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SOME COMPARATIVE EFFECTS OF EARTHWORMS AND LEATHERJACKETS ON UPLAND IMPROVED SOILS

by

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I INTRODUCTION

1) The upland environment

Hill land is unimproved native hill and mountain grassland and heather moors. It is utilised primarily for rough grazing by sheep, cattle and deer in that order of importance. It occupies just over 1/3 (6.5 m.has.) of the agricultural land area in Britain, about 1/4 of the total land area, distributed predominantly in Scotland, Wales, North of England and the upland areas of Northern Ireland. About 2/3 (4.1 m.has.) of this total area being unimproved indigenous grassland. On the wetter west coast in exposed situations, it extends almost to sea level, but usually occurs at altitudes of greater than 250 m. in the drier east. In terms of productivity, its agricultural output is about 7%, representing just over £100M of the total output of British agriculture (Gething et al 1973, Floate 1977).

Many factors account for this low productivity, primarily adverse soil and climatic conditions. High rainfall and low temperatures encourage strong leaching but poor weathering. This causes a net loss of nutrients and bases leading to an increase in acidity and an impoverished base poor vegetation. Many areas are wet and poorly drained and therefore anaerobic due to soil texture and structure, but often a consequence of high rainfall in conjunction with a relief pattern limiting free drainage. This encourages peat formation, primary production exceeding decomposition, the latter slowed both by a reduction in the micro-organisms of decay (Latter et al 1967) and by poor chemical composition of the plant substrates (Coulson and Butterfield 1978). The physical characteristics of the area directly determine the plant material, this is therefore indirectly related to peat accumulation.

The accumulation of organic matter causes a downgrading of the soil system by reducing pH. This is self-perpetuating under such adverse conditions and has important effects on the availability and distribution of the nutrients required for plant growth. Total amounts of nutrients maybe comparable with lowland soils, but those readily available are of low concentration. These are mainly present in organic forms with a slow rate of replenishment. (Floate 1970). The outcome is the reputed low fertility hill soils and a natural herbage poor in quality and quantity, achieving about 20-30% dry matter production of a reasonably well fertilised lowland pasture (Floate 1971).

The exact species composition varies depending on the physical factors. Generally a heath type vegetation is established on the extensive peats, dominated by Nardus, Molinia and Calluna vulgaris with mosses and rushes in the wetter parts. Where the parent rocks are more base rich, the release of nutrients, especially calcium is sufficient to compensate for the severe leaching. A more productive sward composed of Agrostis and Festuca species, with associated herbs is able to develop on brown earth soil. These areas possess the essential soil features associated with good permanent pasture at lower altitudes. This includes higher rates of faunal activity and therefore decomposition, which decreases the thick organic mat, characteristic of hill land areas.

Such are the conditions in these marginal areas that strong restrictions are imposed upon utilisation. Systems must consist of extensive livestock grazing numerically dominated by sheep, these lands account for 65% of all U.K. ewes (Floate et al 1973).

Traditionally the sheep are set stocked in a year round free grazing system. The flocks are self-replenishing and the level of stocking is determined by the needs to supply at least a certain minimum level of winter nutrition. This means that output is low, as the indigenous pastures are poor in quality and characterised by highly seasonal growth. The low numbers of sheep that they can carry through the winter leads to chronic undergrazing during the summer months when grass production is high. Eadie (1971) estimates this surplus to be 80% of total production. The sheep graze selectively and the large proportion uneaten accumulates as a surface mat, exacerbated by slow decomposition and poor nutrient cycling. By autumn and early winter when the breeding ewes need a productive diet for successful mating and accumulation of body reserves prior to the onset of winter, the food on the hill consists largely of senescent herbage, low in protein and digestibility, accentuating the winter feed deficits. This in turn is realised in poor individual sheep performance.

The vegetation of the open hills in its present floristic makeup, is incapable of sustaining a larger head of stock than it does in fact sustain. The limited economic circumstances of the industry constrain the range of possible improvements to the system. Theoretically these fall into two main categories; upgrading native swards by intensive controlled grazing and/or fertiliser applications, or destruction of the native swards, followed by reseeding, fertiliser applications and grazing control (Jones 1967).

It has been known for many years that the grazing animal can initiate vegetation change (Jones 1933). This occurs as long as grazing is intensive and controlled, by promoting a more efficient recirculation of plant nutrients. But the process is comparatively slow, compared to removal of the native sward with subsequent reseeding. This latter treatment, although immediate and effective in increasing production, is costly. Eadie (1971) has shown that such intensive improvements of relatively small areas for use at critical times in ewe nutrition, combined with more efficient use of the unimproved hill land, can lead to significant and economically worthwhile increases in output. Levels of grass utilisation can subsequently be increased to 70%.

Grass potential of peat soils is high in response to added fertilisers, greater than the response on lowland pastures (Crompton 1958). Under the Hill Land Improvement Scheme included in the 1967 Agricultural Act, a comprehensive system of grant aids repay 50% of the actual cost of approved operations, designed to increase the productivity of hill land directly or indirectly (Munro 1970). This had lead to a stimulus in hill land reclamation. Vegetation has been improved through use of fertilisers, especially nitrogen, recognised as a key element in limiting the growth of pasture species and liming, in order to counteract acidity (Newbould 1974). Stocking densities have consequently been raised above the previous very low level of about 1 sheep/ha.

It is now widely accepted that improvement is the key to achieving greater productivity from hill sheep farms, but despite the numerous grants and subsidies offered as an aid to reclamation, progress is still hampered. Permanent physical difficulties such as terrain, climate, elevation, limit areas that are potentially improvable and reduce the economic returns from those areas subjected to relatively expensive improvements. Reseeded pastures can increase yields by 2-3 fold (Eadie 1978) and could last for 15-20 years (Gething et al 1973). But rainfall totals greater than 1300-1500 mm p.a. cause a deterioration of the pasture accelerated by inadequate fertiliser dressings, especially of nitrogen. (Rawes 1963)

Irrespective of man's activities therefore, the soils of hill farms will in general remain of low nutrient content and available energy. The essential aim is to develop a biologically active mull humus with which good pasture is naturally associated.

2) Earthworms and soil fertility

The cost of soil renovation is likely to be prohibitive unless direct methods are supplemented by the use of natural biological mechanisms. Foremost amongst these is the earthworm. Aristotle was the first to appreciate their role calling them "the intestines of the earth". Gilbert White (1770) acclaimed them as the great promoters of vegetation, but it wasn't until Darwin (1881) that factual data on their physical effects on the soil was published. He concluded, "it may be doubted if there are any other animals which have played such an important part in the history of the world as these lowly organised creatures".

Since then, numerous studies have been concentrated upon their effects. Earlier ones included Evans and Guild (1947) in England and Hopp and Slater (1948 and 1949) in the U.S. Both stressed the specific differences in the action of the earthworm on soils, and the quantitative effect of their numbers and biomass. Satchell (1958), Kevan (1955) and Doeksen and van der Drift (1963) review the vast amount of literature available. This includes their effects on the soil's physical and chemical properties, which in turn influences the fertility of the soil and therefore its capacity to produce crops.

The fertility of the soil is in part determined by its pool of nutrients and one of the most important influences affecting the supply is the rate of breakdown of organic matter. Numerous workers have shown that the activity of soil animals can affect this decomposition directly. The value of earthworms in this context has been argued a great deal, much debate centred on whether they actually promote the soil's fertility.

Edwards and Heath (1963) used differentially sized litter bags to exclude various components of the soil fauna, and found that inclusion of earthworms increased the rate of breakdown about three times over their absence. Very little decomposition of litter occurred in the bags of which the mesh size was too small to allow entry of animals.

Van Rhee (1963) observed earthworm populations on old grassed lands and new polders and correlated the amount of breakdown or disappearance of plant remains with the activities of earthworms. A mull soil was produced where earthworms were present, their effects were noticeable after one year. In laboratory experiments, exclusion of worms considerably retarded the breakdown of organic material.

By comminuting plant debris and mixing it with the mineral soil they provide a better substrate for attack by micro-organisms, enhancing humification. Numbers of bacteria have been shown to be far greater in their excrement (Went 1963) and reports from pot experiments show that earthworms can increase the number of micro-organisms in soil by as much as five times (Edwards and Lofty 1977). This is mainly due to the large quantities of available nitrogen returned to the soil in their excretions after consuming plant matter which is rich in nitrogen compounds. This stimulates other microbial decomposition processes as shown by Barley and Jennings (1959). Cultures of Allobophora caliginosa increased the rate of decomposition by 17-20%, due about equally to the direct effects of earthworms themselves and to the stimulation given to other decomposer organisms.

Thus all the available evidence is that earthworms enhance decomposition and make more mineral nutrients available for plant growth. This may be important in improving soil fertility.

On agricultural land earthworms are often the most conspicuous group and may contribute from half to three-quarters of the total weight of fauna (Barley 1961). That their effects are not exaggerated can be seen on lands where they are absent. At Park Grass, Rothamsted, repeated applications of ammonium sulphate increased acidity and completely eliminated the worm population, a thick mat of dead vegetation building up. That the lack of decay wasn't due solely to acidity was demonstrated by mixing the organic matter with the soil upon which it decomposed rapidly (Satchell 1967). A similar situation occurred in grassed orchards where the earthworms were poisoned by copper sulphate spray (van Rhee 1963).

On irrigated pastures in New South Wales, Australia, organic mats up to 4 cm. thick occur with an inverse relationship existing between earthworm number and mat weight (Barley and Kleinig 1964, Noble et al 1970). On introducing earthworms, this discrete layer disappeared. Incorporation of organic matter has also been demonstrated by Vimmerstedt and Finney (1973) after colonisation by earthworms on a calcareous strip mine.

All these studies point to the direct activity of earthworms, in removing organic matter and conditioning it for later decomposition, with the subsequent release of nutrients available for plant growth and the formation of a typically mull type soil.

The quality of material though is important in this respect, as demonstrated by the accumulation of extensive peat in the uplands of Britain. Heavy rainfall, low temperatures and base poor rocks lead to the development of poor quality material. This, together with the absence of earthworms, a reduction in decomposing micro-organisms and lack of large herbivores, accounts for much of the peat accumulation and the contrasting nature of this material with mineral soils. It was estimated that less than 10% of plant production was consumed on blanket bog, compared to at least 80% eaten by animals on mineral soils (Coulson 1978).

In order that the earthworm can contribute materially, conditions must satisfy its basic ecological tolerances, That marginal areas can support earthworm populations has been shown with rehabilitation experiments on marginal grasslands and moors (Mellanby 1958, Dobson and Lofty 1956). Over a span of three years, plots treated with lime and phosphate had higher populations than controls. They have already been shown to survive in a calcareous mine spoil (Vimmerstedt and Finney 1973) and various workers have artificially introduced populations into land that has recently been reclaimed (Hamblyn and Dingwall 1945, Richards 1955, van der Drift 1965 and van Rhee 1969a). Failure has occurred in some cases through not accounting for their environmental tolerances (Stockhill 1959) or through introducing unsuitable species of worm.

In the uplands, total earthworm numbers and biomass are low and accounted for by a restricted range of species related to their tolerance of soil acidity and limited food supply. The above studies have shown that altering conditions to make them suitable for earthworm survival is possible. Evidence that once earthworm populations existed in the uplands are shown by the remains of a mull, humus top soil. This is now overlain by an acid surface mat of vegetation and reverted to heather or Nardus species, within the confines of former well managed fields delineated by derelict walls (Crompton 1958). The change in climate must be significant in this respect but with the addition of lime, essential in all improvement programmes, it may be possible to obtain an organic cycle similar to that found on lowland soils, with the earthworm as the major promoter.

3) The economic significance of Tipula Larvae

Tipula paludosa Meigen, is included in the family Tipulidae, representing the long palped craneflies. They are univoltine with four larval instars and a pupal stage between egg and adult. In the North of England peak emergence of the flies is in late July/early August over a spread of about three weeks (Coulson 1962). This is earlier than in the South of England where peak emergence is about six weeks later, together with other stages in the life cycle (Mayor and Davies 1976). The flight season lasts for about eight weeks.

On emerging, copulation proceeds immediately, the females oviposit the fully mature eggs within the surface layers of the soil very soon afterwards. They hatch in about fifteen days passing through the first two instars rapidly. Third instar is reached by October/ November in the north in which state they overwinter, the stage lasting for about twenty-five weeks with no indication of a diapause. (Coulson 1962). By March/April they pass into fourth instar and enter the pupal stage by mid-July which lasts for about ten to fourteen days.

The larva is therefore the more permanent due to its long duration of about nine months. They are common in all types of pasture soils and widely distributed, being known as 'leatherjackets', due to their tough integument. They feed from the first day onwards (Rennie 1917) until mid-June, being polyphagous and opportunistic in food preferences. (Freeman 1967). As such they are important economic pests, attacking pastures and cereal crops. The larvae usually feed just below the surface destroying the roots and especially the underground stems of the plants, causing severance at ground level. Irregular holes are eaten near the backs of young leaves and often leaf tips may be left at the soil surface or drawn into their soil burrows (MAFF 1979). Farmers are often unaware of any damage until extensive thin or bare patches appear in the crop in spring, by which time the damage is done.

Surveys made in 1948-59 (Cohen 1953), 1952-59 (White 1963) and 1961-65 (George 1966), indicate that populations fluctuate widely from year to year with marked differences between different parts of the country, but peak populations occur on average one year in five. Population level is closely correlated to the incidence and degree of crop damage in any one season (French 1969), therefore surveys to estimate density are a valuable predictive tool to reduce loss by such a pest. The uplands of Britain contain low populations of T. paludosa, except where some form of land reclamation has been undertaken. As such, the area acts as a reservoir, serving to reinfect agricultural land after precautions have been taken to eliminate them. Their presence in the uplands therefore is significant.

4) The comparative aspects of earthworms and larvae of T. paludosa in a recently improved upland environment in Britain

The uplands have been outlined as an extreme environment, economically marginal as well as ecologically, many species being at their northern limits. The fauna is essentially a species poor lowland grassland community, restricted to those organisms that can survive the rigorous conditions. The physical limitations have been divided into permanent and temporary categories, the former precluding improvements but the latter subject to a wide range of treatments according to the nature of these limitations. Soil factors are usually the dominant ones.

But the improvements, in trying to convert an upland moor into something resembling a lowland pasture, requires expensive capital outlay and maintenance costs. It pays little attention to the existing reserves of plant nutrients already held in the organic matter. In improving the soil system, conditions are made more favourable to the development and survival of organisms that live within this system. The earthworm has been shown to be a major component here, a great enhancer of the soil's fertility in the release of plant nutrients during its normal activities. Altering previously unsuitable land may allow establishment of significant populations, with their attendant beneficial effects following.

Unfortunately, many years may elapse before the arrival of a sufficiently well adapted field species, hence the artificial innoculations practised in many continental areas.

In contrast, leatherjackets, although still part of this soil system for the greater part of their life cycle, are opposite in their effects. Their presence is detrimental to the returns hoped to be gained by the improvements, yet their presence is a consequence of these improvements.

The effects of these two organisms are therefore antagonistic.

In the present work an attempt has been made to study some comparative effects of these two organisms.

Firstly to isolate the ecological factors relevant to earthworm survival and distribution, and to try and relate these to the conditions as found in an upland environment, that has recently been subjected to improvement. If survival is proved possible, could they actually colonise the area and in any way make a significant contribution to improvement of the soil environment through their activities in a subsequent increase in yield of plant production?

In order that the merits of earthworm activity can be clearly seen and not obscured by the detrimental effects of T. paludosa larvae, the factors governing the latter's distribution must be determined. More specifically an attempt must be made to deduce the exact effects of the larvae on plant yield and if possible to find a method of reducing their detrimental impact.

