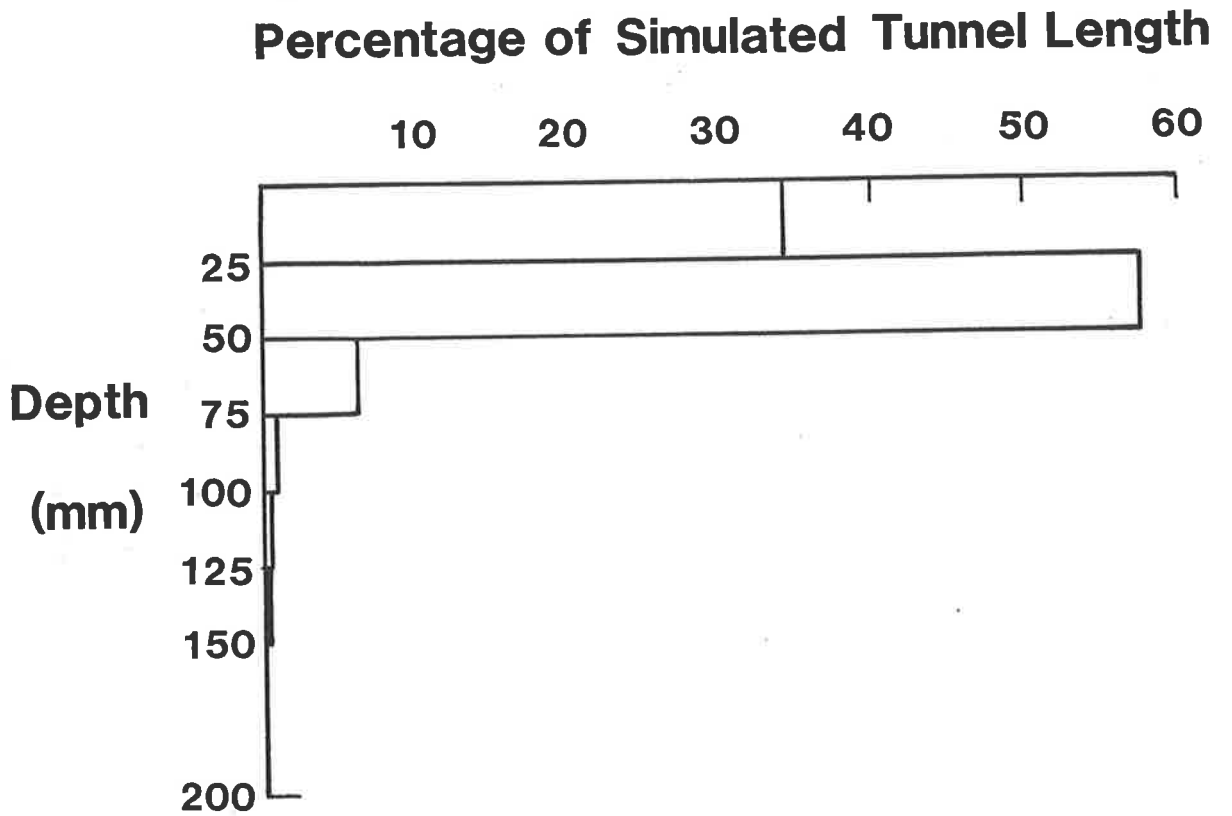
Fig. 6.4 The mean of three years simulated distribution of tunnels per worm for each layer of the profile .

tunnel length against depth presented in Figure 5.3.

Figure 6.5 shows the simulated mean growth rate calculated for all worms. Because of the growth factor as described in equation 6.10 the smallest worms (0.15 g) may reach 1.5 times their initial weight, while the largest worms (0.75 g) achieve only 1.03 of their initial weight. Detailed comparisons of measured (Chapter 5) with simulated (Chapter 6) values of earthworm tunnels and sizes is not considered to be important to the testing of the model, rather the changes to the simulations with changes in parameters were the purpose of the study.

A number of input parameters from the activity and organic matter functions were varied to test the sensitivity of the model. Table 6.3 shows changes in the total tunnel length and the mean maximum worm weight achieved by these changes. The values given are the mean values of the three years. The largest negative potential at which the earthworm becomes inactive is Ψ_{max}. In Chapter 4, I found that earthworms of the species *A. rosea* were inactive in soil at potentials of -50 kPa, while Nordström and Rundgren (1972) found "*Allolobophora*" spp. became inactive at around 2 MPa. Bouché (1971) in Lee (1985) gave the water potential limits of endogées between -20 kPa and -210 kPa. In the standard form the model starts to reduce activity at $|\Psi|_b$ = 50 kPa and totally stops activity at $|\Psi|_{max}$ = 500 kPa. The sensitivity to changes in the (water) activity function were more pronounced for 1977 which was the driest year.

For movement of the earthworms between soil layers only adjacent layers are compared. For simulations with activity ceasing at $|\Psi|_{max}$ = 50 kPa for the year 1986, a band of dry layers (numbers 3 to 6) occurred and trapped a number of worms below this which altered the distribution of tunnels through the profile. This may be due to the limitations of the water movement through the profile or may represent a real situation. The ability of earthworms to detect gradients in water potential is not understood and so it is not clear under what conditions movement through dry layers to more suitable environments will take place.

Setting $|\Psi| < |\Psi|_b$ = 1 led to an increase in tunnel length and as expected this was greatest in the wettest year. The actual tunnelling and ingestion of soil by earthworms in extremely wet conditions is not sufficiently documented to consider whether a water activity of
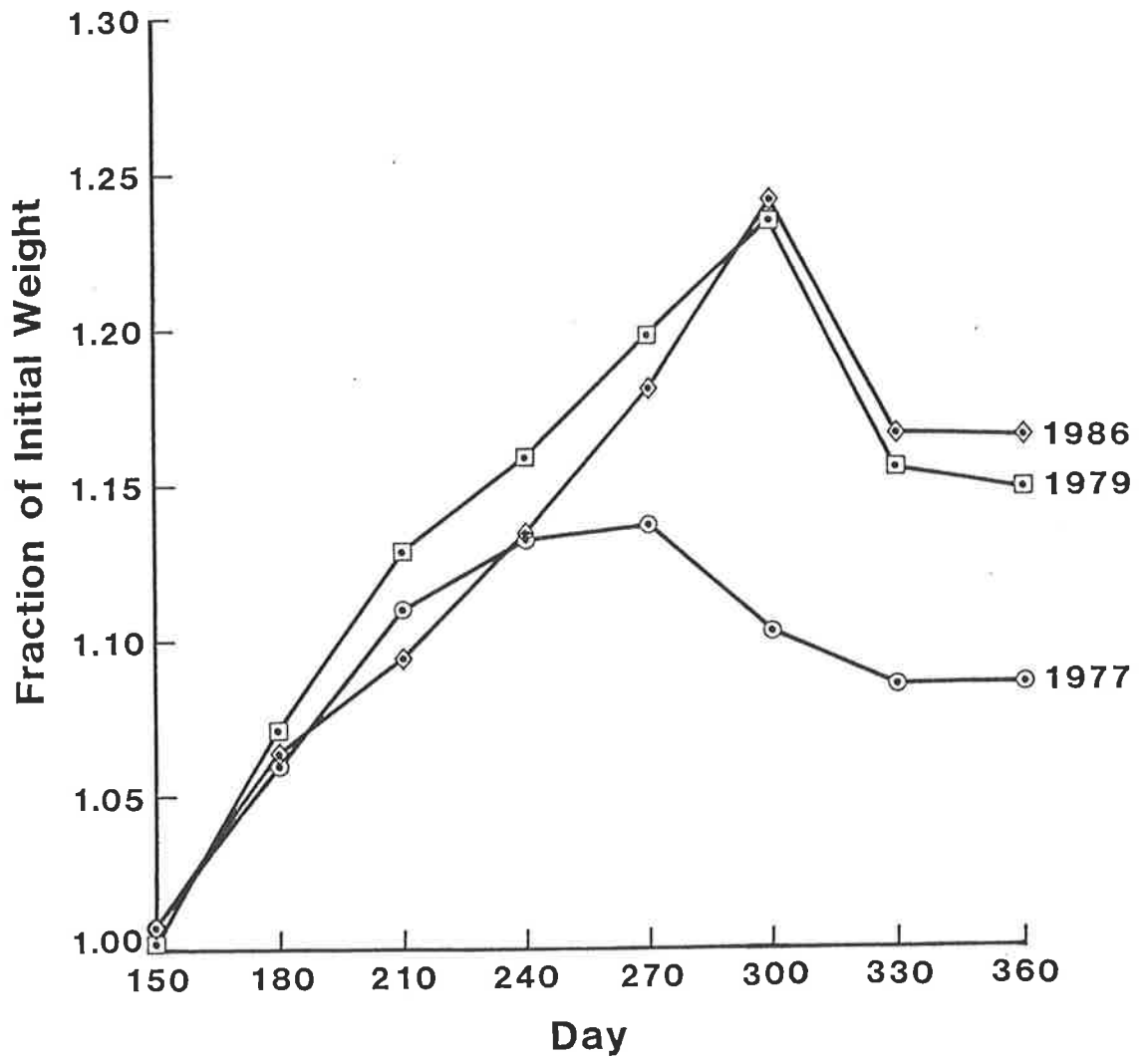
Fig. 6.5 Simulated mean growth as a fraction of initial weight for worms during each of three years. 1977 the driest year for which meteorological data was available, 1979 the wettest year for which meteorological data was available and 1986 the year during which tunnel measurements were made in the field.