The following is a list of the species that occurred in this study:-

Allobophora caliginosa (Savigny, 1826)
Allobophora chlorotica (Savigny, 1826)
Allobophora longa (Ude, 1885)
Allobophora nocturna (Evans, 1946)
Allobophora rosea (Savigny, 1826)
Bimastos eiseni (Levinsen, 1884)
Dendrobaena octaedra (Savigny, 1826)
Dendrobaena rubida (Savigny, 1826)
Dendrobaena subrundicunda (Eisen, 1874)
Eiseniella Tetraedra (Savigny, 1826)
Lumbricus castaneus (Savigny, 1826)
Lumbricus rubellus (Hoffmeister, 1845)
Lumbricus terrestris (Linnaeus, 1758)
Molophilus ater. (Meigen)
Tipula paludosa (Meigen)
Tipula subnodicornis (Zetterstedt)
Pluvialis apricaria (Linnaeus)
Sturnus vulgaris (Linnaeus)
Vanellus vanellus (Linnaeus)

II DESCRIPTION OF SITES

1) Brief History of Upper Teesdale

Upper Teesdale has been settled since pre-history, being under the influence of man since the Mesolithic hunters, the landscape remaining relatively unaltered until about AD 1100, when settlement became more permanent and the forests were cleared (Roberts 1978). By the early 1700's, fields began to be enclosed and improved mainly on the inby lands (see glossary), the upper levels receiving little attention until very recently.

This inbalance of treatment over time, is brought out in this study in a comparison of two upland farms situated in Upper Teesdale. The first is an example of recent improvements, the second subjected to more long term treatments.

2) Site of the Recently Improved Land

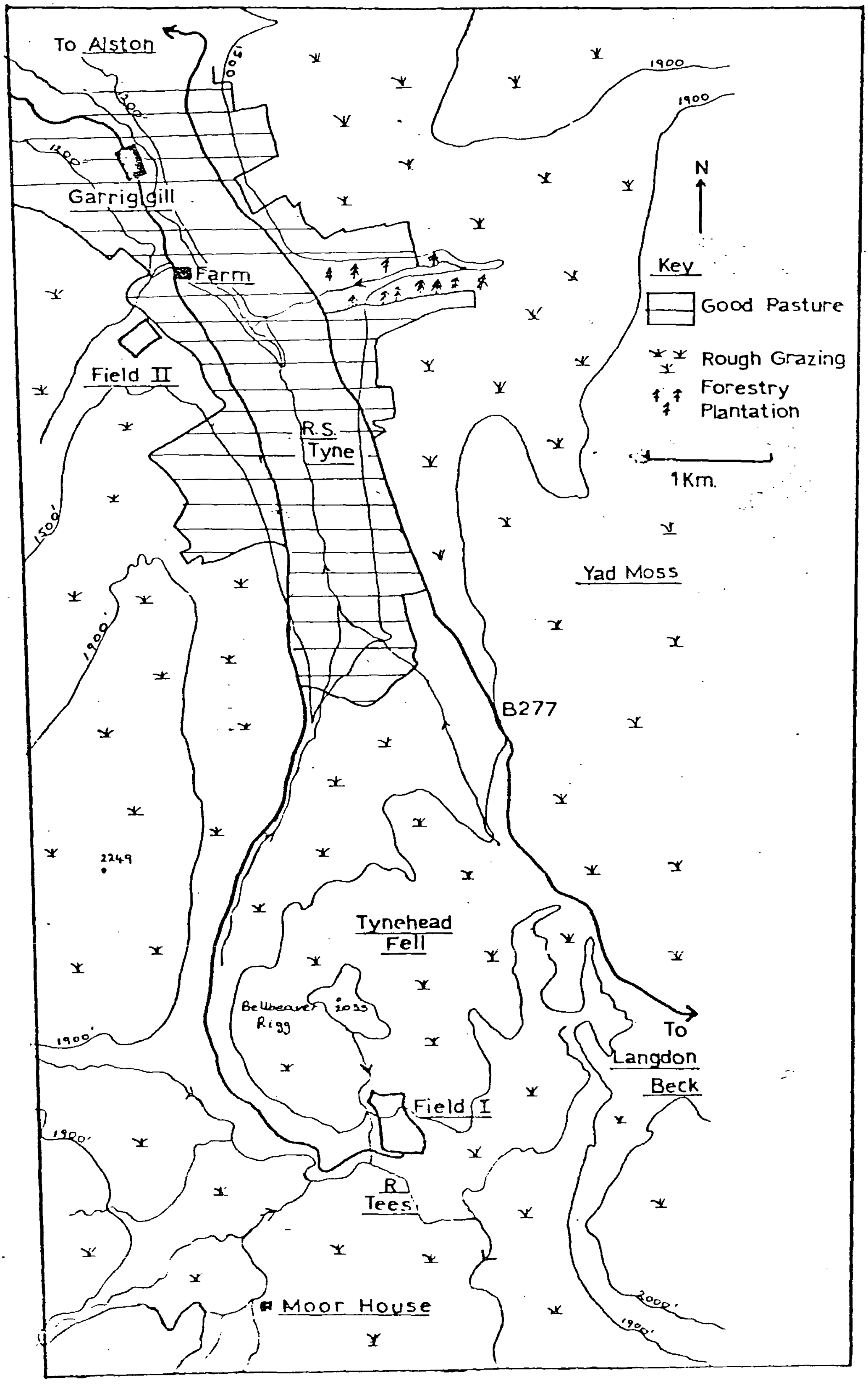
The farm belonging to Mr Tom Carrick, is situated within Cumbria, near the village of Garigill about 8 km. south east of Alston, bordering the Moor House National Nature Reserve (M.H.N.N.R.). It totals about 1093 has. (2700 acs.), of which 80% is classed as outby land (see glossary). Sheep are the sole grazing animal, numbering about 1300.

Because of its situation near to Moor House, use has been made of the meterological data obtained for the Reserve. The climate is rigorous, rainfall averages are high, about 1900 mm per annum, an average temperature of 5.1°C, with a growing season of about 150 days at an altitude of 550 m. (Data for 1968-75).

The underlying geology is the Lower Carboniferous consisting of the Yoredale limestone, sandstone and shale series, in almost horizontal beds.

Two fields were chosen to study within this area, both having been modified within the last 5 years.

DIAGRAM 1 Map showing the location of Mr Carrick's two fields in Cumbria



3) Description of Fields

1 a) Field I (FI) (Diagram 1)

Extent of 16 has. (40 acc.) situated about 7 km. from the farm house. It faces south-south-east at an altitude ranging from 533 m. - 589 m. Its southern edge is bordered by the Upper reaches of the River Tees, which also forms the northern boundary to the Reserve.

Surrounding it is rough unimproved grazing land consisting of acid grassland, species such as Nardus and Molinia together with heather (Calluna vulgaris) except along the river sides where a close cropped Agrostis - Festuca association occurs (photograph 1) on limestone mineral soil. Patches of Juncus squarrosus and Eriophorun vaginatun occur in the more waterlogged parts (photograph 2).

Prior to improvement, the field had carried this typical hill land vegetation on fibrous wet peat, which overlies a heavy textured, gleyed mineral soil. Sheep density was half an ewe plus single lamb per acre. Since 1977 the area has been treated with an aim to increasing grass production and subsequent sheep density.

1 b) Improvements undertaken on FI

In preparation the field was flailmown, rolled, partly burnt and then rotovated twice, in order to remove and destroy the indigenous pasture species and prepare a more favourable seed bed.

Following this the area was treated with lime and compound fertilisers in the following amounts and proportions:-

TABLE 1: Type and amount of fertilisers applied to FI during the course of improvement

Date	Treatment			Amount
May 1977	Ground limestone			3 tons/ac.
May 1980	Ground limestone			3 tons/ac.
June 1978	N	P	K	
	* 12	24	0	6 cwt./ac.
June 1979	* 30	13	0	2 cwt./ac.
May 1980	** 50	0	0	
July 1980	** 50	26	0	

The field was then reseeded two years ago in April 1978 using an upland acid grass mixture containing:-

TABLE 2: The reseed grass mixture

Type	Variety	Amount lbs/ac.
Lolium perenne	Talbot	7
(perennial rye grass)	Melle	9
Phleum pratense (Timothy)	pecora	5
Trifolium repens (white clover)	Huia	3
	Total	24

The field was then rolled three times, bringing the seeds into closer contact with the substrate. Later drainage was undertaken, using open ditches spaced at a distance of about 20 m.

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* Figures denote the plant food ratio in units (multiply by amount to obtain actual amount applied)

** Actual units applied

Photograph 1
<u>Type of vegetation surrounding FI</u> - acid grassland and limestone mineral areas.

View looking S.S.W. from FI shows the heather clad slopes, intermixed with the acid grassland species and the close cropped turf adjacent to the streamside.

Photograph 2
<u>Type of vegetation surrounding FI</u> - the more waterlogged parts.

View looking S.W. Dark brown patches in the background depict the heather, lighter brown areas in the foreground and mid-parts of the picture are patches of <u>J. squarrosus</u> and <u>E. vaginatun</u> situated on the wetter parts.

TABLE 3: Grazing regime

Date	Grazing Control
Mid-July - Mid August	Fenced off. Grazed only by lambs
Rest of the year	Open. Free grazing

This field has therefore received the full range of improvements, the density of stock subsequently being raised to three ewes and their lambs per acre in the summer months (this includes those with no lambs, those with one and others that are gimmers or hoggs) (see glossary for terms).

2 a) Field II (FII) Diagram 1

Extent of 8 has. (20 acs.) at an altitude of 426 m. on relatively flat terrain at a distance of less than 1 km. from the farm. Its northern edge is bordered by Crossgill. Still being surrounded by unimproved rough grazing land, but near its eastern edge runs the track into Garigill, along the margins of which are relatively good pasture land, and cattle are grazed, together with the hill sheep. It carried the same density of sheep as FI, being similar in its physical make-up.

2 b) Improvements undertaken on FII

Improvements began in 1975, preparation roughly following those carried out for the other field. The treatments however differ slightly:-

TABLE 4: Treatments applied to FII

May 1975	Magnesium limestone - X2			3 tons/ac. X2
1975	N	P	K	
	15	15	15	4 cwt/ac.
May 1976 + 1977	* 48	60	0	
July 1976 + 1977 + 1979	34	0	0	
May 1978 + 1979	60	24	0	
July 1979	68	68	68	
May 1980	60	26	0	
June 1980	34	0	0	

* Figures below this refer to the actual units applied, the line above to the plant food ratio.

The field was first reseeded in mid-June 1975 under ideal weather conditions with the same upland grass mixture. This only lasted 4 years, being reseeded again in 1979, together with a complete fertiliser application in July.

Drainage was attempted in 1978 using plastic tile drains, but this proved unsuccessful due to the substrate being originally too wet.

TABLE 5: Grazing regime

Date	Grazing Control
20 November - 1 May	Fenced off. No grazing
1 May - 20 August	Fenced off. Grazed by lambs & ewes
20 August - 20 September	Fenced off. Droughting (see glossary)
20 September - 10 November	Open. Free grazing
10 November - 20 December	Fenced off. Tupping (see glossary)

The regime is therefore more intensive than on FI, distance to the farm no doubt being an important consideration, together with accessibility. The density of sheep carried is therefore greater, three ewes plus twins in summer to one acre.

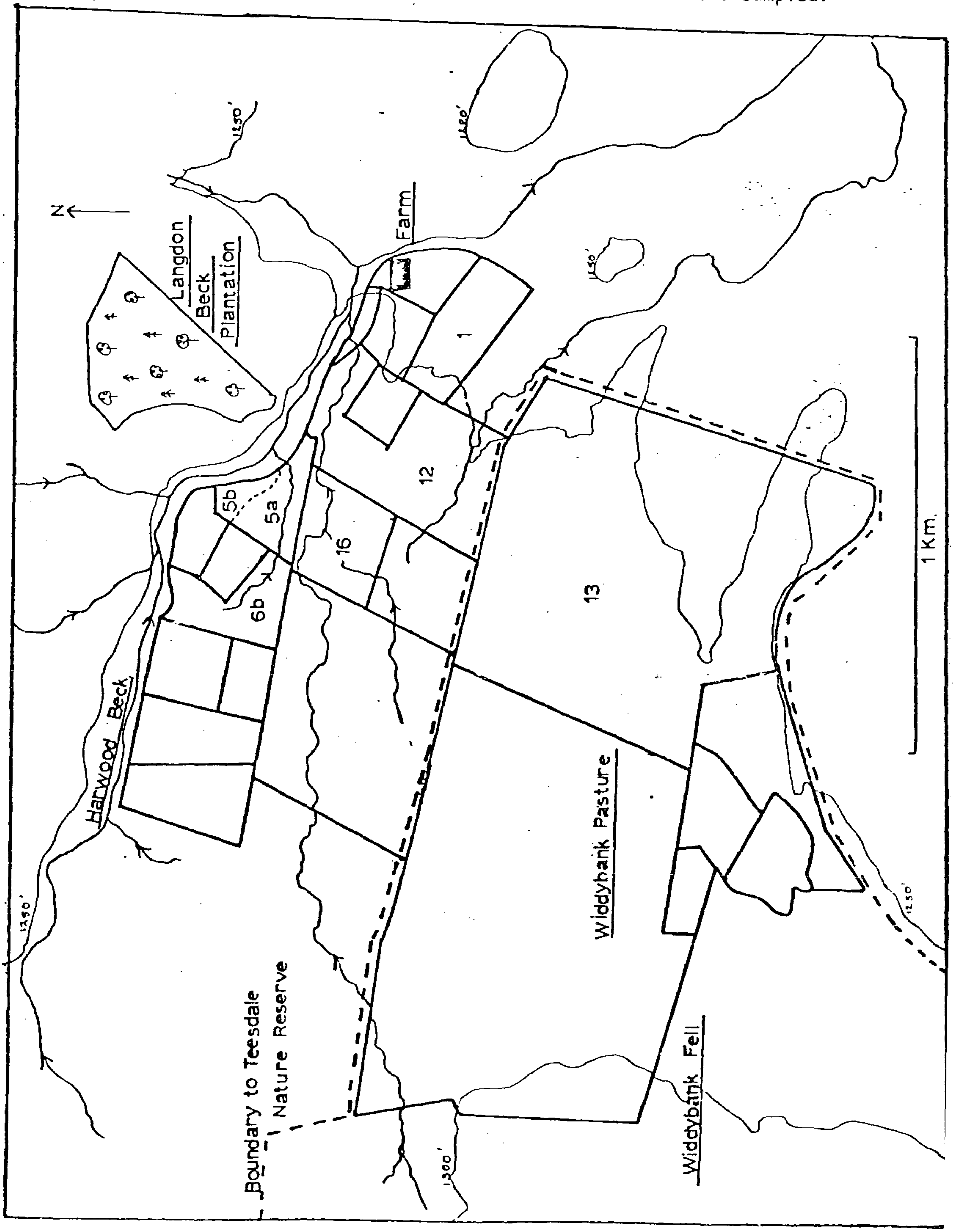
In mid-May 1978, the field suffered an attack by the larvae of Tipula paludusa, resulting in loss of yield amounting to 20-25% of the total.

4) Site of older improved pastures

The second farm is situated lower down the Teesdale Valley in the County of Durham, about 13 km. north-west from Middleton-in-Teesdale, with the newly constructed Cow Green Reservoir lying about 5 km. to the west. Part of the farm (diagram 2) lies within the Upper Teesdale National Nature Reserve.

The farm lies at a lower altitude completely about 365 m., although still classed as an upland farm. It is situated within the valley floor and therefore the majority of the fields are flat.

DIAGRAM 2. Map showing the location of Mr Scott's fields in County Durham. The numbers refer to the fields sampled.



The general climate of the area is also more favourable. Observations on Widdybank Fell (adjacent westwards from the farm), which is 50 m. below the weather station at Moor House, give the average annual rainfall as 1500 mm per annum, an average temperature of 1.6°C higher than Moor House and consequently extending the growing season. But the farm site is about 150 m. below the Widdybank station, consequently temperatures will be higher together with a longer growing season. Piggot (1978) showed that for every 100 m. increase in altitude, mean temperature falls by 0.67°C which shortens the growing season by over two weeks.

The more favourable conditions and terrain mean that a wider scope of management is possible, not being confined solely to rough grazing. Out of a total of 810 has. (2000 acs.) over 121 has. (300 acs.) are classed as inby, 28 has. (70 acs.) of this being utilised as hay meadows. Both sheep and cattle are grazed, the former numerically dominant totalling about 1,000 with cattle about 150.

5) Choice of fields for sampling

The aim was to choose a range of fields differing in age of treatments that were primarily situated on a peaty soil, in order to compare any differences in the earthworm population to that of the recently improved pastures. Unfortunately, the exact age of each field and the time period over which improvements have been carried out, is unknown. The owner, Mr Alan Scott, estimates 20 - 200 years, depending on the location of the field and previous habitation, agreeing well with Roberts (1978) who states a figure of at least 125 years. Therefore, although dating was not possible, they are still much older than those on Mr Carrick's land.

The fields were therefore chosen on the recent treatments of each, whether they had been dressed with farmyard manure or not, as this is known to significantly affect earthworm populations, and knowledge obtained from Mr Scott as to the general nature of the soil.

6) Description of the field sampled

The map (diagram 2) shows the position of each field sampled, only those that were used being numbered.

Fields 1, 5 and 6b are hay meadows cut for hay in June through to July/August, and grazed with sheep only afterwards.

Fields 12, 13 and 16 are natural, indigenous pastures, the former two grazed by cattle, the latter only by sheep. Field 13 lies within the Reserve, the boundary being formed in 1968, effectively curtailing the treatments planned.

Table 6) is an outline of the recent treatments undertaken by Mr Scott.

Table 6) Recent treatments applied to fields sampled in County Durham

Field Number	Size (acs.)	Treatment	Amount
1	11.187	Limed	3 tons/ac/yr 5
5	7.673	slagged	½ ton/ac/yr-1
6b	8.324	N 20 units	
		P 10 units	2 cwt/ac/yr
		K 10 units	
		N	1 cwt/ac/yr
		FYM	
12	23.000	Limed	3 tons/ac/yr-3
		slagged	½ ton/ac/yr-4
		N 20 units	
		P 10 units	2 cwt/ac/yr
		K 10 units	
13	186.000	Limed slagged compound fertilisers	v. small amounts in the last 10 years due to the ruling by the NCC.
		FYM	Small amounts.
16	10.495	Limed slagged compound fertilisers	Applied in the recommended amounts but received no treatment in the last 5 years.

III METHODS

I. FIELD TECHNIQUES

1) Density estimates

Numerous techniques have been devised and modified in order to sample the soil fauna and gain a representative estimate of population levels. The method chosen depends on various factors, from the particular conditions of the site, the salient features of the organism in question and the required level of accuracy. Of all the methods available none are equally suitable for all species and habitats, or even within a particular group.

The project required an estimate of population density for two specific soil organisms i.e. that of earthworms and larvae of T. paludosa over a range of sites and as such a method was needed that could sample both equally well.

a) Comparison of earthworm sampling techniques

Those available for sampling earthworms basically fall into three main categories.

i) Expellants used in the field employing chemical irritants, electrical processes and ground vibration.

ii) Removal of soil samples for later sorting by hand, wet sieving and flotation techniques.

iii) Trapping methods, relying on bait, usually dung as an attractant.

Various workers have concentrated their attention on these techniques in order to assess their relative efficiencies. Evans and Guild (1947) used a chemical expellant of potassium permanganate, later shown by Svendsen (1955b) to result in underestimation of the population density for many species.

Although the use of formaldehyde first described by Raw (1959) gives consistently higher results in comparison, it suffers from the same criticism. Both are influenced by the limited penetration of the solution, dependent on the soil's physical and chemical properties and therefore limiting direct comparison between different soil types. Response of the earthworms differ, death can occur in situ due to toxicity (Raw 1959) and both fail to account for the seasonal activity and life style characteristics of the species.

The extraction of lumbricids by hand from a known quantity of soil has been practised since the mid 19th Century (Hensen 1877). It has been used as a basis for judging the effectiveness of other methods, larger estimates obtained with hand sorting compared to both the chemical expellants (Svendsen 1955b, Raw 1959, Nordström and Rundgren 1972) and the electrical expellant of Satchell (1955a),and Edwards and Lofty (1975). The latter two are impractical in most field situations, as well as being restricted by the difficulty in defining the exact volume of soil that has been effectively treated, and influenced by its variable properties, for example, a greater proportion of earthworms were obtained from the same soil but with a lower pH by Edwards and Lofty (1975).

Compared to a washing and flotation technique devised by Raw (1960) however, on soil with a dense turf, hand sorting recovered only 52% (by numbers) from the sample, although recovering 84% by weight, indicating that it is mainly the smaller species overlooked. The error is less marked therefore when wet worm biomass is estimated.

The same result was concluded by Nelson and Satchell (1972) testing the efficiency of hand sorting by introducing a known number of marked worms into a soil sample. They found the method inefficient for species less than 0.2 g, detection difficult for those darkly coloured, inactive or present in the turf rather than in the soil. Even so, 93% (by number) and 99% by weight were recovered originally, the total increasing to 98% with a second sorting.

Gardefors et al (1971) agree with Satchell (1962) on underestimating smaller species by hand sorting, in their case earthworms less than 0.16 g., but 97% and 96% of the standing crop (expressed as fresh weight) were still recovered in a deciduous woodland and a highly organic old field respectively, in the first sorting.

Trapping (Svendsen 1955a, Boyd 1957a) as a means of determining population level is unlikely to yield accurate results, but is useful for studying activity patterns when population density is low and for the distribution of certain species in different areas.

Concluding, hand sorting seems to be the most efficient method at present for estimating the number and biomass of earthworm populations. Size of the worm, the condition and structure of the soil and the time and care taken all affect its reliability so that much depends on the efficiency of the sorter.

b) Comparison of techniques used for sampling Tipula larvae

Similar analyses have been undertaken for the assessment of the larvae of tipulid species, accurate determination necessary not only for ecological purposes but also for economic reasons. Numerous methods have been devised and tested, many by various government bodies over a number of years.

For many years use was made of a chemical expellant, orthodichlorobenzene (ODCB), developed by T.W. Evans and published by Dawson (1932). Barnes (1941) considered the method accounted for about 80% of the population, but its efficiency wasn't critically assessed until Milne et al (1958) found it to be about 85% efficient from November to May, dropping steeply to zero by July. Later, Shaw et al (1974) found the efficiency to be far less than that of Milne et al (1958), being affected by temperature, soil characteristics, stage of development of the larvae and the weather.

Extraction by hot water (HWP) relies on driving the larvae to the surface through the heat carried by the rising water through the sample turf, which must be sectioned and carried back to the laboratory. Efficiency is 100% up to pupation, thereafter dropping only about 5-10%, but the time required for completion varies from 45 - 150 minutes depending on the nature of the turf; the wetter and more peaty the turf is, the longer the response.

The Agricultural Development and Advisory Service (A.D.A.S.) has adapted the method above using small cores, 6-10 cm. in diameter and 5-6 cm. deep employing a dry heat (Murdoch pers. comm.). In this way several hundred cores can be processed in the lab and time not wasted sampling in the field.

Hand sorting, with later washing on a bed of sieves, or flotation in magnesium sulphate (Salt and Hollick 1944) is considered the best method for full recovery of all stages of the life cycle, although very laborious and time consuming. It seems from the data available though that this method is conclusively the best, agreeing with that for earthworm sampling.

2) Field sampling methods

a) Population estimates through hand sorting

An absolute number was required therefore the most efficient method was chosen for both species being sampled. Hand sorting allowed a known number of cores of a certain volume to be taken at each site and therefore comparisons could be meaningfully made between the different locations.

b) Number of cores taken

Of all the studies related to earthworms most show that they are not randomly distributed in the field, aggregations occurring due to the presence of local concentrations of food (Svendsen 1957 a and b, Boyd 1957a), the particular physico-chemical characteristics of the soil (Guild 1952 a and b) or the habits of each species, as in cocoon production and deposition (Satchell 1955). This makes sampling in order to obtain a consistent, representative figure very difficult.

Abrahamsen (1972) considers the mean number of individuals/core important for the precision of the estimated density, relating this to the coefficient of variation, the resulting dispersion pattern being explained through the Poisson Distribution.
In this way, an adequate number of cores can be estimated by prior sampling with later modifications if necessary.

In this study the number of sites to be sampled and their distance from Durham made preliminary sampling impossible. Also through a study made by Zisci (1958) it was known that percentage recovery declined the larger the sample due to increasing tediousness leading to inefficiency. As this method is primarily dependent on the efficiency of the sorter the samples had to be kept to the most acceptable minimum.

Consideration was given to the earthworm as little data has been published on the distribution of tipulid larvae within the soil. It seems that once they are present within a field the even cover of their food supply means that they are regularly distributed in relation to it.

The number of cores chosen, was therefore 30. In Abrahamsen's study (1972), this number lead to slight over-dispersion of the earthworm population, but here the result showed clumping, indicating aggregation and so was thought to be acceptable.

It also fell within the range used for sampling tipulid larvae, Rayner (1978) using 20-100 and just below that used in a survey of leatherjackets in south-west England by Mayor and Davies (1976) when 32 cores were taken.

c) Depth of core

Most soil animals live in the surface zone of the soil, 95% in the top 5 cm. Leatherjackets live at a maximum depth of 7.5 cms (Milne et al 1958), the majority of workers taking cores 5-6 cms deep (Mayor and Davies 1976, Rayner 1978) and Rennie (1917) stating that larvae have rarely been found below 15-20 cm.

Qualitative evidence by Svendsen (1955a) in his work at M.H.N.N.R. taking cores of 20 cm. deep showed that within this depth the bulk of the lumbricid population occurred. On normal mineral soils though, deep burrowers such as Lumbricus terrestris can be missed due to their escaping in the time it takes to drill a core (Raw 1959).

Large, deep burrowing animals were not envisaged on the recently improved areas, but the species composition was unknown on Mr Scott's land which had variable soil types and depths. Therefore the depth of core taken was never less than 10 cm., but was modified according to conditions pertaining at each site, limited ultimately by the actual depth of soil.

d) Size of core

For convenience of calculations, together with the sheer weight of 30 cores that had to be carried over variable distances and terrain, and with the intention of creating as little disturbance as possible to the fields, the size of core used was 1/100 of a square metre.

3) Field Collection

a) Time of sampling

The samples for population determination were collected in late April/early May, this was considered to be representative of one of the most active times for earthworms, as they are highly seasonal (Satchell 1967), together with being at a peak in numbers and biomass (Hopp 1947). Although these estimates may be smaller than those from autumn sampling (Evans and Guild 1947), the level will give some indication of the general population level.

Estimates of the population level for the tipulid larvae will have accounted for winter mortality, which is usually about 30-50% (Mayor and Davies 1976).

Photograph 3

FI and control area

View looking north-westwards from a south-easterly direction. In the foreground is the area chosen as a control, consisting predominantly of poor grassland species including Nardus, and D. flexuosa with rushes on the more waterlogged parts. In the background is FI, the open drainage ditches running along the contours.

The bare dark brown patches are areas of peat, the surface vegetation absent due to tipulid larvae attack.

b) Density estimate on recently improved pastures

Due to its location near the River Tees and adjoining a limestone mineral grassland, it was decided to sample FI in a parallel transect beginning about three-quarters of the way up the field sampling every 15 paces in between the drainage ditches, and therefore outside their influence. This transect was continued outside the fence towards the mineral area and again within the mineral area. The cores were placed whole into polythene bags, labelled and sealed.

As a control, the area chosen was as depicted in the foreground of photograph 3, broadly the vegetation that was present before improvements were undertaken, consisting predominantly of a mosaic of Nardus, Deschampsia flexuosa, Eriophorum vaginatum and Juncas squarrosus. Here, 30 cores were taken in a single line, separated by about 3 paces, each being bagged, labelled and sealed as above.

On FII no significant topographical features were present to warrant choosing a particular sampling method, therefore cores were taken at random.

c) Density estimate on older improved pastures

On all fields, the cores were taken randomly. Field 5 though was divided into two sections (a and b, diagram 2), due to there being a marked discontinuity within the field in the form of a steep vertical ridge about 4 m. high, separating the flat alluvial plain bordering a stream from the rest of the field. This feature was though significant enough to affect the distribution, therefore each was sampled with half the number of cores and treated as a separate field.

On return to the laboratory the cores were stored at 8°C until sorted.

d) Hand sorting the soil

Each core was sectioned in half, separating the surface mat of vegetation from the mineral soil below, in the case of the older improved pastures. On the more recent ones, which effectively had no mineral soil, the top 5 cm. was sorted separately from the material below.

Sorting was carried out in a wide, white enamel tray with strong desk lamps overhead. The mat of vegetation was pulled into individual pieces, the roots especially searched amongst due to many earthworms and leatherjackets associated intimately with them. This was re-sorted once individually divided.

The soil half was sectioned into smaller manageable units, finely crumbled and spread thinly over the tray, the animals being noticed due to their colouration or wriggling. As the leatherjackets were in the fourth instar at the time of sampling and already quite noticeable, the extra accuracy claimed for their later detection by the flotation technique was considered unnecessary. But as a check on efficiency, the sorted material was put into Tullgren funnels for one week. This recovered only 3% more of the total leatherjacket population and 12% of the earthworm total. The method was therefore considered satisfactory for both species, especially as the material from FI and FII was required for experimentation and therefore needed to be as close to its natural state as possible, not treated with various chemicals.

This method also seemed detailed enough to collect the ootheca which were washed and stored in small collecting bottles with a little water.

e) Weighing and recording

The earthworms were counted and identified as far as possible if mature in the total of 30 cores, and their fresh weight recorded. This measure is subjective due to the variable amounts of water contained in their body tissues, ranging from 75-90% of body weight (Grant 1955), but they are never fully hydrated in unsaturated soil, therefore the water content can vary between wide linits.

As an aim to standardising the measurement the worms were washed free of adhering soil and vegetation matter, the excess water removed from the body by rolling on filter paper. Barley (1961) states that 1/8th of the total body water is removed in this way, plus that from the nephridia. They were then weighed en masse from each field sampled.

Although this accounts for some variation in moisture content, it does not correct for the amount of soil held in the gut, which can be up to 20% of the total live weight (Edwards and Lofty 1977). This can be overcome by storing the worms overnight in damp sphagnum moss, but due to the very small size of earthworms found, many became mutilated on pulling the vegetation apart later resulting in death and very quick decomposition. Storing them therefore would lead to underestimation of the measurement so that weighing immediately after sorting was favoured.

The leatherjackets were counted for each site sampled, no weight measurements being taken. These were kept in containers in groups of about 15 on moist paper with adequate food for later use. Larger numbers were not put together because of their cannabalistic tendencies at this instar (Chiswell 1956).

(f) Collection of samples for soil analyses

Using a cover 1/1000 of a square metre cores were taken 5 cm. in diameter and 10 cm. deep.

(i) On recently improved pastures

On FI, 5 cores each were taken at 5 sites in a transect following the slope as for the larger cores. Each collection of 5 cores were placed in polythene bags, labelled and sealed with the minimum inclusion of air to reduce chemical alteration of the soil due to aeration.

On FII the same number were taken but randomly sampling the field and the above procedure was followed.

(ii) On older improved pastures

On all fields 9 soil cores, of the same dimensions were randomly taken. These were divided into 3 groups, bagged labelled and sealed.

The majority of tests were carried out immediately after return to the laboratory but where this proved impossible they were stored at $1^{o}C$ in order to minimise alterations due to microbial activity.

4) Laboratory determination of soil samples

The method of soil analysis concentrated on those factors that were thought significant in affecting earthworm populations, as well as trying to observe changes in the soil properties over time. Bengston et al (1975) accounted for the distribution of earthworms in natural biotypes broadly through two main divisions, the vegetation forming the food supply and the habitat, the latter specifically through moisture, temperature, pH and calcium content.

The equipment needed to monitor temperature sufficiently accurately was not available, the location of the sites from Durham also made this determination impossible.

The analyses were carried out through modification of the Department of Geography, University of Durham, Soil Science Handbook (1980), in association with Allen (1974).

a) Determination of soil pH

Carried out immediately on return from the field, as air drying affects the pH status (Allen 1974). Measurement depends very much on the soil:water ratio, as the usual effect of diluting the soil with distilled water is to increase the pH of the suspension. This is greatest in alkaline and neutral soils.

The soil core was sectioned at 1 cm. intervals for at least 4 cms., thereafter at 2 cm. intervals in order to determine the depth to which liming had reached through leaching and drainage. This was done for all field soils. For the control no variation was apparent down the profile, therefore only the top surface layer was used as this was considered the most relevant.