Table 6.3

Changes in tunnel length produced and maximum worm weight

obtained by altering some input parameters

Parameter	Change in total tunnel length per worm (%)	Change in maximum worm weight (%)
Ψ_{max} = -5000kPa, Ψ_b = -500kPa	+ 23.7	+ 3.0
Ψ_{max} = -50.0kPa, Ψ_b = -5.0kPa	- 29.2	- 14.5
$\Psi < \Psi_b$ =1	+ 25.4	+ 9.2
T_a = 10	+ 6.3	+ 3.8
T_b = 20	- 7.3	- 1.4
p = 0.00065	+ 0.8	+ 1.6
p = 0.0013.W	- 5.9	- 8.0
2 x OM_i	+15.9	+ 22.1
0.5 x OM_i	- 2.9	- 13.5
0.5 x OM_i, 2 x OM_v	- 3.1	+ 4.1

one is appropriate under these conditions. Certainly Bouché (1971) gives lower limits to the optimum water potentials for endogées, which is why a minimum was used for the standard model parameters.

The standard temperature parameters used in the model allow for an optimum range of 10° C between 15° and 25° C, which is spaced between the published values of 12° C by Graff(1953) and 25-27° C by Reinecke (1975). The setting of a minimum of 15° C means that at some stages of most days earthworm activity will be below maximum. This may be realistic since earthworm activity has circadian rhythms (Ralph 1957, Edwards and Lofty 1977).

The horizontal variance of organic matter in the soil layers was not chosen in response to published values but rather resulted from trial and error. It is obviously a parameter which is important, since keeping the mean amount of organic matter constant but altering its variance is the only change to the model which alters in opposite directions the tunnel length produced and the worm weight.

No attempt is made in the model to allow for reproduction, or mortality of the existing population but in life some production is obviously diverted to or lost by these mechanisms. Simulations were continued to day 360, but because of the activity functions and the setting that a weight loss of 7% of the individual maximum stopped each earthworm from being active, (line 250 of Appendix 2), changes after day 300 were minor.

The model can be used, through the activity functions, to consider the suitability of a soil profile for earthworm prosperity. Through the use of rainfall and soil temperature data from different sites comparisons of suitability could be made. The distribution of the simulated earthworm tunnels through the soil profile can likewise be tested for alternate sites if the profiles of organic matter content are known and if the effects of different contents of organic matter in the soil have been quantified. Other geophagous species for which energy budgets are known could be tested using this model to indicate if similar depth profiles of tunnels occur.

There are however a number of limitations to the model which could be refined if more detailed information was available. The temperature range used for maximal earthworm activity in this model is based on published values, but acclimatization of earthworms and the

conditions under which the measurements are made may affect the results. More detailed information from field studies of temperature preferences and the relationship between temperature and water may enable refinements to be made. Similarly the importance of parameters such as soil texture are not considered in this model. Without measurement of the relative importance of sand and clay proportions in the soil to the welfare of earthworms such inclusions are impractical.

With refinement of temperature optima the use of temperature as a control of daily activity could be avoided. Allowance for periods of reduced activity as with circadian rhythms could be made. Refinements of this type may enable simulations to respond with more sensitivity to variations between years. At the moment it is not possible to ascertain whether the small changes between years reflect actual limited variation or reflect deficiencies in the model.

Chapter 7
General Discussion and Conclusions

7.1 General Discussion

The purpose of this chapter is to integrate the experimental information obtained here with published results to improve understanding of earthworms and their tunnels in relation to soil physical properties. Some of the experimental work given in previous chapters has been published and is set out in Appendices 1, 3, and 4. From integration of ideas conclusions will be drawn and suggestions for new lines of enquiry made. It is evident from Chapters 1 and 2 that while the anatomy and some of the physiology of some earthworm species has been defined, the relationships of earthworms and their tunnels with soil structure and other physical properties is not fully understood. These gaps in our understanding make it impossible to assess accurately the importance of earthworms to agriculture or more specifically to soil structure and plant root growth. The exception to this may be in rigidly defined pot type experiments with the plant and earthworm species defined and soil properties carefully measured. However it is difficult to extrapolate the importance of earthworms to root growth and soil structure in the field from simple pot experiments performed in controlled environments.

As discussed in Chapter 1 there was a need to develop suitable techniques for the measurement of direct physical force in the tunnelling of earthworms and to attempt to relate this to known soil mechanical properties (eg penetrometer resistance) and to the forces exerted by the elongation of plant roots. Because two discrete layers of muscles are involved in earthworm locomotion it was necessary to consider both the axial and radial forces generated by the separate layers, so that the importance of soil displacement by direct pressure could be considered and compared with other tunnelling mechanisms, such as soil ingestion.

It was also important to consider changes to and the fate of soil ingested by earthworms. Whereas chemical studies have looked at changes in plant nutrient mineral composition of casts, physical changes occurring as soil passes through the worm gut and excreted have not been considered, except for shape description (Bal 1973). The shape,

strength and physical modification of soil excreted as casts were considered here.

Earthworm tunnels have been regarded as significant pathways for water and air movement through soil and for plant root growth, so field studies were undertaken to determine tunnel structure. Information about earthworm behaviour was used in a simulation model to consider factors influencing tunnelling behaviour.

The mean ingestion rate for earthworms tunnelling through discs of compacted soil as described in section 3.1.3 and extrapolated to an entire day was 1300 mg dry soil per gram fresh weight of earthworm per day. This value is near the mid point of the range given by Bolton and Phillipson (1976 a) of 800 - 1900 mg dry soil per gram fresh weight of earthworm per day. This compatibility of rates suggests that tunnelling into compacted soil (of density 1.51 tm^{-3}) by *A. rosea* can proceed at a similar speed to tunnelling into soil with a published density of only 0.72 tm^{-3}. It should be recalled that Rushton (1986) found a reduction in tunnel length with increasing density between 1.38 and 1.66 tm^{-3} but that this was for *L. terrestris*, an anécique earthworm, while Dexter (1978) found no correlation between soil strength and tunnel length for *A. caliginosa*, which is an endogée.

Since there is only minor loss in weight of soil in the passage through the earthworm gut the rate of soil ingestion must correspond with the egestion rate. Published values of egestion rates (described in section 5.1.3) vary greatly and range from 0.4 g/ worm / day (Barley 1959 b) to 2 g/ worm/ day (Bolton and Phillipson 1976 a). It is apparent that not only can earthworms tunnel without detectable loss of speed into compacted soil but that the soil can be egested at a rate sufficient to maintain this tunnelling speed. It does not follow that the maximum sustainable rate is the only rate used. It may well be that rapid tunnelling is employed only to create a new tunnel system or to move through compacted soil to a more favourable environment (as from the soil in a matchbox experiments in Chapter 3) but that once this goal is achieved tunnelling rates may be reduced. Also extrapolation of activity from a few hours to an entire day is likely to be inappropriate. Movement to a more favourable environment does not necessarily require detection of improved conditions but may be a simple geotropic response.