The method used was as follows:-

(i) Calibrate meter against buffer solutions 4 and 7 (one on either side of the expected mean).

(ii) 1 cm. section of soil added to 50 ml. beaker, together with enough distilled water to make a smooth paste when stirred with a glass rod (about 2:1 by volume water:soil) left for at least 30 minutes.

(iii) Re-stir mixture, immerse electrode in slowly, wait for needle drift to cease and record measurement to one decimal place.

(iv) Wash electrode with distilled water after each reading.

A reading 24 hours later is sometimes recommended (Allen 1974) in order to account for the changes in partial pressure of carbon dioxide in the atmosphere. But this effect is small in soils having a $pH < 7.0$ and so was thought unnecessary.

b) Soil Moisture

This determination was carried out immediately on return to the laboratory. In each case the procedure was:-

(i) 50-100 g. of fresh soil placed into a weighed crucible $(= W_1)$.

(ii) Dried at 105°C for 4 days.

(iii) Removed from oven, cooled in a desicator and reweighed $(= W_2)$.

(iv) Calculated fresh moisture as a percentage of fresh weight by

$$\frac{(W_1 - W_2)}{W_1} \times 100$$

Because of the one week time interval between sampling FI and FII when the weather proved very hot and dry, in order to aid comparisons between these areas, FI was partly sampled at the same sites as previously. The results showed no significant differences caused by the weather.

c) Organic carbon

Determined by loss on ignition of over dried soil, giving only an approximate indication of the amount of organic matter due to bound water and volatile salts lost at the temperature of ashing, therefore a lower temperature was chosen, but a longer period of combustion. This value is less variable than that obtained by use of the rapid titration method of Walkley and Black (1934) for non-calcaeous soils (Ball 1964). The procedure adopted was:-

(i) Oven dry soil for 4 days at 105°C, weigh crucibles (= W_1).

(ii) Weigh about 1 g. dried soil into the weighed crucibles (= W_2).

(iii) Combust to ash for 5 hours at 450°C in a muffle furnace.

(iv) Remove, cool on a desicator and reweigh (= W_3).

(v) Calculate percentage carbon by:-

$$\frac{W_2 - W_3}{W_1 - W_2} \times 100$$

d) Total nitrogen

Determined by a modification of the Kjeldahl 1883 digestion distillation system, with the conversion of organic nitrogen to ammonia and its subsequent estimation. The procedure used is that as set out in the Geography Department Handbook (1980), University of Durham.

(e) Cation Exchange Capacity

(i) Exchangeable Calcium (Ca)

(ii) Exchangeable Magnesium (Mg)

(iii) Exchangeable Potassium (K)

(iv) Exchangeable Sodium (Na)

Extracted from 5 g. aliquots of air dried soil by ammonium acetate buffered to pH 7 and estimated by atomic absorption spectrophotometer (AAS). The procedure being followed as set out in the Geography Department Handbook (1980), University of Durham.

5) Choice of worm species for experimental purposes

a) Preliminary sampling to determine species composition in an upland environment

The various factors that affect earthworm distribution have already been mentioned. In order to know these limiting factors, the detailed ecology of each species must be investigated. This requires long term study, therefore for the experimental part, species were used that were known to inhabit and could survive such areas and therefore would be the most appropriate.

As a preliminary investigation in order to determine the species composition on upland areas, a site was chosen at Harwood Beck at an altitude of 426 m. about 3 km. north of Mr Scott's farm. This area resembled the *Agrostis/Festuca* association on the limestone mineral soil at the Cumbrian site, being next to a river and consisting of close cropped turf. Formalin extraction was used because of its speed, an accurate population level not being the aim.

A plot of one square metre was roughly sectioned and a very weak solution of formalin, about 30 cm^3 to 2 gallons of water applied with a watering can through a rose. The vegetation was short enough not to obscure the worms as they emerged. These were quickly picked out, washed immediately in fresh water and stored in jars containing damp moss in order to keep them alive. A second application of solution was made at an interval of about 10 minutes later.

(b) Identification

The problem was to familiarise myself with the worms and to identify them in the live state. A local anaesthetic called Ms 222 used for aquatic invertebrates by physiologists was tried in the recommended proportions of 1:10,000 with distilled water. This proved unsuccessful even after increasing the quantity used to over 100 X the recommended dose.

A brief spell at freezing temperatures also failed to reduce their activity long enough, as once placed under microscope lights they quickly revived.

In the end ethyl acetate proved quite successful, a cotton wool ball dampened, placed in a dish with the worm and sealed. Although it caused writhing and ejection of coelomic fluid, this quickly ceased once it had succumbed. Depending on the size of the worm, the time left in the container varied between 1 and 2 minutes. This reduced their activity sufficiently, in order to note the salient features characteristic of each species according to the revised key by Gerard (1964). After identification they soon recovered in a clean dish with a little water, kept separately from those not undergoing this treatment, in order to see the mortality rate, if any. Although a few did die, the rate was very low, as long as care was taken not to leave them too long under the influence of the anaesthetic and under the hot microscope lights. A small proportion of those identified using this method were killed in 4% formalin as a check on identification. It proved sufficiently accurate.

The great majority of specimens identified were those of the genus Allobophora. Although Guild (1951) found members of this genus tolerant of a wide range of pasture types, altitude and soil acidity, Gerard (1960) noticed that sexually mature individuals of A. longa and A. nocturna went into an obligate aestivation beginning in May/June, with A. chlorotica, A. caliginosa and A. rosea having a facultative quiescent state depending on conditions.

These features mitigated against using this group, plus the fact that Satchell (1955) had classed the genus into his acid intolerant category and Laverack (1960) showed that A. longa would not burrow into a soil having a pH $<$ 4.5. Numerous workers (Svendsen 1957 a and b, Nordström and Rundgren 1973 and 1974, Bengston 1976, Phillipson et al 1976), demonstrated that the Allobophora association is dominant in pasture or deciduous areas with a mull type soil, being absent or in very low numbers from peaty soils.

c) Actual species chosen

The aim therefore was to select species that could survive the conditions of the recently improved peat soil, but was common and numerous enough to enable collection of adequate numbers. Guild (1951) noted that although altitude would no doubt reduce earthworm metabolism and reproduction it wouldn't per se limit earthworms, but indirectly through lack of suitable soil habitats. Therefore it was considered feasible that those species, able to survive the conditions in Durham, would also survive at the site in Cumbria, earthworms shown to be present on the mineral soil adjacent to the field.

Ideally a large active species was required that could eventually produce an effect on the decomposition of peat. Standen (1979) showed that Lumbricus rubellus, Lumbricus castaneus, and Dendrobaena rubida had high surface activity indices when sampling a range of seven mineral sites close to my location. All have been shown tolerant of acidic conditions, L. rubellus and L. castaneus classed as ubiquitous and D. rubida as acid tolerant (Satchell 1955), digesting a large proportion of raw humus (Piearce 1972b).

d) Collection of species chosen

From Svenden's work (1955) and later Boyd's (1957a) the three species were known to aggregate and actively move into dung. Therefore a cattle grazed pasture on Mr Scott's farm was selected for collection.

Dung pats found most suitable were those of intermediate age, these were turned over and all the worms quickly picked up before they could retreat below the soil surface. They were carried back to the department in jars containing a little soil with dung where they were later sorted, first by eye into groups and more specifically using the ethyl acetate method.

The numbers of L. rubellus and L. castaneus collected were adequate, but those of D. rubida were not. The former two species were therefore used.

II EXPERIMENTAL SECTION

6) Survival and effects of earthworms and leatherjackets on yield of grass sown in three soil types

Observations on the effects of earthworms on soil structure and plant growth have lead to numerous efforts to test these on the yield of crops, through use of experiments with artificial cultures. Results have proved positive in many cases, but some were heavily criticised due to the difficulty of testing earthworm activity whilst holding constant all other factors that influence plant growth. Inconclusive results have been obtained through failing to account for release of nutrients from dead worms (Chadwick and Bradley 1948, Nielson 1951) or from adding excessively unrealistic numbers, making the results highly subjective (Kahsnitz 1962). But when these factors are accounted for, positive results can still be achieved (Russell 1910, Hopp and Slater 1948 and 1949, Waters 1951, van Rhee 1965, Atlavinyte 1968).

Compared to the claims advanced for earthworms, leatherjackets are in stark contrast being destructive pests. Numerous reports of attacks are evident (Cohen 1953, Mayer and Davies 1976, A.D.A.S. Bulls 1970 -1980). But although they have been found in appreciable numbers on farm lands, often no recognisable loss in crops occur. The knowledge of their density on Mr Carrick's land, together with the loss of yield he had suffered due to their presence on FII in 1978, made an interesting parallel with earthworms of the effects they have on yield of grass.

a) Experimental layout

Three types of soil were used in order to compare the relative survival and effects. These included the recently improved field soils and their control, compared to a "normal" mineral soil, that collected from the limestone area, added to the soil dug from a site that had numerous moles present and therefore known to be able to support a rich earthworm fauna.

Each soil type was hand sorted, all living animals being removed. It was then sieved and bulked into large bins being thoroughly mixed. The pH was tested, because due to the quantity needed, the lower layers of the field soil had to be used, which were effectively out of the influence of liming. Bulking had increased the acidity overall compared to the relevant surface zone at the site, therefore it was limed to raise the pH. The three soils therefore had a starting pH of:-

Field soil	6.2
Control soil	4.1
Mineral soil	5.8

Four treatments were planned for each soil type:-

(i) Control - no animals.

(ii) Dead - dead specimens of L. rubellus and L. castaneus of similar weight and the same number of species as in (iv).

(iii) Tipulid - 14 specimens of Tipula paludosa larvae added to each pot within this treatment.

(iv) Earthworm - L. rubellus and L. castaneus 2 of each species/pot.

Practical restrictions were placed on the amount of replicates due to a number of reasons. These included:-

(i) A limited amount of soil.

(ii) A limited number of pots of a suitable size.

(iii) Numbers of worms and larvae available.

(iv) Space.

(v) Time spent sorting the soil at the end of the experiment in order to sort the total number of pots within a reasonable time period of one another.

For these reasons the two treatments with no live animals were replicated three times, the other two, four times, making a total of 48 pots.

The pots used were plastic with a diameter of 26.5 cm., a 23.0 cm. depth and an area 0.05 m^2 of a square metre sunk into gravel at the greenhouses in Durham.

In order to aid comparisons between this site and the actual fields in Cumbria, the number of larvae used, was a scaled down density estimate to fit these pot dimensions, amounting to 14/pot.

In order to see any significant effects due to earthworms, an average density of 390/m^2 was chosen as found within a hay meadow over limestone at Moor House (Svendsen 1955). But, in scaling this down for the pots used 20 worms would still be needed for each making a total of 240 worms to collect. Therefore, although far outside any ecological density and probably too small a number to produce any conclusive results, only 4 worms/pot could be used, 2 of each species due to the limitations imposed.

The grass mixture used was supplied by Jackson Seeds of British Seed Houses Limited, and was the same variety used by Mr Carrick, aiming to relate the results specifically to his crop. This was sown at 15 g/pot in early June.

The animals were introduced by pouring them onto the surface with a little water and leaving them to find their own situation. Both top and bottom of all pots were covered with mesh netting to prevent escape in the animal pots and to keep the conditions for germination equal. (The top netting was later removed for growth of grass and unfortunately this meant colonisation by earthworms from outside and loss of utility.)

These were checked several hours later to ensure that all animals had burrowed and to replace any failing to do so. All burrowed successfully.

The pots were watered regularly when rainfall proved inadequate.

b) Harvesting the material

At the end of August, the material from each pot was clipped to 0.5 cm. from the surface and weighed. A subsample was taken after being well mixed, weighed and dried to a constant weight at a temperature of 40°C, in order to convert all yield measurements to a dry weight figure and reduce variations due to water content.

Each pot was then sorted by hand for tipula larvae, earthworms and their ootheca.

7) Growth rate of earthworms under controlled conditions

In conjunction with the survival experiments the actual growth rate of the two species of worm used was investigated in more detail under controlled conditions.

The earthworms were kept individually in earthenware pots 16 cm. in diameter by 15 cm. deep in two soil types, the field soil and the 'normal' mineral soil. Three replicates each of L. rubellus, L. castaneus and immatures were used, the latter being either of these two as difficulty was experienced in efficiently distinguishing between them. A layer of gravel was placed in the bottom of the pots and both ends were sealed with netting. They were kept at 80°C in a constant temperature room with a photoperiod normal for the time of the year. Once a week, the soil was hand sorted, the worms recovered, washed and rolled on filter paper to remove the excess water, then weighed. The soil was moistened after each weighing and once inbetween the week's interval to prevent drying out.

8) The effects of earthworms and leatherjackets on germination and the subsequent yield of rye grass and clover

Evidence for the effects of earthworms and tipulid larvae on the final yield are numerous, but their influence before the plants grow are relatively unknown. It was decided therefore to look at the differences in percentage germination between the two animals, compared to a control.

For ease of absolute counting the size of the earthenware pot was 16 cm. diameter and 15 cm. deep. A 'normal' mineral soil was used in all cases, 5 replicates within each treatment. The treatments consisting of:-

(i) Tipulid - 5 *tipula* larvae/pot.

(ii) Earthworm - 5 specimens of *L. rubellus* to each pot.

(iii) Control - no animals.

A total of 15 pots. They were sown with the same grass mixture in mid-July. The pots were sealed with mesh netting top and bottom and watered as necessary.

Two weeks after sowing the percentage germination of grass and of clover was measured.

9) The consumption of vegetation by Larvae of Tipula paludosa

As an aim to gaining more specific detailed knowledge of the actual amounts that these larvae eat at different weights, a series of controlled experiments were set up. These were conducted over a month from early June to early July, before their pre-pupal phase.

The larvae were grouped into two size classes, 'small' and 'large', kept singly in glass containers about 10 cm. deep on moistened tissue roll. They were fed over one week on various diets of common grass species consisting of the following treatments:-

(a) Shoots only.

(b) Roots only.

(c) Shoots and roots together.

    (i) Over 1 week

    (ii) Over 24 hours.

    (iii) Over 72 hours.

(d) Roots of both grass and clover separately.

The containers were covered with mesh to prevent escape and allow aeration and held at 8^{0}C in a constant temperature room, the photoperiod normal for the time of year.

The amount consumed was converted into a dry weight figure but those for the larvae are wet weight estimates. A wet:dry weight ratio was carried out for the two size classes but not used in conversions, because the limited supply of animals prevented taking a subsample each time. But it was found to be significantly different, the small size ($\bar{X}$ wt = 0.174 g.) with 18% of their initial weight remaining and the larger ($\bar{X}$ wg = 0.308 n = 5 on both occasions) with 14% ($P < 0.05$). The larger animals were therefore having a larger proportion of their body weight as water.

IV RESULTS AND DISCUSSIONS

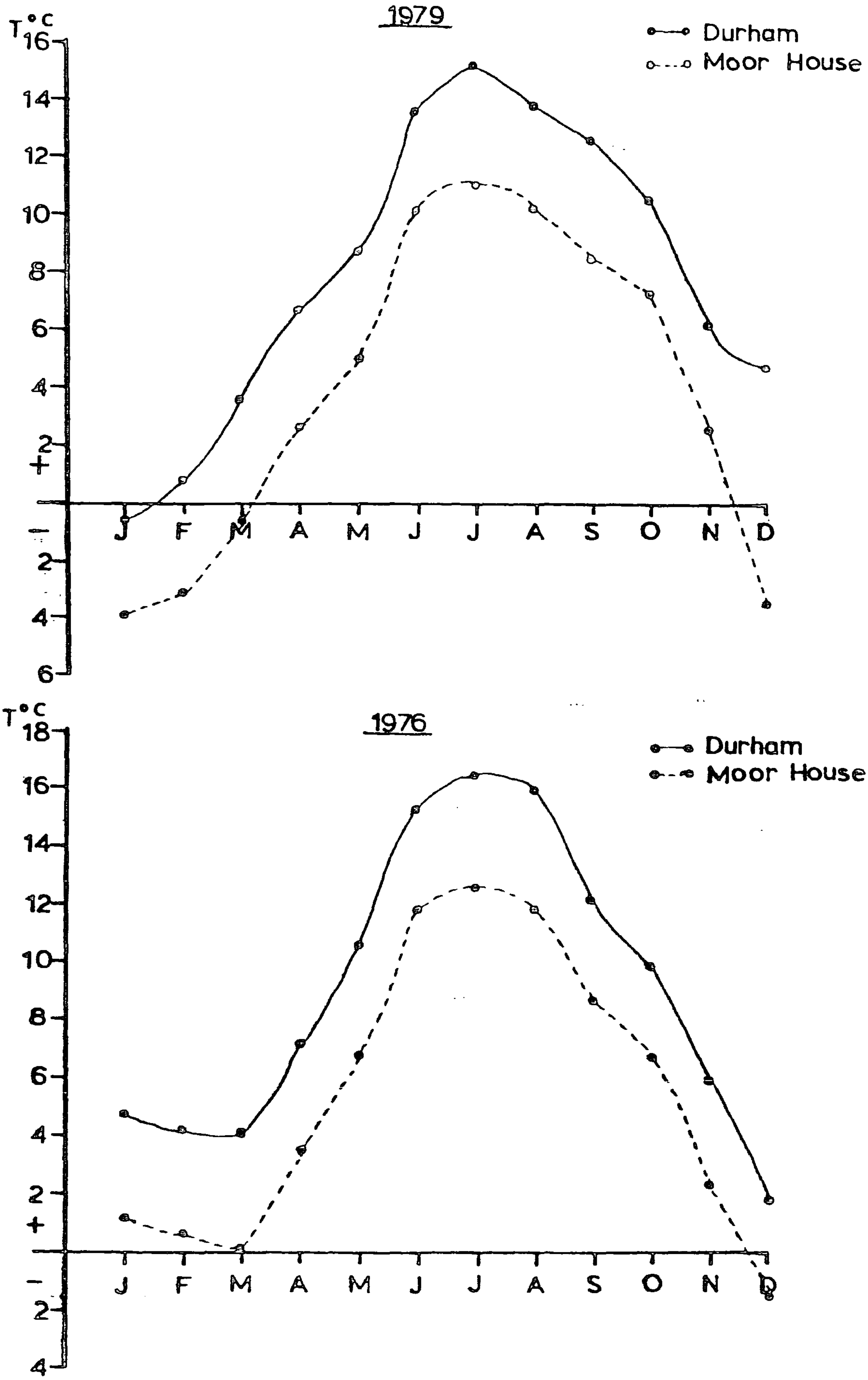
1) The determining conditions for earthworm survival in an upland environment

(a) Climate

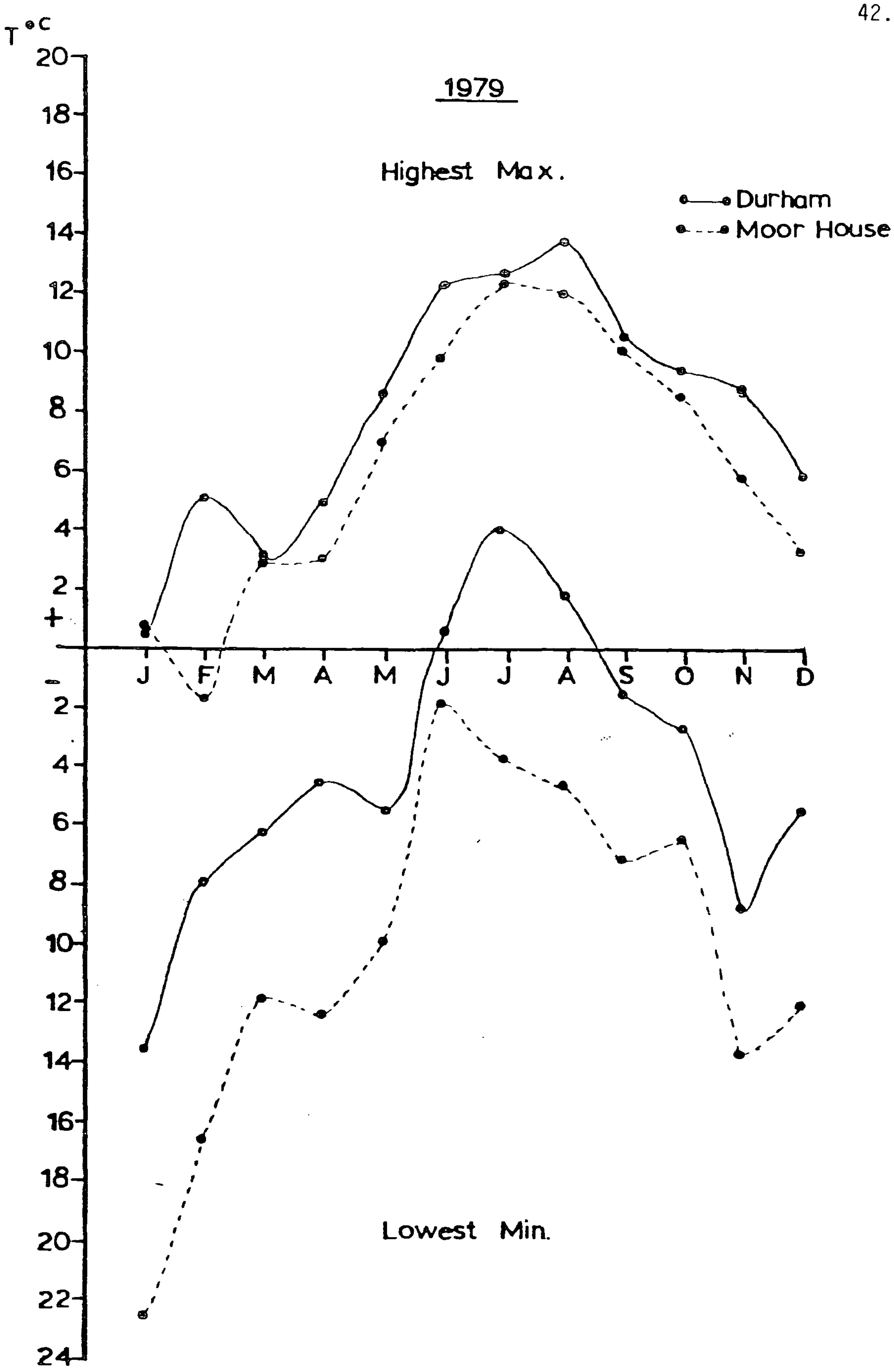
The climate within the M.H.N.N.R. has been described by Manley (1936, 1943) as sub-artic, being similar to that at sea level in Southern Iceland. Yet even here earthworms are able to survive and colonise (Bengston et al 1975). As pointed out by McFadyen (1956), the air temperature as measured 1.5 m. above the ground by a Stephenson screen is not necessarily a close approximation to the temperature at or near the soil surface where the animal lives. Mean monthly air temperatures are about 4^{o}C lower throughout the year at Moor House, compared to Durham (Graph 1), but grass readings show the lowest minimum to be below freezing all year round for Moor House (Graphs 2 and 3). But even this is not relevant to the organism in question. The most relevant mean temperature in the field occurs at greater depth. Shown by Table 7, soil temperatures at 5 cm. at no time drop to less than 0^{o}C for the winter months (Phil Holmes, Warden, M.H.N.N.R., pers. comm.).

TABLE 7: Comparison of air temperature and soil temperature at 5 cms. Weekly mean and overall monthly mean for the year 1979 T°C

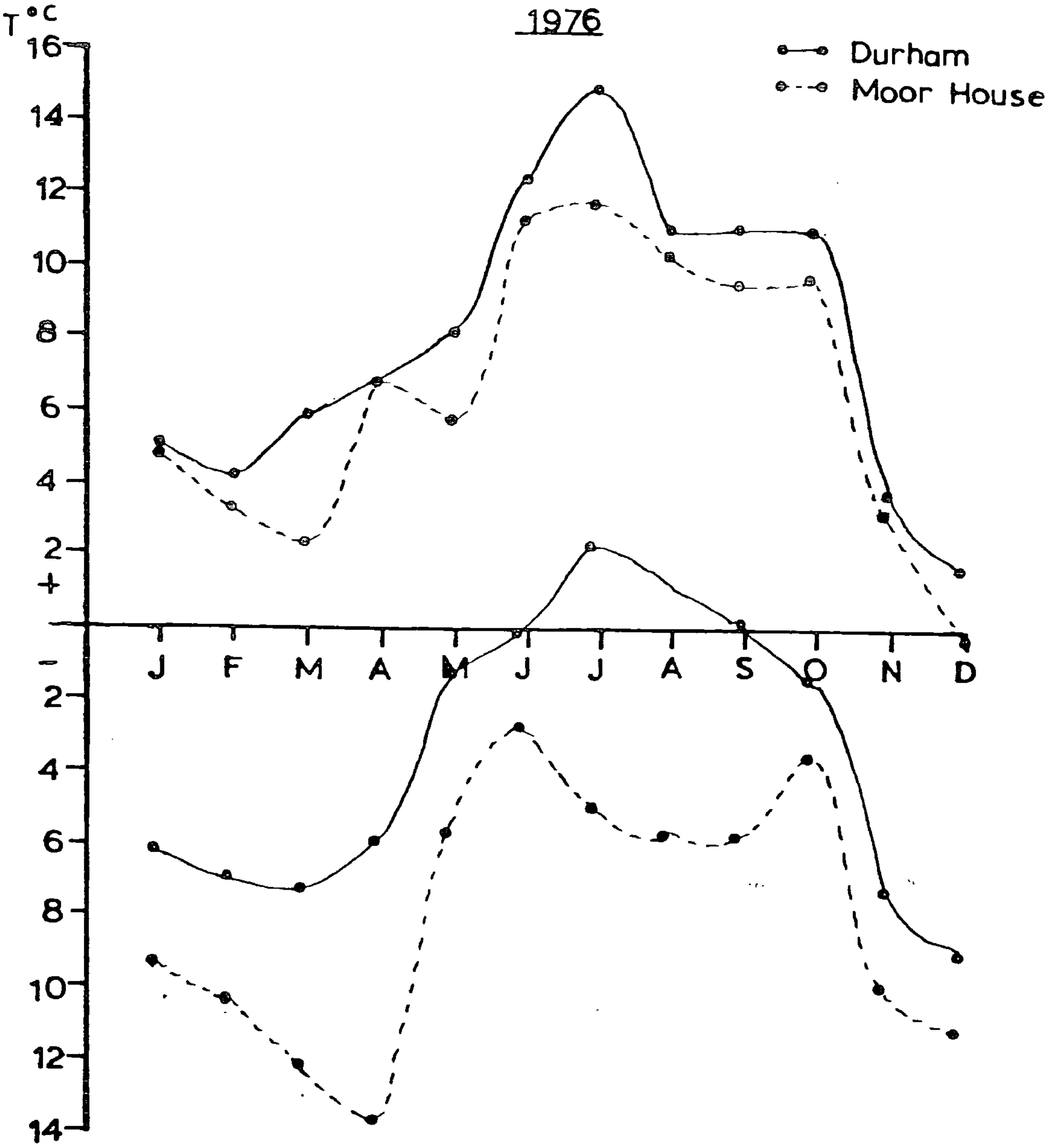
	January			February			March			April		
	Mx.	Mn.	5 cm.	Mx.	Mn.	5 cm.	Mx.	Mn.	5 cm.	Mx.	Mn.	5 cm.
	$\bar{2}.1$	$\overline{9.5}$	0.4	0.9	$\overline{5.8}$	0.1	2.9	$\overline{0.8}$	0.2	2.1	$\overline{3.3}$	0.3
	$\bar{3}.1$	$\overline{7.3}$	0.2	$\overline{1.9}$	$\overline{5.7}$	0.1	2.8	$\overline{1.8}$	0.2	4.3	0.4	0.9
	0.9	$\overline{3.2}$	0.3	$\overline{3.1}$	$\overline{5.3}$	0.1	$\overline{1.5}$	$\overline{4.4}$	0.1	8.2	0.6	3.4
	$\bar{2}.3$	$\overline{7.2}$	0.1	0.9	$\overline{2.6}$	0.2	1.1	$\overline{3.1}$	0.1	6.3	0.5	3.4
$\bar{X}$	$\bar{1}.65$	$\overline{6.8}$	0.25	$\overline{0.8}$	$\bar{4}.85$	0.125	1.325	2.525	0.15	5.225	$\overline{0.7}$	2.0



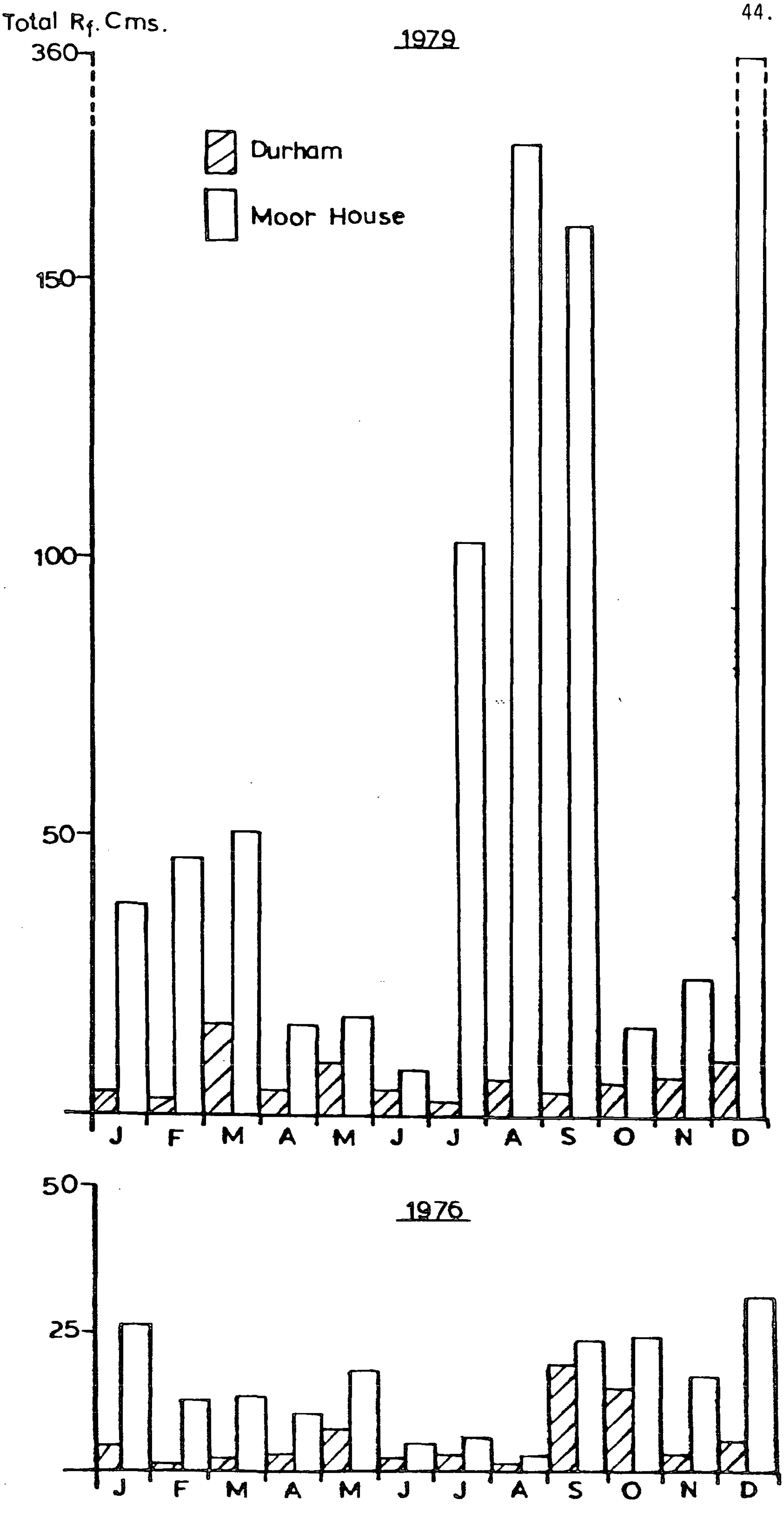
GRAPH 1 : Mean monthly air temperature at Durham and Moor House for the years 1976 and 1979



GRAPH 2 : Grass minimum readings at Durham and Moor House for the year 1979



GRAPH 3 : Grass minimum readings at Durham and Moor House for the year 1976



GRAPH 4: Total rainfall in cms at Durham and Moor House for 1976 and 1979

No data was available for December, but as the lowest minimum air temperature almost always occur in January they can be taken as representative of the most extreme period.