As mentioned in Chapter 3, Bouché (1977) suggested that endogées have limited

muscle development, but Lee (1959 a) described a more complex situation for megascolecoid earthworms and stated (Lee 1985) that it may also be more complex for lumbricids than Bouché proposed. It is likely that the evolution of muscle development was favoured as a means of resistance to removal from their tunnels, as well as an adjunct to tunnelling. The importance of the setae to the axial forces must also be mentioned since they provide the anchorage that makes movement possible. Without anchorage provided by the setae, friction between the worm and the soil would be inadequate, especially since friction is reduced further by mucus secreted by the worms to provide smooth movement along the tunnel. It seems likely that the maximum thickness of the secretions along the tunnel walls will not exceed the extension of the setae if the worm is to maintain maximum grip.

Radial pressures measured for *A. rosea* had a mean value around 230 kPa. It was suggested that this would be insufficient to cause compaction around tunnels in most agricultural soils since the soil is likely already to have been compacted to greater pressures than this (at the same water content), so that repeated compression at lower pressure would not increase compaction. If this is the case, the diffusivity of air from tunnels to the bulk soil will not be reduced by the pressures caused during tunnelling. Similarly, the movement of water from earthworm tunnels to the bulk soil is unlikely to be inhibited by compaction. However the chemical linings of the tunnels (as described by Jeanson 1964) may alter the diffusivity properties of the tunnel walls.

While compaction of soil around tunnels will not usually occur, it is possible to estimate the conditions under which an earthworm will be able to displace a soil aggregate of known size within a bed of similar sized aggregates, such as may be the case in a fine seed bed. Applying the axial forces derived in section 3.1 of this thesis to equation 2 of Whiteley and Dexter (1982) shows that :

$$\frac{F_{max}}{\rho . g . D^3} = A_1 \left(\frac{d}{D}\right)^{A_2}, \qquad (7.1)$$

where F_{max} is the force required to displace an aggregate vertically within a bed of similar

aggregates and in this case the axial force generated by the worm is used, ρ is the density of the aggregate, g is the acceleration due to gravity, D is the aggregate diameter, d is the depth from the surface of the bed and A_1 and A_2 are adjustable parameters given in Whiteley and Dexter (1982). The probabilities that *A.rosea* can displace vertically an aggregate has been calculated from the values given in Table 3.1 and are shown in Figure 7.1. It can be seen that in seed beds the loose, aggregated structure will enhance the ability of earthworms to move by pushing soil aside and that with smaller aggregates in the bed, a worm could move at greater depths by this mechanism.

The tunnelling of earthworms through soil can thus take place by a number of mechanisms or combinations of mechanisms. Figure 7.2 presents the "decision" making process for earthworms when actively tunnelling, in contrast to grazing along an existing tunnel.Estimates have been made in this work of the ability of earthworms to displace soil by simply pushing it aside. The physical limitations to earthworms sucking particles from the soil matrix have to my knowledge not been estimated. An initial approximation is possible because earthworms are able to move vertically up glass surfaces, where the setae will give no grip, by using suction from the mouth to secure them. Thus the suction is sufficient to hold the weight of the worms (Roots 1956), which for *A. rosea* may be up to 1 gram. If this suction acts over an area of the mouth, which may be 0.5 mm diameter, then a minimum suction developed by the species is 51 kPa. Parry (1954) found that spiders were able to collect pore water at matric potentials to 50 kPa which indicates that the value calculated here for earthworms is similar to that attained by other soil animals. Other possible mechanisms involved in tunnelling include first weakening the soil by wetting. As the strength of Urrbrae fine sandy loam is decreased by a factor of 1.68 for each percent increase in gravimetric water content, as shown in equation 4.24, the wetting of soil may provide a useful adjunct to the previously-described mechanisms.

Cast material shrank with drying, increasing the density of the individual casts to greater than the density of the individual soil aggregates. This increased density (or decreased voids ratio) implies that the largest included voids in the casts will be smaller than the largest included voids in the soil aggregates. This decrease in large voids is consistent with
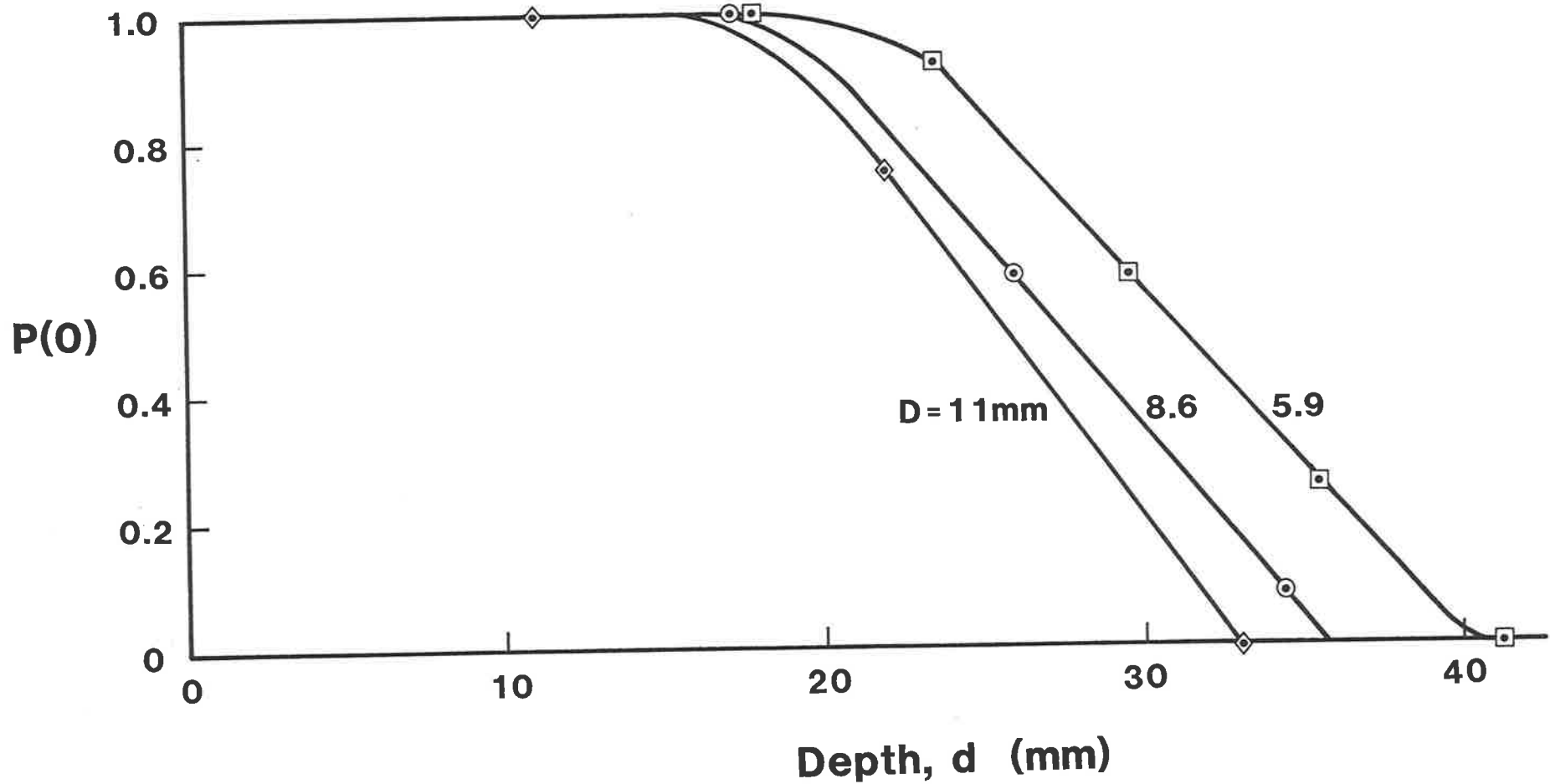
Fig. 7.1 Probability that *A. rosea* can exert an axial force sufficient to displace vertically an aggregate of diameter D, at depth d within a bed of similar aggregates.
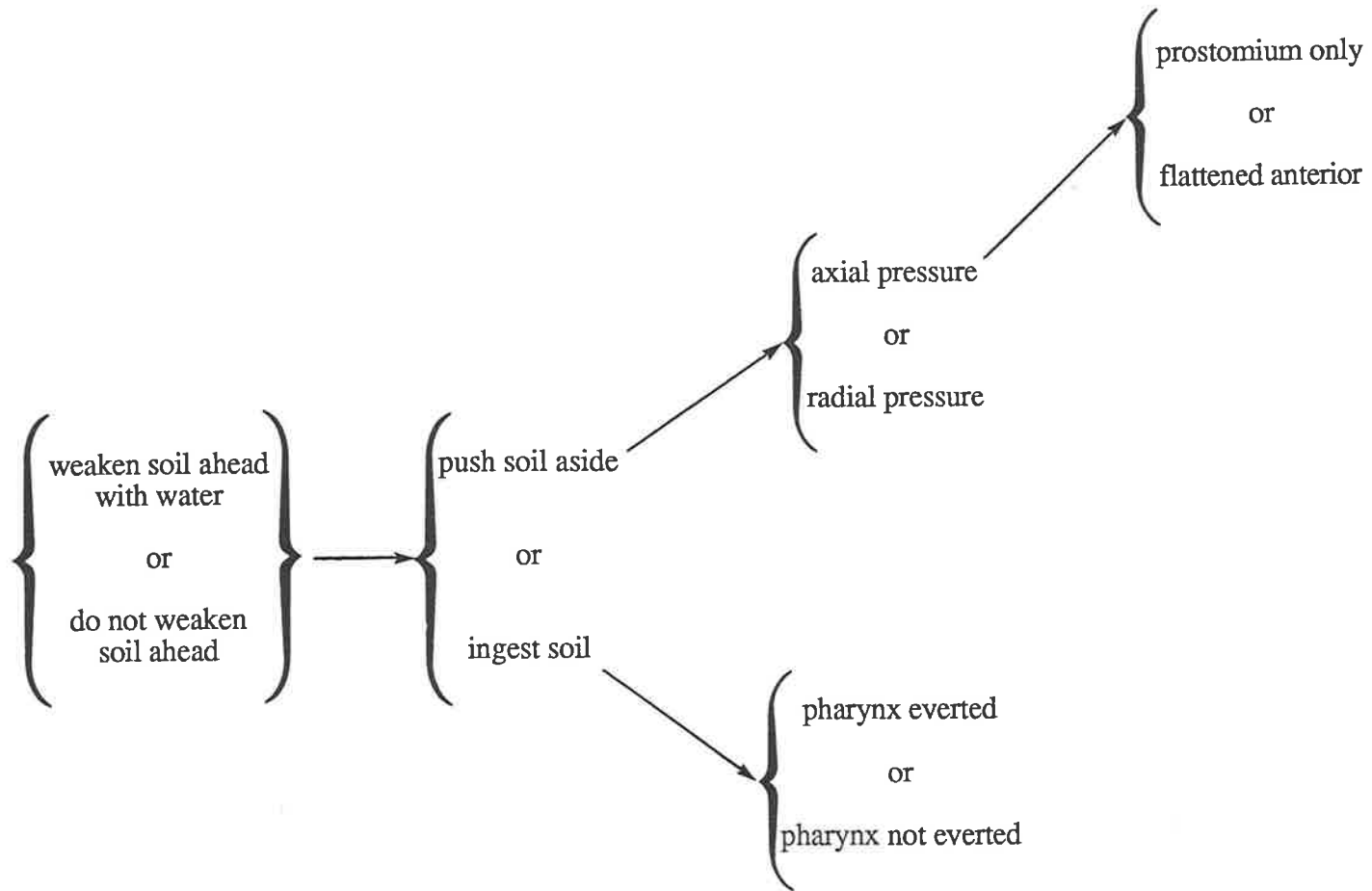
Fig. 7.2 Suggested decision making process for an earthworm tunnelling in soil.

homogenization of the cast as it passes through the worm gut. The largest voids in a soil sample are the determinants of tensile strength (Braunack et al 1979, Hadas 1987), and thus it is to be expected that dense homogeneous casts will be stronger than bulk soil aggregates. Hadas (1987) found that aggregates from cultivated soil were stronger than aggregates from a non-cultivated site. He attributed this increased strength to shearing and compaction during tillage resulting in improved orientation of the particles within the aggregate. This is analogous to the shearing and compaction that occurs in casts. Nevertheless, while dry individual cast pellets may be more dense than the bulk soil aggregates, the packing together of incompletely dry casts may be such as to give a decreased bulk density.

The dry bulk density of the wet casts is 1.15 tm^{-3} and the density of the dry casts is 1.67 tm^{-3} therefore, provided that there are no differences in the amount of material present extensive shrinkage must have occurred. Assuming the shrinkage is equal in all directions, which is reasonable as I have suggested material is homogenized in the passage through the earthworm gut, the size of the dry casts relative to the wet casts can be calculated. The radius of the wet casts is 1.13 times the radius of the dry casts. Bal (1973) suggested that he had observed that wet modexi had a diameter 1.5 times that of dry modexi, but this is obviously an over-estimation since if no material was lost the dry volume would be only 0.3 times the wet volume and the density increase as a result of such shrinkage would be such that unrealistic densities would be predicted.

Soil ingested by earthworms is sheared in the gut at very low pressures. This is possible because of the low density (and high water content) of the material as it passes through the gut. It is also shown by the density and water content of the fresh cast. Extensive shearing accounts for homogenization of the material in passage through the gut. Fresh casts shrink considerably with oven-drying, producing material more dense than the bulk soil aggregates. In a natural situation drying would not be as severe and the cast material may be stabilized at densities and water contents significantly different from those found in the oven dry state.

Only the shape of fresh cast material was measured in Chapter 4 and so the extent to which the shape of casts alters with drying has not been assessed. Fresh material was

convenient for measurement as the age of the cast was known. Since cast material will continually change, as a result of drying, weather, treading and microorganisms until it is indistinguishable from the bulk soil, fresh cast material presents the maximum difference from the bulk soil. If sufficient distinct cast material existed in bulk soil used for shape measurement, a bimodal distribution would occur with one peak representing cast material and one representing the bulk soil. Between the two peaks the shape of decaying cast material would be represented. As was stated in Chapter 4 none of the bulk soil material assessed appeared to be recently biologically influenced.

The shape of composite casts, consisting of aggregated masses of excreted pellets and slurries, as sometimes occurs at the openings of tunnels to the surface will differ from the individual pellets assessed here. Whether the composite material could be divided into distinct component parts of the same shape as the pellets has not been tested, but may be necessary if surface cast shape were to be used as an indicator of biological activity. If different species are to be introduced into new areas as has been suggested for South Australian agricultural areas (Barley 1959 b, Rovira et al 1987) an assessment could first be made of the shape of soil aggregates and casts found at the site and comparison made after the introduction. This would provide an alternative assessment of the numbers and effect of the different species and would also provide a measure of the zoological ripening of the soil, as described by Bal (1982).

The increased strength of dry casts may not only result from density increase but may be enhanced by fungal hyphae binding the material together (Parle 1963). The opening of new surfaces to attack by microorganisms as a result of the shearing of soil in the earthworm gut (Rovira and Greacen 1957) may enhance the binding. Large composite casts, by definition made as a packing of small casts and with much larger void spaces, would not be expected to have the same strength as the smaller casts.

The extremely low shear strengths of fresh cast material indicate that initially cast material can be easily broken down by physical action or dispersion. When casts have dried and shrunk with a consequent increase in density, they will be more resistant to breakdown.

At the site where work for Chapter 5 was performed, the maximum activity of earthworms in the soil profile is at depths less than 200 mm, as shown in Figure 5.4. The

distribution of organic matter through the profile as seen in Figure 5.5 appears to decrease exponentially from the soil surface to a depth of approximately 200 mm, below which a low residual level persists. Even at the soil surface the measured content of total carbon (1.35%) is smaller than that found in many soils. The amounts of carbon present and the shape of the distribution are similar to the values of Piper (1938) as presented in Oades et al (1981). The profile has an A1-A2 horizon boundary near the 150 mm depth, with the A2 containing moderate amounts of gravel and stone (Chittleborough and Oades 1979). The coincidence of soil and biological features around 200 mm depth suggest that they may be interrelated.

While the exact date of introduction of *A. rosea* and *A. caliginosa* earthworms is not known, it cannot be prior to European settlement, which in this case was approximately 150 years ago. A2 horizons in red-brown earths are attributed to at least moderate weathering (Oades et al 1981) which requires a time scale at least two orders of magnitude greater than the 150 years maximum residence by these peregrine earthworms. Thus while the soil horizon structure may influence the depth of activity of the earthworms, they have apparently not altered the horizon boundaries.