Recordings made by Horobin (1971) over the months October - December 1968 at 1 cm. depth in the same area, show that at no time did the temperature fall below freezing, the lowest recorded being +1.3°C at an altitude of 625 m. on Great Dun Fell.

The variables which concern the meteorologist therefore are not significant in influencing the animal.

Although sudden drops in temperature to less than 0°C have been known to kill large numbers of earthworms (Hopp and Linder 1947, Bro Larsen 1949) the significance of the vegetation acting as a buffer must be taken into account. Butterfield (1974) recorded -9°C in the middle of an Eriophorum tussock but -1°C in Juncus litter.

Reports have also shown that certain surface active species can retreat to lower layers. Bornebusch (1953) referred to D. octaedra and Abrahamsen (1972) to D. rubida and L. rubellus as retreating due to the cold, although Nordström and Rundgren (1974) did not support this view for D. octaedra in their study.

The years 1976 and 1979 were chosen because they were within the time period of the alterations in land use and both represented extremes of climate, 1976 was a 'good year', i.e. warm and dry, and 1979 a 'bad year', i.e. cool and wet. This can be clearly seen in the summary table (Table 8) and the monthly figures for the relevant meteorological data plotted as a series of graphs 1-4.

TABLE 8: Summary of meteorological data for the years 1976 and 1979 at Durham and Moor House

	Air Temperature 1°C		Rainfall mms		No. Frost days		Grass min. Readings	
	1976	1979	1976	1979	1976	1979	1976	1979
Durham								
H. Mx.	29.3	24.9	193.2	166.0	122	146	11.8	12.2
L. Mn.	- 5.0	-10.9	17.5	25.3			-13.5	-22.5
Moor House								
H. Mx.	25.6	22.4	302.4	3588.0	352	352	14.9	13.7
L. Mn.	- 9.7	-15.9	29.0	78.9			- 9.0	-13.6

H. Mx. = highest maximum)
L. Mn. = lowest minimum) for the year

But although such measurements are important in defining the climatic environment of the organism, they give no information on the actual micro-climate experienced by that organism.

High temperatures are unlikely to be limiting to earthworms in the study areas and soil temperatures rarely fall to below freezing. Satchell (1967) concluded that optimum temperature for motor activity within the earthworm is about 10°C. Temperatures at Moor House, would probably never reach high values beneath the surface, as although the black peat soil would absorb much heat, this energy would be dissipated in evaporating its contained water, of which a plentiful supply is available through rain and snowfall (Graph 4).

L. rubellus and L. castaneus both have high reproductive rates producing up to 106 and 65 cocoons per individual respectively (Evans and Guild 1948). Their survival and fecundity is related to environmental conditions in that being surface active they are more liable to dessication, heat and predation. Some evidence exists that earthworms are able to acclimate (Grant 1955) which may also aid their survival during extended periods of cold.

There is no reason to suppose that survival of earthworms is not possible on Mr Carrick's land based on the relevant meteorological data and evidence exists that they are already firmly established at this altitude and area (Svendsen 1955a, Standen 1979).

b) Soil acidity - pH (Table 9)

That lumbricids are directly sensitive to the acidity of the soil has been known since the early 20th Century. Later Russell (1973) denoted a value of 4.5 as being critical for earthworm activity, but as shown by Laverack (1961) this depends on the species being considered. Satchell (1955) found a direct correlation with pH of the soil and the presence or absence of worms and their distribution. Later studies by Piearce (1977a) and Nordström and Rundgren (1973) confirm this fact.

The chemical analyses confirm that the pH of the recently improved soil is well within the range tolerated by both L. rubellus and L. castaneus (Table 9), the former being the most resistant in the experiments of Laverack (1961), able to survive at a pH of 3.8. Although the lower layers of the peat correspond to this value at one sampling site, the majority of the population occur in the upper layer where the pH is higher. Compared to the control, the pH has been increased significantly.

TABLE 9: pH of FI and FII compared to a control peat soil

		Sampling Sites				
	Date sampled	Top 1	2	3	4	Base 5
FIELD I	9.5.80					
Depth = 1 cm. intervals unless marked * = 2 cm.	a	4.3	5.8	6.1	5.5	4.8
	b	4.1	5.5	5.9	5.2	4.8
	c	4.0	5.3	5.7	4.7	5.3
	d	3.9*	4.9	5.5	4.2	5.3
	e	3.9*	4.4	5.3*	4.1	6.4*
	f	3.8*	4.0	4.5*	4.0	
** CONTROL	9.5.80					
	a	3.0	3.3	3.3	3.3	3.4
	b	3.0				
	c	3.1				
	d	3.1				
	e	3.1*				
	f	3.2*				
FIELD II	19.5.80					
	a	6.0	5.9	5.0	5.2	6.2
	b	5.3	6.0	6.0	5.2	5.9
	c	4.4	5.8	4.1	4.9	5.9
	d	4.0	5.8	3.8	4.5	5.3
	e	3.9*	5.6*	3.8	4.1*	4.3
	f	3.8*				

** N.B. pH of the soil at depth wasn't continued for the control due to lack of variation down the profile.

Higher pH values are shown for FII by fertiliser treatment compared to FI, reflecting the greater number of years of treatment. The full effect of the lime penetrates to about 5 cm. on these soils whereafter a sharp decrease in pH occurs, but still these layers are significantly influenced to have less acid soil than the original peat as demonstrated through the control soil.

Only one site showed an inverse trend of pH with the depth, sample site 5. Being at the base of the hill it would be under the influence of drainage bringing more alkaline water from up slope. The surface layer is still sufficiently alkaline to support earthworms.

Compared to Mr Scott's fields, the longer term treatments haven't significantly affected the values from those of FI or FII (Table 11 and 't' test Table A).

Table A: pH - 't' test table of significance comparing all fields sampled

	1	5a	5b	6b	12	13	16	FI	C	FII
1		S*	NS	S*	NS	NS	S*	NS	S*	NS
5a			NS	S*	S*	NS	S*	NS	S*	NS
5b				NS	NS	NS	NS	NS	S	NS
6b					S*	S*	S*	S*	S*	S*
12						NS	S	NS	S*	NS
13							NS	NS	S*	NS
16								NS	S*	NS
FI									S*	NS
C										S*
FII										

S* $p < 0.01$
S $p < 0.05$
NS Not significant $p < 0.05$

c) Percentage Moisture (Table 10)

Water constitutes a large percentage of the body weight of earthworms necessary for respiration, excretion, locomotion and burrowing and with no protection from dessication, it plays an important part in their economy. Despite this, they possess marked physiological tolerance to dessication, the majority are able to sustain a loss of at least 50% (Grant 1955). Behavioural means such as retreating to lower layers, aestivating or diapause also confer protection. Many can survive long periods submerged, including L. rubellus although when given a choice they prefer to remain above the water level.

The use of a percentage figure has been critised as it is not the total amount of water contained in soil that is important, but the relative availability of this water. Therefore, use of the pF, or the force with which water is held is more relevant (Nordström and Rundgren 1974). Peat can hold 2-3 times more water as an equal volume of mineral soil. Much of it is contained in hygroscopic pores and therefore unavailable. But peat also contains a larger amount in capillary pores.

TABLE 10: Percentage water content of Mr Carrick's fields FI and FII, compared to a control peat soil

			Sampling sites					
		Date Sampled	Top 1	2	3	4	Base 5	$\bar{X}$
% water content	FIELD I	9.5.80	39.84	31.07	77.30	80.72	96.40	65.66
	CONTROL	9.5.80	82.40	85.20	83.84	85.74	86.10	84.65
	FIELD II	19.5.80	27.92	61.55	58.37	64.95	66.35	55.83

From an analysis of the water content of FI (Table 10) it seems unlikely ever to become limiting, well within the range found lower down the valley (Table 11) where earthworm populations are high. Between the newly improved fields no significant changes in water content have occurred over time since treatments, few differences were shown even by the fields undergoing longer term treatments (Table 11 and 't' test table B). Although water content allows a broad general comparison, the Geography Handbook (1980), University of Durham, states that samples cannot be adequately compared unless they have been equilibrated to a standard moisture content, such as field capacity.

TABLE 11: Chemical analysis of Mr Scott's fields, Teesdale, for pH, percentage moisture & percentage carbon 23/7/80

	Depth 1 cm. intervals	Field Number 1	5a	5b	6b	12	13	16
pH (mean of 3 samples)	1	4.9	4.7	4.8	6.4	4.9	6.3	4.7
	2	4.9	4.6	4.7	6.2	4.8	5.3	4.7
	3	4.9	4.6	4.7	6.0	4.8	4.5	4.7
	4	4.9	4.6	4.7	5.7	4.8	4.2	4.7
	5	4.9	4.6	4.7	5.7	4.9	4.2	4.7
	$\bar{X}$		4.7	4.7	5.7	4.8	4.9	4.7
% Moisture	$\bar{X}$	35.02	50.63	58.59	33.13	35.05	47.46	56.90
	SD	3.19	15.69	3.19	2.80	5.18	5.65	2.72
	N 3							
% Carbon	$\bar{X}$	45.70	19.33	19.60	67.98	64.37	62.86	28.12
	SD	4.51	2.20	4.29	5.46	10.45	1.29	22.93
	N 3							

TABLE B : Percentage moisture 't' test table of significance comparing all fields sampled

	1	5a	5b	6b	12	13	16	FI	C	FII
1		NS	S*	NS	S*	S	S*	NS	S*	S*
5a			NS	NS	NS	NS	NS	NS	S*	NS
5b				S*	S*	S	NS	NS	S*	NS
6b					NS	S	S*	S	S*	S*
12						S	NS	NS	S*	S
13							NS	NS	S*	NS
16								NS	S*	NS
FI									NS	NS
C										S
FII										

S*	$p < 0.01$
S	$p < 0.05$
NS	Not significant

The differences between the values obtained for FI and for FII were reflected in the large standard errors (Table 14). This emphasises the great variability over the fields. The influence of the slope was shown on FI, higher values were obtained from the base of the field.

Where moisture content is high, aeration is usually low, especially at depth and also contributing to an increase in acidity of the soil. The aeration status of the soil is very difficult to measure and the value obtained very subjective.

d) Percentage Carbon (Table 12)

The amount of organic matter in soil greatly influences the distribution of species of earthworm and the size of populations, but as measured by loss on ignition fails to distinguish soil organic matter in terms most relevant to earthworm nutrition. A continual supply is necessary which must be palatable and sufficiently nutritious to support the organism. This is adequately demonstrated in mor soils which support few lumbricids compared to fertile mull soils.

In this study the approximate amount of carbon for Mr Carrick's fields was not significantly different to the control, even on FII with longer term improvements ('t' test table C).

TABLE C : Percentage carbon 't' test table of significance comparing all fields sampled

	1	5a	5b	6b	12	13	16	FI	C	FII
1		S*	S*	S*	S	S	NS	S*	S*	S*
5a			NS	S*	S*	S*	NS	S*	S*	S*
5b				S*	S*	S*	NS	S*	S*	S*
6b					NS	NS	S	NS	S*	NS
12						NS	NS	NS	S*	NS
13							NS	S	S*	S
16								S	S*	S
FI									NS	NS
C										NS
FII										

S* $p < 0.01$ NS Not significant

S $p < 0.05$

Percentage carbon content was high in all cases, the material consisting of remains of acid blanket peat. But percentage carbon content in FI and FII was not significantly different to 6b or 12 therefore the actual material must be different in its chemical and physical composition, as the structure of organic matter is not comparable in organic and mineral soils.

Evans and Guild (1948c) offered organic matter at various stages of decomposition to A. chlorotica and L. castaneus and monitored effects on cocoon production. A high rate was obtained on partially decayed organic matter, which included dung and peat and a low rate on the two extremes of decay, the differences being highly significant. Piearce (1972a), investigated the diets of lumbricids on soils ranging from lowland to upland pastures and found that the surface litter feeders had a relatively high proportion of undecomposed as well as decomposed organic matter in their faeces, with only a little mineral material. At the upland pasture the proportion of raw humus in earthworm crop and gizzard was particularly high. Therefore this seems to suggest that organic remains can be digested by the two species used in this study.

e) Total nitrogen (Table 12)

Russell (1973) states that the level of available nitrogen is probably an important factor governing the size of earthworm populations. Linked to carbon it determines the quality of the material available. Although the figures for total nitrogen on the improved soils are high,(average for lowland soils is about 0.1 - 0.6% Floate 1977), they are not significantly different from the control area (Table 14), which seems to support the fact that total amounts in peat generally are high, although availability may be low (Floate 1971). Much nitrogen is held in organic form and only slowly becomes available through decomposition. Despite high total amounts the quality expressed through the C:N ratio is poor, the ratio being 2-3 fold above the level, (20:1), at which mineral nitrogen can be directly utilised by plants (Edwards et al 1970).

TABLE 12: The percentage carbon and percentage nitrogen of Mr Carrick's fields together with the C:N ratio, compared to the control peat

		Sampling sites					
	Area	1	2	3	4	5	$\overline{X}$
% Carbon	FIELD I	90.82	57.30	83.20	89.80	89.70	82.16
	CONTROL	89.50	91.30	90.20	91.80	89.20	90.40
	FIELD II	86.33	85.29	83.86	84.22	83.08	78.55
% Nitrogen	FIELD I	1.44	1.34	1.92	2.04	1.81	1.71
	CONTROL	1.19	0.70	1.86	1.18	1.46	1.28
	FIELD II	0.45	0.74	0.59	0.34	0.70	0.56
C:N ratio	FIELD I	62.98	42.63	43.37	43.93	49.66	48.51
	CONTROL	75.21	130.42	48.44	78.06	61.26	78.67
	FIELD II	192.70	114.95	91.60	250.65	118.70	153.72

FI and Control sampled 9.5.80
FII sampled 19.5.80

The high solubility of nitrate was reflected in the very low results obtained for FII, emphasising the need for continuous applications in order to offset the effects of leaching.

That nitrogen is important for the protein nutrition of earthworms has been shown on Silpho Moor, an acid Callunetum occupied almost solely by Bimastos eiseni. After 8 years of applying birch litter containing 2-3 times the nitrogen content of heather to simulate natural leaf fall, the population increased from <1 worm/20 m^2 to 1-5 worms/m^2 (Satchell 1967).

f) Cation exchange capacity (Table 13)

Out of all the cations analysed, the one most directly important for earthworm survival is calcium (Satchell 1955). It is of secondary important to pH, as the avoidance of acid soils, means that there is no opportunity for lack of calcium, which is characteristic of acid soils, to play a decisive role.

Piearce (1972a) showed that some species, (amongst them L. rubellus and L. castaneus) possess complex calciferous glands able to excrete excess calcium absorbed from the diet. Greater concentrations of calcium were found in the surface litter layers.

Here the act of liming has greatly increased the amount of Calcium on both fields, compared to the control. The levels are now far in excess of that required for earthworm survival.

TABLE 13: Cation exchange capacity of FI and FII compared to the control peat

		Top		Sampling sites		Base	
		1	2	3	4	5	$\bar{X}$
p.p.m. Ca	FIELD I	122.0	257.0	136.0	236.0	188.0	187.80
	CONTROL	18.0	24.0	36.0	27.0	22.0	23.40
	FIELD II	90.0	254.0	145.0	185.0	280.0	190.80
p.p.m. K	FIELD I	6.0	3.3	7.2	5.2	5.3	5.40
	CONTROL	5.6	5.4	5.5	5.5	12.4	6.88
	FIELD II	4.8	5.8	3.9	5.6	4.8	4.98
p.p.m. Mg	FIELD I	9.1	9.0	10.2	11.8	10.2	10.06
	CONTROL	4.6	3.4	4.8	5.5	6.9	5.04
	FIELD II	30.0	56.0	38.0	41.0	61.0	45.20
p.p.m. Na	FIELD I	4.9	3.7	4.6	4.3	4.2	4.34
	CONTROL	4.8	4.7	4.5	5.1	6.1	5.04
	FIELD II	3.0	3.5	2.7	3.1	2.9	3.04

FI and Control sampled 9.5.80

FII sampled 19.5.80

A positive correlation is also usually associated with the rate of decomposition, liming increases bacterial activity. This should eventually lower the C:N ratio to a more favourable value for the fauna.