It has been proposed that continual cycling of the top soil by earthworms may be associated with the formation of horizons higher in organic matter than the bulk soil because of the inclusion of litter layers. Shipitalo and Protz (1987) found in a comparison of tillage and no tillage corn production that after only seven years the amount of organic carbon was greater at all depths and substantially higher below 200 mm in the no tillage system. This was attributed to the action of earthworms. Since changes were detected by Shipitalo and Protz (1987) in only seven years, the similarity of carbon profile shown in Figure 5.4 with that from the 1938 data used by Oades et al (1979) indicate that a steady state in organic matter distribution has been established at the site for at least 50 years.

The close relationship between organic matter and earthworm activity is supported by the similarity in shape of their distributions with depth as can be seen in Figures 5.4 and 5.5. The two earthworm species found in the field work are widespread and are known to be suited to environments disturbed by man (Lee 1985). Further, inputs of organic matter to the soil profile at this site are likely to occur mainly at or near the soil surface. From this it would seem

likely that the carbon profile is one of the critical factors determining the depth of action of these species. If new species are to be introduced to this environment as has been suggested by Barley (1959 b) and by Rovira et al (1987) I would suggest that anécique ecotypes, which would not compete directly with the endogées present and which may increase the organic matter levels at depth by dragging surface material deep into burrows, would be most appropriate.

That the tunnels mapped in this work are not vertical is of major importance, since the chance of a plant root which is growing vertically meeting a tunnel is proportional to the sine of the angle between the tunnel and the vertical. Many plant roots, notably the seminal or tap roots of dicotyledons, grow vertically and as these roots may be impeded in their downward growth by compacted layers or ploughpans the presence of non-vertical pores provides access for the roots to a greater soil volume. Figures 5.6, 5.7, and 5.8 show that the deeper the earthworm tunnels are in the soil, the nearer to vertical they become. Thus a plant root, initially growing vertically, but which meets and grows along an earthworm tunnel, perhaps through a hardpan, will be directed more rapidly deeper into the soil the further the association continues. The significance of the angle of earthworm tunnels to plant roots could be assessed by examining the angles of the major axes of plant roots with depth in soil and comparing this with the angles of earthworm tunnels. Small-scale pot experiments, growing plants with and without worms, are unlikely to provide a realistic environment for interactions between roots and tunnels, particularly since both roots and earthworms (Evans 1947) tend to follow the edges of the pot. The interaction would therefore differ markedly from that I have shown in the field.

From my observations during the measurement of tunnels in the field I conclude that the endogée species that were considered here commence a tunnel system, possibly at a crack in the soil surface, by rapid movement of soil. Tunnelling may involve some pushing of the soil aside but is predominantly by rapid ingestion of soil. This rapidly-ingested soil will similarly be passed rapidly through the gut and excreted as casts. Unless there are large voids in the soil, the casts will be deposited at the soil surface. Although the surface soil may be rich in organic matter, the worm will rapidly tunnel into the soil to meet the pressing need for a

refuge safe from predators and desiccation. The initial construction may be several times the length of the worm and may have several surface openings. The hypothesized rapid tunnelling and corresponding rapid transit through the gut are consistent with the measurements of gut transit time by Bolton and Phillipson (1976 a). Once a safe haven is constructed the worm feeds by browsing or grazing along the tunnel length, perhaps extending its length in the process. Browsing may be more extensive along root surfaces as was implied by Rovira et al (1987). Regions of organic rich soil may be ingested along the tunnel, creating tunnels of uneven diameter, or at particular sites, thus creating cavities. This grazing will involve gut transit times much longer than that during the initial tunnel construction, permitting improved digestion of food. During grazing, the transit times may be comparable with those measured by Barley (1959 b), which were much longer than those of Bolton and Phillipson (1976 a). The grazing procedure will provide selected food and need not be continuous, so that the activity can be confined to times when the environment, particularly temperature and water are most suited to activity. This is compatible with the diurnal rhythms described for several earthworm species by Lee (1985). If the temperature of the surface soil becomes uncomfortably hot, a deeper tunnel may be constructed to provide less extreme conditions, but most of the tunnelling will be near the soil surface where food is more abundant. It is suggested that a burrow will be actively used for a period of up to several weeks. As both *Aporrectodea rosea* and *A. caliginosa* are parthenogenetic there is no need to search for other individuals and this may explain why only one mapped tunnel system contained more than one adult earthworm. When the food available in a tunnel has been eaten out, a new tunnel is constructed. New constructions are thought to have at least one surface opening. Old tunnel systems may provide void space for the deposition of cast material.

Figure 7.3 is a first attempt to relate the mean survival time of tunnels to the their depth in the soil. Although only two points are plotted from the results given in section 5.2.3 it is reasonable to consider that tunnel lifetime will be longer at greater depth since the forces that act on soil are usually most extreme near the soil surface. This applies to biological activity, which as has been shown here for earthworms, is maximal near the soil surface as well as to physical factors such as raindrop impact or treading by animals, which are confined to the soil
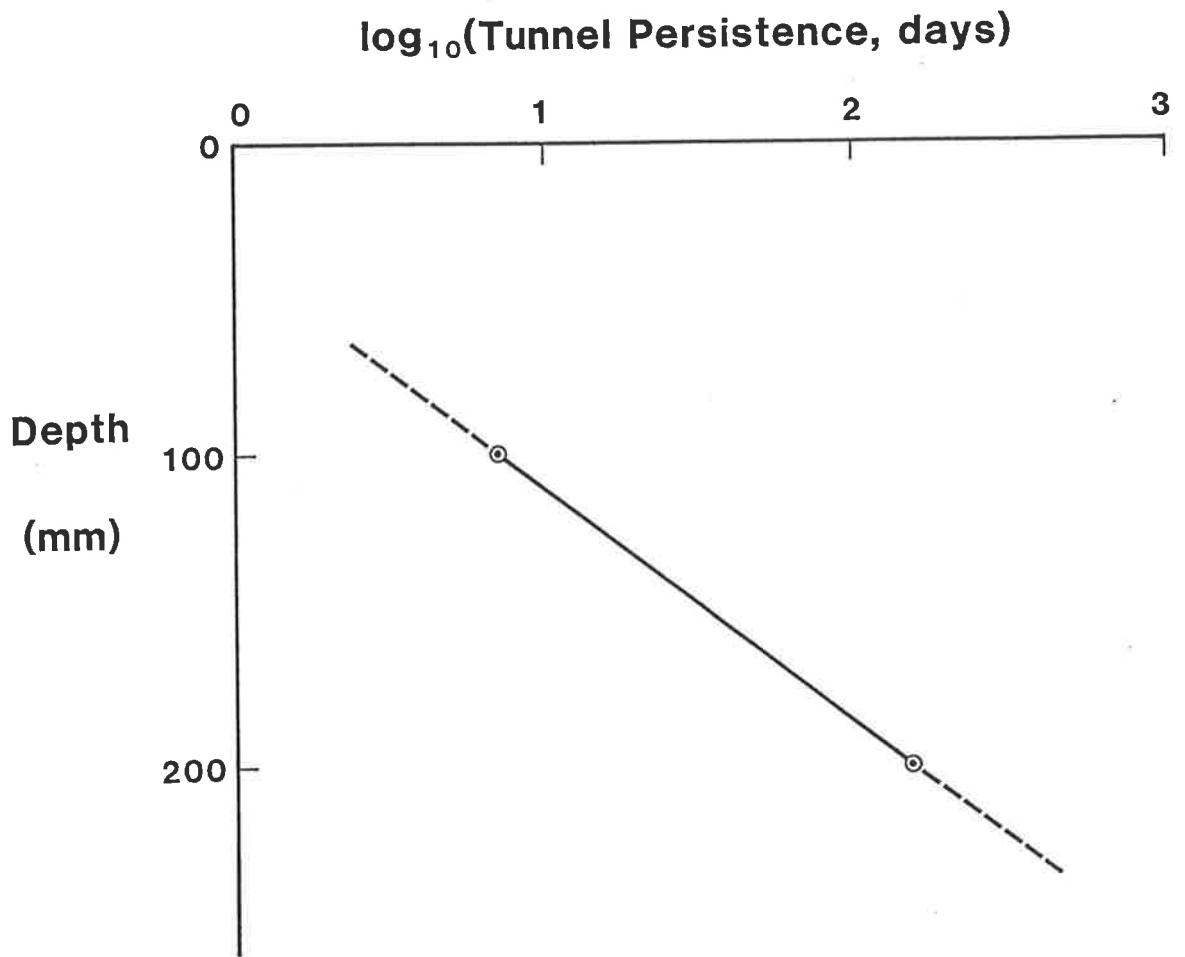
Fig. 7.3 Estimated time of tunnel persistence in permanent pasture as a function of depth.

surface, and to environmental influences such as temperature and water content fluctuations which are greatest at the soil surface. It is interesting to speculate what factors may alter the slope of the line relating persistence of tunnels with depth. Obviously agricultural activities, such as traffic and tillage, will destroy large numbers of tunnels and may alter the relationship from a straight line, while seasonal growth of grass roots which intercept tunnels, must be a factor leading to the destruction of tunnels. This suggests that destruction rates will vary seasonally. If this is the case, periods of maximum destruction may correspond with periods of maximum earthworm numbers and therefore of maximum tunnel production.

In section 5.3 the influence of tunnels on the breakdown of aggregates was considered. Breakdown results from the destruction of a tunnel by fracture of the soil aggregate containing it, and it was shown that the larger the diameter of the tunnel through the aggregate the less force was required for fracture. As stated in Chapter 3 penetrometers are not appropriate models for worms moving through soil, so artificial tunnels for these experiments were produced by removal of wet soil and not by radial strain produced by blunt penetrometers, although whether this is an appropriate model for the changes induced by earthworms is not sure. Section 3.2.3 shows that tunnelling by earthworms led to a greater reduction in strength of soil discs than would be predicted from Figure 5.12 as a result of radial strain.

The computer model described in Chapter 6 integrates some of the environmental factors influencing the growth and movement of individual endogée earthworms. It was important for the earthworm section of the model that a water balance model incorporating root growth was available to provide a simulated soil profile in which to simulate earthworm activity. Climatic data from any available site could be applied to the model to assess the depth of tunnelling. However limitations to the model include the lack of information on the horizontal distribution (spatial heterogeneity) of organic matter in soils and on the ability of earthworms and the range over which they are able to detect such changes.

If decay rates of tunnels as estimated in Chapter 5 were included it would be possible to test the validity of such measurements and to estimate changes in soil macroporosity caused by endogée earthworms. If similar data can be obtained for anécique earthworms the

introduction of such species to an environment devoid of such deep tunnelling species could be simulated. Population dynamics under the different conditions may influence the activity of the anéciques. Inclusion of life cycle data such as predation, parasitism and competition would require major modification of the model as it currently exists.

The acclimatization of earthworms to new temperature and water regimes provides a challenge for the model. The model cannot predict changes due to acclimatization but it does provide a method to examine the level of change required for an earthworm from a different climate to achieve a desired level of activity. This can be done by varying the activity functions.

7.2 Suggestions for future work

From the work described and the discussion it is apparent that several paths for future studies are open.

(1) Methods devised in Chapter 3 to measure the forces involved in tunnelling provide a way of comparing the muscle development of different species and thus to clarify the importance of muscle complexity when classifying earthworms into ecological groups.

(2) To test whether endogée earthworms are determining the shape of the organic matter profile, experiments could be performed by creating soil columns with uniform organic matter distribution, except for a surface litter layer. Inclusion of earthworms in some of the columns, combined with measurement of the carbon distribution over time would enable the importance of the earthworms to carbon redistribution to be assessed. This could help to isolate whether earthworms are determining the shape of the organic matter profile or whether the organic matter profile is determining the zones of earthworm activity.

(3) If different species are to be introduced into new areas as has been suggested for South Australian agricultural areas (Barley 1959 b, Rovira et al 1987) an assessment could first be made of the shape of soil aggregates and casts found at the site and comparison made after the introduction. This could provide an alternative assessment of the numbers and effects of the introduced species.

(4) To test whether initial tunnelling and gut transit times are more rapid than when the tunnel is more developed, experiments could be performed in large scale pots and studied using neutron radiography. This would enable in situ measurement of tunnel construction.

(5) More information on the relationship between life span of tunnels and depth in the soil profile is needed. This would enable the influence of tunnels on the movement of water and air through the profile to be better understood, and would facilitate comparisons of the mechanisms leading to tunnel breakdown.

(6) To understand the movement of endogée earthworms through the soil both the spatial distribution of organic matter, and the ability of these earthworms to detect gradients of organic matter content need to be clarified. More precise definition of the limits of acclimatization of earthworms to new environments is needed to test their suitability to new environments.

(7) The development of a computer simulation of earthworm tunnelling in a realistic soil profile offers the prospect of testing relationships between earthworms and the environment, by using meteorological data from other sites. Further if the decay rates of tunnels described in this thesis were included in the model changes in soil macroporosity could be simulated. If data on the energy budgets and tunnel structures of anécique earthworms were measured the model could be extended to simulate changes to the macro-pore space distribution caused by the introduction of new species.

7.3 Conclusions

On the basis of experiments performed in this thesis, the following conclusions can be drawn.

(1) The pressures exerted by *Aporrectodea rosea* :

in the axial direction reach a maximum of 116 kPa and have a typical value of 73 kPa,

in the radial direction had a maximum of 330 kPa and a mean value of 230 kPa,

the suction from the mouth has been estimated to reach at least 51 kPa, and

the internal pressures shearing soil were estimate to attain a maximum of 742 Pa and typically were 260 Pa.

(2) The pressure applied by *A. rosea* to penetrate soil is approximately one-twentieth of that required by a blunt penetrometer and is approximately one-quarter of that applied by plant roots.

(3) The shape of fresh cast material is smoother and more nearly spherical than the shape of similar-sized aggregates from the bulk soil.

(4) Dried cast material has greater tensile strength than similar sized aggregates from the bulk soil, but fresh cast material has extremely low shear strengths. For *Aporrectodea rosea* a mean value of the shear strength of fresh casts was 364 Pa.

(5) Tunnels created by *Aporrectodea rosea* and by *A. caliginosa* are not vertical near the soil surface but tend toward vertical at increasing depth.

(6) Most activity of *A. rosea* and *A.caliginosa* in a pasture is in the top 200 mm of soil, but the maximum number of tunnels found is between 300 and 400 mm depth. From this it can be predicted that the life span of earthworm tunnels and other biopores in general increases with depth.

(7) Knowledge of the energy budgets for these endogée earthworms, and knowledge of appropriate soil and environmental data make it possible to simulate their growth and tunnelling.

APPENDIX 1

McKenzie B.M. and Dexter A.R. (1987)

Physical properties of the casts of the earthworm

Aporrectodea rosea

Biol. Fertil Soils 5 : 152-157

McKenzie, B. M. & Dexter, A. R. (1987). Physical properties of casts of the earthworm Aporrectodea rosea. *Biology and Fertility of Soils, 5*(2), 152–157.