Of the other cations, none are directly important for earthworm survival, only as they affect the growth of the plant and therefore the food supply. The influence of fertiliser treatments on the soils was clearly shown by the amounts of magnesium extracted. FII received applications of magnesium limestone rather than pure calcium carbonate.

Sodium was not a constituent of any treatment but significant reductions still occurred on both FI and FII compared to the control (Table 14).

These figures represent total amounts rather than amount available but Gore and Allen (1956) compared the CEC of 5 different peat types at M.H.N.N.R. and found that the exchangeable and total Na^+, K^+, Mg^{++} and Ca^{++} were similar only exchangeable Fe values were much lower than the total amount of Fe present.

TABLE 14: Comparison of the chemical analyses for Mr Carrick's fields with that of the control peat using students 't' test

Chemical analysis		FI	C	FII	Comparisons	t	Result
% Water	$\bar{X}$	65.06	84.65	55.83	F1 vs F2	0.64	NS
	SD	28.14	1.52	15.90	F1 vs C	1.55	NS
	SE	12.58	0.68	7.11	F2 vs C	4.03	S*
% O.C.	$\bar{X}$	82.16	90.40	78.55	F1 vs F2	0.40	NS
	SD	14.22	1.12	13.85	F1 vs C	1.29	NS
	SE	6.36	0.50	6.19	F2 vs C	1.90	NS
% N	$\bar{X}$	1.71	1.28	0.56	F1 vs F2	7.63	S*
	SD	0.30	0.42	0.17	F1 vs C	1.88	NS
	SE	0.13	0.19	0.08	F2 vs C	3.50	S*
C:N	$\bar{X}$	48.51	78.67	153.72	F1 vs F2	3.53	S
	SD	8.55	31.25	66.14	F1 vs C	2.08	NS
	SE	3.82	13.97	29.58	F2 vs C	2.29	NS
pH	$\bar{X}$	5.10	3.08	5.0	F1 vs F2	1.52	NS
	SD	0.31	0.15	0.55	F1 vs C	11.65	S*
	SE	0.22	0.06	0.24	F2 vs C	4.09	S*
p.p.m. Ca	$\bar{X}$	187.8	23.40	190.80	F1 vs F2	0.068	NS
	SD	59.42	3.57	77.85	F1 vs C	6.18	S*
	SE	26.57	1.59	34.81	F2 vs C	4.80	S*
p.p.m. K	$\bar{X}$	5.40	6.88	4.98	F1 vs F2	0.58	NS
	SD	1.42	3.08	0.76	F1 vs C	0.97	NS
	SE	0.63	1.38	0.34	F2 vs C	1.33	NS
p.p.m. Mg	$\bar{X}$	10.06	5.04	45.20	F1 vs F2	6.06	S*
	SD	1.13	1.28	12.91	Fs vs C	6.62	S*
	SE	0.50	0.57	5.77	F2 vs C	6.92	S*
p.p.m. Na	$\bar{X}$	4.34	5.04	3.04	F1 vs F2	5.45	S*
	SD	0.45	0.63	0.2(	F1 vs C	2.034	NS
	SE	0.20	0.28	0.13	F2 vs C	6.48	S*

✓ at 8 degrees of freedom = 2.306 (except pH)

NS - not significant at $p < 0.05$ level

S - significant at $p < 0.05$ level

S* - significant at $p < 0.01$ level

FI - Field I

FII- Field II

C - Control

Comparisons of the total nutrient concentrations in mineral and organic soils is difficult because of the differences in availability. Total concentrations are much higher in mineral soils than in peat, but a higher proportion of the nutrients are usually extractable from peat. Expressed on a soil volume basis rather than on a weight basis, the nutrient content of peat is about 4-6 times less than a mineral soil (Heal and Smith 1978).

g) Conclusions

This study of the factors relevant for earthworm survival showed it would be possible for the two chosen species to survive on the newly improved peat soils. A cosmopolitan range of species is already present on the limestone mineral soil, adjacent to the streamsides so that the determining ecological conditions must be satisfied here.

Out of all the factors studied which might reduce survival of earthworms in the field, the quality and quantity of food is of significant importance. This is the one determining factor as Satchell (1967) pointed out that although some species (namely B. eiseni and D. octaedra) are adapted to live in extremely eutrophic situations such as mor humus, their total biomass remains small despite abundant energy supplies. Organic horizons still exist, so that the worms may be physiologically unable to exploit fully mor forming litter as food.

This implies that they can utilise humus only to a limited extent and Handley (1954) suggested that the organic nitrogeneous material in mor is less easily digestible than that in mull.

On fields FI and FII, the vegetation consists of pasture plant species which will eventually contribute a mull type litter. The various fertiliser applications will increase the nutrient content of the material, so that a shift from mor forming vegetation will occur. Theoretically this should support a greater total biomass of worms, together with species of a narrower ecological range.

h) Summary of results

Measurement of factors important to earthworm survival were taken from the newly improved field soils and from a control area of peat. The factors measured were climate, pH, moisture content and calcium level. These were found to be within the limits of earthworm tolerance, for these particular species, although the type and quantity of available food may be restricting at the present.

2) The physical factors influencing field distribution of earthworms

a) Density estimates

Table 15 shows the comparison of the density estimates of total earthworms and ootheca on all sites sampled. Total numbers were compared using Chi squared,

TABLE 15: Comparison of the numbers of earthworms and ootheca found on sites sampled in June and July 1980

Field No.	Total No. worms	No. worms per m^2	Total weight g^{-1}	Av. weight g^{-1}	Wt/m^2 g^{-1}	No. ooth	No. Ooth per m^2
1	140	467	21.33	0.15	71	46	153
5a	41	273	7.21	0.18	48	13	87
5b	83	553	7.20	0.09	48	3	20
5a + 5b	124	407	14.41	0.13	48	16	53
6b	178	593	28.69	0.16	96	47	157
12	81	270	10.54	0.13	35	61	203
13	40	133	6.28	0.16	21	12	40
16	38	127	3.28	0.09	11	11	37
FI	4	13	0.83	0.20	3	2	7
FII	-	-	-	-	-	-	-
Lst. Min.	67	223	6.63	0.10	22	20	67
Control	-	-	-	-	-	-	-

significant differences were found on the blanket bog (control area), FI and FII and fields 1, 5(a and b) and 6b ($p < 0.01$). The first three differed from the expected because of low density and the latter three because of high densities. The same differences were reflected in the ootheca number, but included field 12 and not field 5.

The number of worms in the fields containing the high density estimates are comparable with those in lowland pastures (Table 5 pg 124 Edwards and Lofty 1977). The lower estimates for Mr Scott's fields are comparable with deciduous woodland. No earthworms were found on FII and very few on FI, although a significant population exists on the adjacent limestone mineral soil.

Total numbers of ootheca differed widely amongst the fields, but generally they were positively related to the total number of worms. Highest numbers were found on field 12, which may have increased the density estimate of earthworms later in the season.

b) Factors affecting distribution

(i) Total numbers

The table (Table 15) shows the absence of earthworms in the newly improved field soil (FI and FII). Yet having analysed their chemical composition and finding it not totally inimical to earthworm survival, a multiple regression was carried out on all fields including FI and FII, in order to determine the major phyico-chemical factors that are actually limiting their distribution.

For total numbers this is shown in Table 16 indicating the slope of the line b, its standard error, together with the F ratio for each characteristic which produced a significant reduction in the error of the sum of squares.

TABLE 16: Significant factors in the multiple regression equation accounting for the presence of total numbers of earthworms

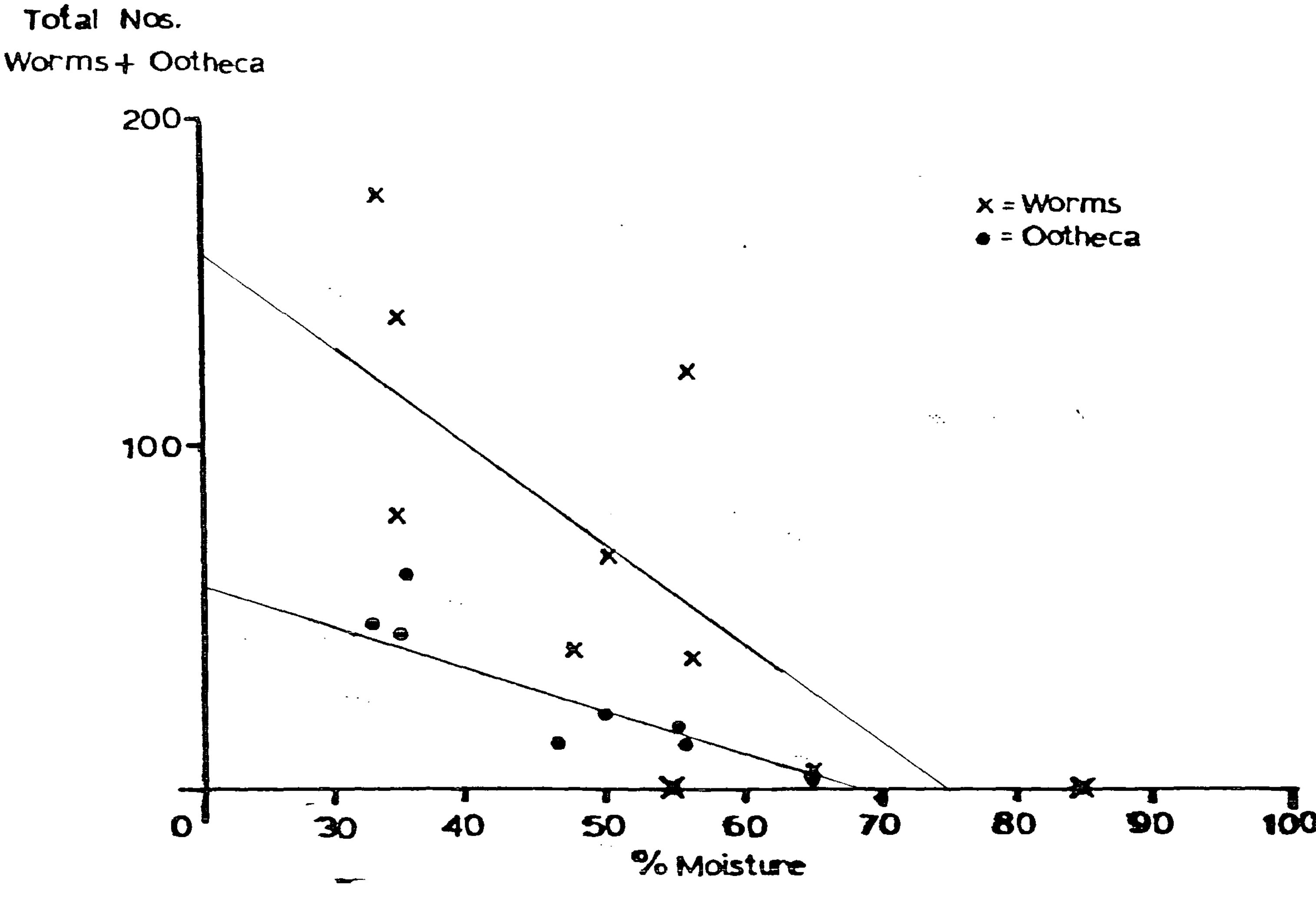
Variable	F	b	SE
% Moisture	10.716	- 2.878	0.879
Peat	5.273	-49.489	21.550
Clay	14.178	-69.159	18.367
FYM	6.310	194.111	17.872

R^2 for significant variables	94.20
Total R^2	99.00

These four variables explain nearly 95% of the distribution, inclusion of another six variables practically accounting for their complete distribution.

(1) Percentage Moisture

Over 50% of the total distribution is accounted for by this one factor alone. This is reflected in the trend found on Graph 5. A negative correlation was obtained between water content of the soil and number of worms (r = -0.741).



GRAPH 5: Variation in total numbers of worms and ootheca with percentage moisture for all fields sampled

Regression equations:

No. worms $y = -2.949\,x + 220.324$ $r = -0.741$

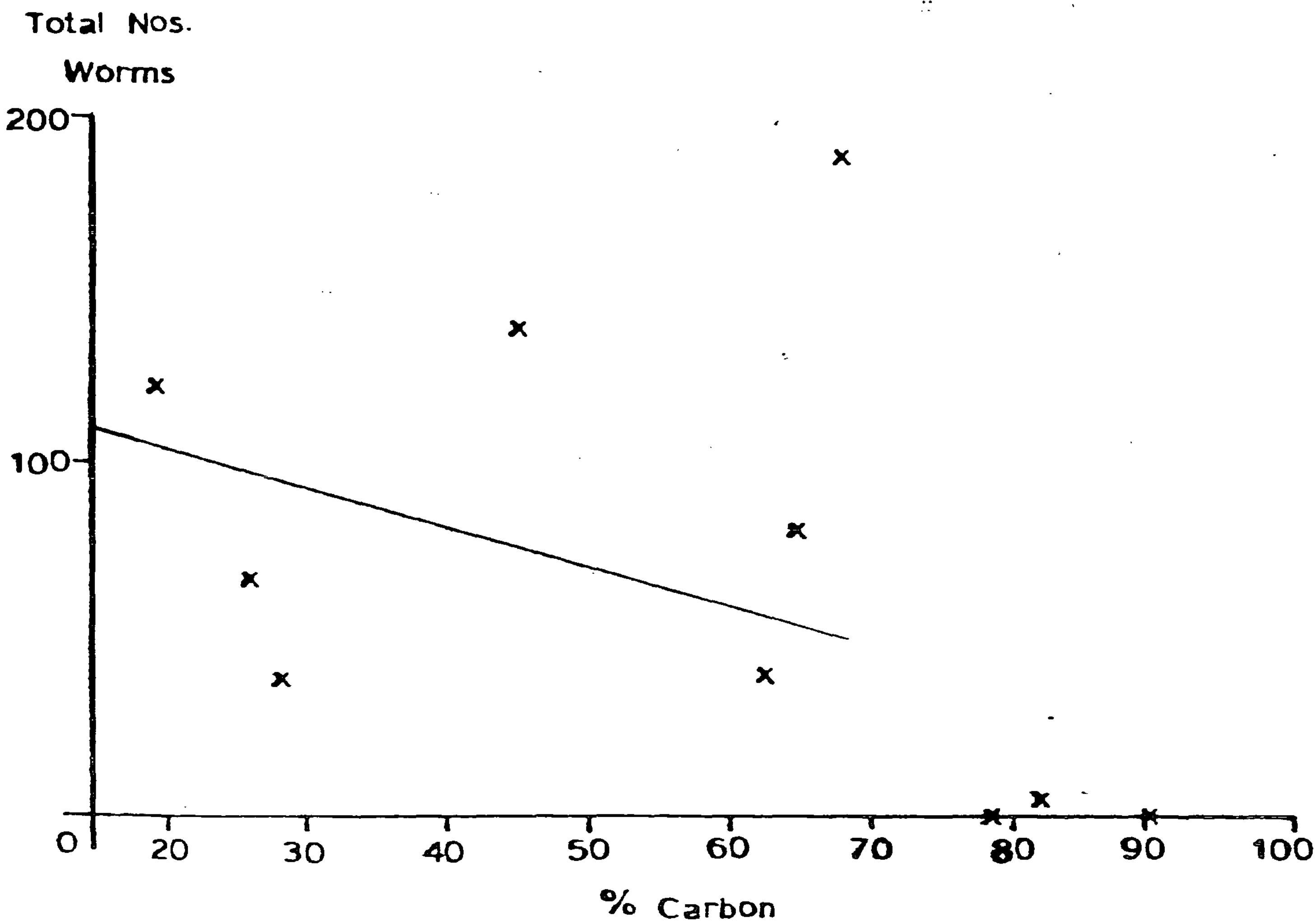
No. ootheca $y = -1.171\,x + 82.314$ $r = -0.8422$

But even with this the scatter is high, some discrepancy being found. No significant differences were found between the moisture content of fields 5a and 5b and FI and FII ('t' test Table B) yet the former supports one of the largest earthworm populations.