APPENDIX 2

Computer Simulation Model

referred to in Chapter 6

```fortran
1                          Appendix 2
2        common om(12),var(12),act(15),burr(12),pf(12)
3        common weight(12),weightx(12),lay(12),food(12),grfact(12)
4        common depth(12),ihyb(12),rval(6)
5        common rho(13),thick(14),z(13)          ! rho t/m**3
6        common wc(13),wcs(13),sw(13)             ! water g/g
7        common wat(12),dwat(12),watp(12),wats(12)     ! mm/layer
8        common hsw(13),hn2(13),hn1(13),hsat(13)      ! suction, m
9        common com(13),con(13),scon(13)            ! conductiv, mm/day
10       common flow(13),flmax(13)             ! mm/day
11       common temp(12),tav(12),amp(13)          ! C
12       common a(12),b(12),c(12),en(12)          ! water retention
13   !
14   c  INITIAL OPERATIONS
15   !
16       read(6,1) pri,wloss,resp1,resp2,workf,growf,potgrowth
17   1     format(f4.1,f6.2,f7.4,f5.1,f7.4,f5.1,f7.4)
18       write(5,2)
19   2   format (1x,'burr1  burr2  burr3  burr4 burr5 burr6 burr7 burr8
20    x   burr9 bur10 bur11 bur12')
21       write(5,3)
22   3   format (1x,'jday  weig1 weig2 weig3 weig4 weig5 weig6
23    x  weig7 weig8 weig9 wei10 wei11 wei12 ')
24       if(pri.le.0.5) go to 9
25       write(5,4)
26   4   format(1x,'l1 l2 l3 l4 l5 l6 l7 l8 l9 l10 l11 l12 h1 h2 h3 h4
27    x  h5 h6 h7 h8 h9 h10 h11 h12')
28       if(pri.le.1.5) go to 9
29       write(5,5)
30   5   format(1x,' act1  act2  act3  act4  act5  act6
31    x  act7  act8  act9  ac10  act11 ac12' )
32   9   read (6,12) lday,jwrt,iran,dist,hswi,p,fm,alfa
33   12    format (2i4,i10,3f6.1,2f7.4)
34       read (3,13) nsd, june
35   13    format(2i4)
36       do 14 i=1,12
37       read (6,15) a(i),b(i),c(i),wcs(i),rho(i),flmax(i)
38    x  ,thick(i),om(i),var(i)
```

```
39    15    format (7f8.3,2f6.3)
40    14    continue
41          do 17 n= 1,12
42          read(6,18) lay(n),weight(n),grfact(n)
43    18    format(i4,2f6.2)
44          weightx(n)=weight(n)
45    17    continue
46    !
47          rho(13)=rho(12)
48          thick(13)=thick(12)                    ! layers, mm
49          thick(0)=1.0
50          z(0)=0.0
51          do 19 i=1,12
52          z(i)=z(i-1)+(thick(i-1)+thick(i))/2.0          ! depth, mm
53          y=ran(iran)
54          en(i)=2.0/b(i)-2.0                 ! exp. for hsw(i)
55          sw(i)=-b(i)/abs(b(i))              ! sign of teta,+,-
56          wc(i)=(exp((alog(hswi)-a(i))/b(i))-c(i))/sw(i)   ! g/g, initial
57          hsat(i)=exp(a(i)+b(i)*alog(c(i)+sw(i)*wcs(i)))    ! suction at a.e., m
58          wats(i)=wcs(i)*rho(i)*thick(i)            ! mm/layer at sat.
59          watp(i)=(exp((5.07-a(i))/b(i))-c(i))         ! w.p.,mm/layer
60        x /sw(i)*rho(i)*thick(i)
61          call water(hsw(i),hn2(i),hn1(i),a(i),
62        x  b(i),c(i),sw(i),en(i),wc(i),wat(i),rho(i),thick(i))
63          con(i)=4.67e4*fm/exp(2.0*a(i)/b(i))*rho(i)
64        x  *rho(i+1)/(1-2*b(i))/(2-2*b(i))
65          com(i)=con(i)*2000.0/(thick(i)+thick(i+1))/(-1.0-en(i))
66          scon(i)=con(i)*hsat(i)**en(i)
67          avail=avail+wat(i)-watp(i)
68    19    continue
69          wc(13)=wc(12)
70          hn2(13)=hswi**(en(12)/2.0)
71          hn1(13)=hswi**(en(12)+1.0)
72          h01=200.0**(en(1)+1.0)
73          com0=con(1)*2000.0/thick(1)/(-en(1)-1.0)*rho(1)/rho(2)
74          runoff=0.0
75          n=0
76          aleaf=p*15.0e-6            ! kg dm/m**2
```

```
77        aroot=p*15.0e-6            ! kg dm/m**2
78        wstr=0.0
79        alai=0.0
80        regn=0.0
81        drain=0.0
82        act(-1)=-2.0
83        act(0)=-1.0
84        act(13)=-1.0
85    !
86    c   START OF NEW DAY
87    !
88    20  read (3,25) jday,rh,rain,ep,tx6,ti6
89    25   format (i4,f5.2,f6.1,3f5.1)
90        epa=0.35+0.75*ep
91        tav(1)=0.5*(tx6+ti6)
92        amp(1)=0.5*(tx6-ti6)
93        amp(0)=1.32*amp(1)
94        degrees=64.0+jday
95        tav(10)=16.42+5.86*sind(degrees)
96        do 26 i=1,12
97        amp(i)=amp(0)*exp(-z(i)/90.0)
98        tav(i)=tav(1)+(z(i)-25.0)/675.0*(tav(10)-tav(1))
99    26   continue
100       if (jday.lt.nsd) go to 21
101   !
102   c   CROP  GROWTH
103   !
104       nday=nday+1
105       alai=16*aleaf             ! leaf area index
106       aep=epa*sqrt(alai**2/(1.0+alai**2))
107       root=2.0e5*aroot          ! m root/m**2
108       r0=alfa*root*1000.0
109       sumupt=0.0
110       do 27 i=1,12
111       call wupt(r0,alfa,z(i),hn1(i),h01,en(i),wat(i),dwat(i),wc(i),
112     x con(i),rho(i),thick(i),0.0,watp(i),upt)
113   27   sumupt=sumupt+upt
114       umax=amin1(1.0,aep/sumupt)
```

```
115        avail=0.0
116        trans=0.0
117        do 28 i=1,12
118        call wupt(r0,alfa,z(i),hn1(i),h01,en(i),wat(i),dwat(i),wc(i),
119      x  con(i),rho(i),thick(i),umax,watp(i),upt)
120        call water(hsw(i),hn2(i),hn1(i),a(i),
121      x  b(i),c(i),sw(i),en(i),wc(i),wat(i),rho(i),thick(i))
122        avail=avail+wat(i)-watp(i)
123    28  trans=trans+dwat(i)
124        phot=trans*rh*0.01
125        aroot=aroot+phot*0.36*exp(-0.02*nday)
126        aleaf=aleaf+phot*0.66*exp(-0.01*nday)
127        sumtr=sumtr+trans
128        wstr=trans/(aep+0.001)
129    !
130    c   RAINFALL AND FILLING OF LAYERS
131    !
132    21   if (rain.le.0.0) go to 22
133        regn=rain+regn
134        rai=rain
135        ainf=0.0
136        do 23  i=1,12
137        defi=wats(i)-wat(i)
138        if (rai.le.defi) go to 24
139        wc(i)=wcs(i)
140        rai=rai-defi
141        ainf=ainf+defi
142        rai=amin1(rai,scon(i))
143    23   continue
144        drain=drain+rai
145        rai=0.0
146    24   wc(i)=wc(i)+rai/rho(i)/thick(i)
147        runoff=runoff+rain-ainf-rai
148        do 29  i=1,12
149        call water(hsw(i),hn2(i),hn1(i),a(i),
150      x  b(i),c(i),sw(i),en(i),wc(i),wat(i),rho(i),thick(i))
151    29   continue
152    !
```

```
153    C   WATER REDISTRIBUTION IN SOIL AND EVAPORATION
154    !
155
156    22    esp=(epa-aep)*wc(1)/wcs(1)
157          dt=4.0/24.0
158          do 38 j=1,6
159          tim=5.0+4.0*j
160          flow0=amin1(esp,(com0*(hn1(1)-h01)))
161          flow(0)=amax1(flow0,0.0)
162          do 35 i=1,12
163          temp(i)=tav(i)+amp(i)*sind(tim-9.0-300.0/z(i))
164          flow(i)=com(i)*(hn1(i+1)-hn1(i))-con(i)*hn2(i)*hn2(i+1)
165          flow(i)=amin1(flow(i),flmax(i))
166          flow(i)=amax1(flow(i),-flmax(i))
167    35    continue
168          sumes=sumes+dt*flow(0)
169          drain=drain-dt*flow(12)
170          do 37 i=1,12
171          wc(i)=wc(i)+dt*(flow(i)-flow(i-1))/rho(i)/thick(i)
172          if (wc(i).le.0.01) wc(i)=0.01
173          call water(hsw(i),hn2(i),hn1(i),a(i),
174        x  b(i),c(i),sw(i),en(i),wc(i),wat(i),rho(i),thick(i))
175    37    continue
176          if (jday.lt.june) go to 38
177    !
178    c   WORMS
179    !
180          do 100 i=1,12
181          pf(i)=alog10(hsw(i)+0.01)+2.0
182          actlow=temp(i)/15.0
183          acthigh=0.2*(30.0-temp(i))
184          acttem=amin1(1.0,actlow,acthigh)
185          actpf=amin1(1.0,pf(i),(3.70-1.0*pf(i)))
186          actt=amax1(0.01,acttem)
187          actp=amax1(0.01,actpf)
188          act(i)=actt*actp
189    100   continue
190          do 101  n=1,12
```

```
191        i=lay(n)
192        if(ihyb(n).eq.1) go to 101
193        foodupt=0.0
194        work=0.0
195        growthpot=potgrowth/grfact(n)
196        resp=resp1*weight(n)*temp(i)/resp2
197        if(food(n).le.0.008) go to 104
198        comf=amin1(act(i)/(act(i-1)+0.001),act(i)/(act(i+1)+0.001))
199        if(comf.gt.0.95) go to 111
200        if(act(i-1)-act(i+1)) 102,102,103
201    102 lay(n)=lay(n)+1
202    103 lay(n)=lay(n)-1
203        go to 111
204    104 diam=10.0*(weight(n)*0.07)**0.333      ! length=18.2*diam.
205        do 105 k=1,6
206        rval(k)=ran(iran)
207    105 continue
208        rval(2)=amax1(rval(2),rval(3),rval(4),rval(5))
209        omu=(om(i-1)+var(i)*rval(1))*act(i-1)
210        omh=(om(i)+var(i)*rval(2))*act(i)
211        omd=(om(i+1)+var(i)*rval(6))*act(i+1)
212        if(omu.ge.omh) go to 106
213        if(omh.ge.omd) go to 107
214    106 if(omu.ge.omd) go to 108
215        depth(n)=depth(n)+dist*act(i)*0.89
216        burr(i)=burr(i)+dist*act(i)
217        foodupt=omd*rho(i)*dist*0.785*(diam**2)/1000.0
218        if(depth(n).le.thick(i)) go to 110
219        depth(n)=depth(n)-thick(i)
220        lay(n)=lay(n)+1
221        go to 110
222    107 updown=abs(omd-omu)/(omd-omu)
223        depth(n)=depth(n)+dist*act(i)*0.7*rval(1)*updown
224        burr(i)=burr(i)+dist*act(i)
225        foodupt=omh*rho(i)*dist*0.785*(diam**2)/1000.0
226        if(depth(n).le.thick(i)) go to 109
227        depth(n)=depth(n)-thick(i)
228        lay(n)=lay(n)+1
```

```
229          go to 110
230     109  if(depth(n).ge.0.0) go to 110
231          if(depth(n)+thick(i-1)) 113,113,114
232     113  depth(n)=-depth(n)
233          go to 110
234     114  depth(n)=depth(n)+thick(i-1)
235          lay(n)=lay(n)-1
236          go to 110
237     108  depth(n)=depth(n)-dist*act(i)*0.89
238          burr(i)=burr(i)+dist*act(i)
239          foodupt=omu*rho(i)*dist*0.785*(diam**2)/1000.0
240          if(depth(n).ge.0.0) go to 110
241          depth(n)=depth(n)+thick(i-1)
242          lay(n)=lay(n)-1
243     110  work=workf*weight(n)
244     111  foodupt=foodupt-work-resp
245          growth=amin1(growthpot,foodupt)
246          foodupt=foodupt-growthpot
247          food(n)=food(n)+foodupt
248          weight(n)=weight(n)+growth/growf
249          weightx(n)=amax1(weight(n),weightx(n))
250          if(weight(n).lt.wloss*weightx(n)) ihyb(n)=1
251     101  continue    ! NEXT WORM
252     38   continue
253          if (jday.lt.june) go to 20
254          ny=jday/jwrt
255          if(ny*jwrt-jday) 41,40,41
256     40    write(5,42) burr(1),burr(2),burr(3),burr(4),burr(5),burr(6)
257        x ,burr(7),burr(8),burr(9),burr(10),burr(11),burr(12)
258     42    format('0',3f7.0,9f6.0)
259          write(5,43) jday,weight(1),weight(2),weight(3),weight(4),
260        x weight(5),weight(6),weight(7),weight(8),weight(9),weight(10)
261        x ,weight(11),weight(12)
262     43    format(1x,i4,12f6.3)
263          if(pri.le.0.5) go to 41
264          write(5,44) lay(1),lay(2),lay(3),lay(4),lay(5),lay(6),lay(7),
265        x lay(8),lay(9),lay(10),lay(11),lay(12),ihyb(1),ihyb(2),ihyb(3)
266        x ,ihyb(4),ihyb(5),ihyb(6),ihyb(7),ihyb(8),ihyb(9)
```

```
267        x ,ihyb(10),ihyb(11),ihyb(12)
268     44    format (1x,12i3,i7,11i3)
269           if (pri.le.1.5) go to 41
270           write(5,45) act(1),act(2),act(3),act(4),act(5),act(6),act(7)
271        x ,act(8),act(9),act(10),act(11),act(12)
272     45    format(1x,12f6.3)
273     ! 38  continue
274     41    if (jday.lt.lday) go to 20
275           stop
276           end
277     !
278           subroutine water(hsw,hn2,hn1,a,b,c,sw,en,wc,wat,rho,thick)
279           arg=a+b*alog(c+sw*wc)
280           hsw=exp(arg)
281           hn2=exp(en*arg/2.0)
282           hn1=exp((1.0+en)*arg)
283           wat=wc*rho*thick
284           return
285           end
286     !
287           subroutine wupt(r0,alfa,zi,hn1,h01,en,wat,dwat,wc,
288        x con,rho,thick,umax,wp,upt)
289          vl=r0*exp(-alfa*zi)
290          rz=vl*thick/1000.0
291           geo=7.5-0.5*alog(vl+0.1)
292           up=6.28*con*wc*rho*(hn1-h01)/geo/(-en-1.0)
293           upt=amax1(0.0,up*0.005/(up+0.005))
294           upt=upt*rz
295           adwat=amin1(upt,(umax*upt),(wat-wp))
296           dwat=amax1(adwat,0.0)
297           wc=wc-dwat/(rho*thick)
298           return
299           end
300
301
302
303
304
```

```
305    3.0 0.930 0.0067 25.0 0.0030 15.0 0.0013
306    365 240  9876541 12.0 120.0 120.0 0.0330 0.0035
307    16.340  8.410  0.377  0.300  1.300  1.000  25.000 0.030 0.030
308    16.340  8.410  0.377  0.300  1.300  1.000  25.000 0.027 0.027
309    16.340  8.410  0.377  0.300  1.300  1.000  25.000 0.025 0.025
310    15.430  6.530  0.330  0.290  1.400  1.000  25.000 0.022 0.022
311    15.430  6.530  0.330  0.290  1.400  1.000  25.000 0.019 0.019
312    15.430  6.530  0.330  0.290  1.400  1.000  25.000 0.016 0.016
313    15.430  6.530  0.330  0.290  1.400  2.000  50.000 0.015 0.015
314    16.960  5.600  0.450  0.415  1.200  2.000  50.000 0.011 0.013
315    16.960  5.600  0.450  0.415  1.200  2.000  50.000 0.010 0.012
316    16.960  5.600  0.450  0.415  1.200  3.000 200.000 0.009 0.011
317    16.960  5.600  0.450  0.415  1.200  3.000 200.000 0.008 0.010
318    16.960  5.600  0.450  0.415  1.200  3.000 200.000 0.007 0.007
319      1 0.25 0.25
320      2 0.65 0.65
321      3 0.50 0.50
322      4 0.35 0.35
323      5 0.75 0.75
324      6 0.15 0.15
325      7 0.16 0.16
326      1 0.18 0.18
327      2 0.20 0.20
328      3 0.22 0.22
329      4 0.24 0.24
330      5 0.26 0.26
331
332
333    burr1 burr2 burr3 burr4 burr5 burr6 burr7 burr8  burr9 bur10 bur11 bur12
334    jday  weig1 weig2 weig3 weig4 weig5 weig6  weig7 weig8 weig9 wei10 wei11
335    wei12
336    l1 l2 l3 l4 l5 l6 l7 l8 l9 l10 l11 l12 h1 h2 h3 h4  h5 h6 h7 h8 h9 h10 h11 h12
337     act1 act2 act3 act4 act5 act6 act7 act8 act9 ac10 act11 ac12
338    0 15377. 30666. 4244. 1246. 172. 138.  11.  0.  0.  0.  0.  0.
339     240 0.300 0.680 0.548 0.403 0.766 0.192 0.201 0.226 0.247 0.268 0.289 0.312
340      1 2 1 1 2 2 1 1 1 2 2 1   0 0 0 0 0 0 0 0 0 0 0 0
341     0.962 0.706 0.990 0.713 0.685 0.651 0.950 0.937 0.915 0.869 0.885 0.849
342
```

APPENDIX 3

McKenzie B.M. and Dexter A.R. (1988)

Axial pressures generated by the earthworm

Aporrectodea rosea

Biol. Fertil. Soils. 5 : 323-327

McKenzie, B. M. & Dexter, A. R. (1988). Axial pressures generated by the earthworm Aporrectodea rosea. *Biology and Fertility of Soils, 5*(4), 323-327.

APPENDIX 4

McKenzie B.M. and Dexter A.R. (1988)

Radial pressures generated by the earthworm

Aporrectodea rosea

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