(2) Peat

18% of the variation was accounted for by this factor, indicating that total earthworm numbers are lower in soils with high peat content. Although classed separately from organic carbon, the factor labelled 'peat' can be taken as representative of it; a negative correlation was obtained with organic carbon and earthworm number.

The trend is shown on Graph 6.



GRAPH 6: Variation in total numbers of earthworms with percentage carbon for all fields sampled

Regression equation: $y = -1.0829\ x + 128.45$ $r = -0.435$

But Table 11 shows that field 6b had the largest organic matter content, not being significantly different to either of the two newly improved fields, FI and FII, yet 6b had the largest earthworm total, a density estimate far in excess of what most workers recover, although with a slightly lower wet weight biomass.

The wide scatter of points reflects these exceptions which may be related to the type of organic matter present.

(3) Clay

Nordström and Rundgren (1974) obtained a positive correlation with clay and total numbers. The negative correlation with clay found here is difficult to explain. The majority of the worms were very small immatures and these are difficult to identify. The majority of adults belonged to the genus Allobophora and have been assigned to the Endogée category by Bouché (in Phillipson et al 1976). A. chlorotica is intermediate in character, where the burrow systems are extensive and shallow, primarily horizontal and between the mineral/organic contact layer. The negative association with clay therefore seems unexpected, as a certain proportion would be needed to stabilise the burrow system. Piearce (1972b) also found a large proportion in the faeces of A. caliginosa.

The result could possibly be due to the arbitrary classification of soil type, a proper textural analyses may have given different results. The fact that many of the worms occurring at these sites were immature may be of some significance in producing a negative relationship. A different result may have been produced with mature species of worm.

(4) Farm Yard Manure (FYM)

The positive correlation with FYM is expected as it constitutes one of the most favourable forms of food to earthworms, being high in available nitrogen. As shown at Rothamsted, the Broadbalk plots (continuous arable) receiving FYM at 14 tons/ac. increased the worm total to 3-4 times over the control. On Park Grass (meadow mown) receiving 14 tons FYM and 6 cwt. guano every 4th year leading to totals 3 times greater than unmanured plots (Satchell 1967).

As shown by the outline of treatments to Mr Scott's land (Table 6) the majority of fields had FYM applied and difficulty was experienced in finding fields without this application. The earthworm totals reflect this treatment (Table 15), the two lowest density estimates being obtained on untreated areas i.e. fields 12 and 16. The number of worms on field 13 was also very low, possibly due to the improvement treatments being stopped at the request of the N.C.C.

These results are difficult to compare with those of other workers, as they are not based on individual species. Nordström and Rundgren (1974), used total biomass and abundance; and obtained positive correlations for clay and abundance and for pH and biomass, with no correlation for organic matter, but the yearly moisture regime exerted some influence. However their study was conducted in rich deciduous woods.

(ii) Total weight

Using total weight in this regression, the significant variables were exactly the same as those for total number. The high correlation obtained with total number (r = +0.96) would enable either measurement to be used when estimating density and as the latter is easier and quicker, a subsample from this could be taken, weighed and used to construct a correlation.

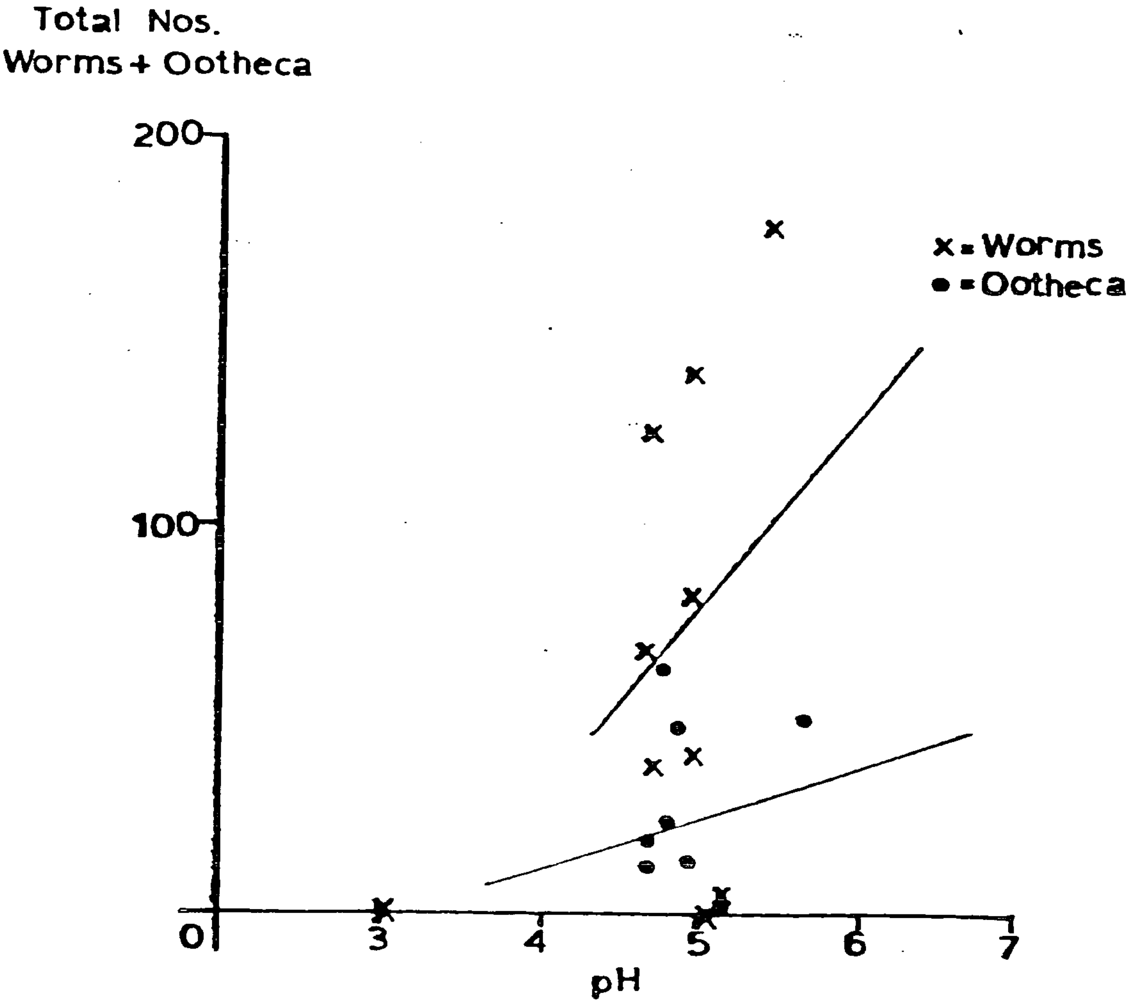
(iii) Average weight

The regression of independent variables with average weight of worms produced no significant reduction in accounting for their distribution. The weights fall within a narrow range (Table 15) none being significantly different, therefore this lack of significance is expected.

(iv) Number of ootheca

Only 2 variables were significant in affecting their total numbers accounting for 83%. Inclusion of another 8 variables brings the total explained to 99.7%.

The trend shown on Graph 7, is the same as that for total earthworm numbers, displaying the general dislike of soil acidity by earthworms.



GRAPH 7: Variation in total numbers of worms and ootheca with pH for all fields sampled

Regression equations: No. worms $y = 47.021\ x + 157.940$ $r = 0.4956$

No. ootheca $y = 13.020\ x + -40.346$ $r = 0.4048$

TABLE 17: Significant factors in the multiple regression equation accounting for the presence of total numbers of ootheca

Variable	F	b	SE
% Moisture	22.702	- 1.196	0.251
pH	6.904	-18.471	7.029
R^2 for significant variables	82.69		
Total R^2	99.69		

(1) Percentage Moisture

The water status of the soil is again of overriding importance, alone explaining 69.5% of the total distribution. The trend is very clear when plotted (Graph 5) a high negative correlation was obtained with a close scatter of points. Although a certain minimum level of water is necessary to prevent dessication of the cocoons, obviously at values greater than about 50% this becomes detrimental possibly related to the aeration of the soil.

Differences in time of hatching of ootheca may influence the total number found. Thus field 5 (Table 15) had a low number of ootheca but a high total earthworm population - the opposite situation occurred in field 12. The smallness of the average weights indicates that a significant proportion hatched this season.

(2) pH

pH in this regression accounts for 13% of the total numbers of ootheca. A positive correlation occurs (r = 0.4048) indicating that as the pH increases and the acidity of the soil drops, the number of ootheca increases.

Although the multiple regression analysis may indicate the major factors controlling an earthworm population, it doesn't account for the inherent aggregations or micro-variations within the area. For example, grazing and the subsequent deposition of dung may influence micro-distribution of some species. As shown in Table 15, field 12 had one of the lowest earthworm densities. Yet a large aggregated earthworm population was known to occur here beneath the dung pats.

The ground directly beneath these pats was not sampled during the study and this may have caused a bias towards the genus Allobophora, as these, unlike L. castaneus and L. rubellus, are not attracted to dung, being present more in the intervening patches of open soil. (Boyd 1958). This can lead to a misinterpretation of the actual species composition together with the density estimate.

This of course could have been overcome by more thorough sampling but it serves to show that a large earthworm population can survive on a medium high in organic matter, such as field 12 (Table 11), in localised situations such as dung. Relating to Mr Carrick's fields, sheep dung is not as preferred by earthworms compared with cattle dung but at high stocking densities a large volume of material would be available. This would supplement and increase the quality of food available to the worms.

(v) Other factors affecting earthworm distribution and population levels on the study sites

The distribution of earthworms can be partly explained through the physico-chemical features, Satchell (1967) contended that moisture and available food were the primary determinants. But probably what is more significant in this case is the relationship between population density and the age of the pasture. The absolute age of the pasture is not known for each field therefore the correlation is difficult to prove. But abundance and distribution must be dependent on historical factors, as well as recent ecological ones. Earthworm populations maybe low not because they can't exist under the present conditions but because they have been previously absent in the locality. That significant populations can occur in upland pastures has been shown by Guild (1951a), a density of 72,000/ac. was obtained on a two year rye grass pasture, with the soil still very acid. The density although low, is comparable with that found on arable land in Hertfordshire, U.K. (Edwards and Lofty 1977). Guild (1948b) found that areas treated for a few years can increase populations by fourfold, continuous improvements can lead to population increases of eightfold over the original level. This was reflected in the multiple regression for total earthworm number, a variable, 'present treatment' was included, to depict that fields were still being managed. Although not significant, it was included in the total R^2 value, indicating a positive trend.

But Mr Carrick's fields in Cumbria are surrounded by a typical upland pattern of vegetation, effectively isolating the fields from any external, natural colonisation, and density of worms in these areas are low (Table 18).

TABLE 18: Earthworm numbers/m^2 on different vegetation types within the M.H.N.N.R. (from Svendsen 1955a)

1st grassl.	Juncus Moor	Nardus grassl.	Mixed Moor	Blanket peat	Calluna Moor	Eriophorum area
389	-	12	0.01 - 0.05	Nil	0.1 - 0.5	0.1

Apart from this, the migration rate of worms by their own activity is slow, Roots (1956) calculating the maximum rate of locomotion to be 0.4 m/min in the most surface active species. Rate of advance by A. caliginosa populations into newly limed pastures was estimated by Hamblyn and Dingwall (1945) to be 10 m/yr., faster than that found later by van Rhee (1969) for colonisation of newly drained polders (6 m/yr.) and by Richards (1955), who found colonies spreading over a quarter of an acre in 9 years.

But these colonies and their advance depended on artificial innoculation. In fields as isolated as Mr Carrick's, reliance on significant colonisation by natural means would be very slow and probably quite rare.

Although close to the limestone grassland supporting a relatively high density population when sampled by means of the transect, numbers declined from the centre of the area outwards, being met by the zone of J. squarrosus bog effectively inhibiting movement closer to the field.

(vi) Conclusions

From these analyses, it seems that the water content of Mr Carrick's soil must be reduced in order to increase the favourability of the environment. Drainage of peat poses inherent difficulties, effective at distances of only <3.5 m apart (O'Toole 1970), but even then, drainage causes uneven shrinkage of the top layer, subsidence, fluctuating water tables and other problems.

Liming will be essential to maintain a high pH and stimulate soil organisms to decompose the organic matter and reduce the peaty nature of the material.

The obvious benefits of applying FYM have been shown through the introduction of ootheca with their later development into earthworms and the build up of a substantial population. But the economics of using this material must be favourable. Where cattle are absent and long distances must be covered over unkept tracks, the costs far outweigh the benefits, an obvious disadvantage in Mr Carrick's case.

(vii) Summary of Results

(1) Using multiple regresssion, 4 factors were found significant in explaining the distribution of total numbers of earthworms, namely, percentage moisture, peat, clay and FYM. Together they accounted for 94% of this distribution.

(2) Total weight (wet weight biomass) could be explained by the same 4 factors as above.

(3) The distribution of total numbers of ootheca could be explained by 2 variables, percentage moisture and pH, accounting for 82.7% of the distribution.

(4) Although the regression practically accounts for total distribution, within the context of the newly improved field soils, isolation from a significant colonisation source must be taken into account.

3) The physical factors influencing the field distribution of leatherjackets

a) Density level

T. paludosa larvae are generally distributed and present in most soils, not necessarily only on farmlands, but of course here their presence is more noticeable. As shown by Table 19 their density was relatively low in the sites sampled, in comparison to the unusually high figure for FI, all were non-significant when compared by χ^2, except for this field ($p < 0.01$).

TABLE 19: Comparison of the numbers of leatherjackets found on the sites sampled

sampled	July 1980							May 1980			
	1	5a	5b	6b	12	13	16	FI	FII	Lst.	Cont.
Tot. No.	10	1	4	2	6	5	8	69	1	13	0
No./m^2	33	6	27	7	20	17	27	246	3	43	0

According to Rayner (1978) leatherjackets are known to cause occasional severe damage to lowland grasses, but more frequently to reseeded upland pastures. This appears to be the situation here, FII experienced a severe attack in May 1978 after reseeding, now FI is experiencing a similar attack.

An attempt was made using multiple regression to explain this distribution and account for the differences in population density. The multiple regression produced no variables significant in affecting *Tipula* numbers. However, single correlations were helpful in some respects.

b) Factors affecting distribution

(i) Moisture

Positive correlations were obtained with peat $r = +0.417$, and a category designated as 'close to stream' $r = 0.415$ i.e. the distance the sampling site was from the nearest fresh water source. Although the correlation with percentage moisture of the sample was very low $r = 0.1993$ (but still positive), both these variables can be related to the moisture status of the soil. Peat contains high amounts as shown by the mean figures of 65% for FI and 55% for FII, (Table 14) and figures of 58% and 56% obtained for 5b and 16 respectively (Table 11), sites very close to a stream. The density estimates reflect these figures.

Milne et al (1965) attributed the drastic reduction in number of T. paludosa in Northumberland in 1955 to very low rainfall causing heavy mortality in the egg stage. Maercks (1943) related the density of T. paludosa to the rainfall in the period of the year in which the eggs hatch, in this species autumn and correlated high larval densities with high rainfall. Barnes (1925) has shown that in Britain species of this family are most abundant in wet habitats and Coulson (1962) has advanced the theory that higher water status within the soil in July and August at high altitudes is responsible for the earlier emergence of this species, because conditions are suitable for oviposition, whereas at lower altitudes the soil is dry and hard and not suitable until some weeks later.

It seems therefore that moisture is essential for their survival because they are susceptible to dessication especially in the egg and first instar stages. Rainfall although substantial in the lower Tees Valley where Mr Scott's fields are situated, (unfortunately no accurate details being available for this precise area), is still far greater on Mr Carrick's land and August totals averaged 1746 mms for 1979, compared to 67.3 in Durham at the equivalent date (Graph 4). (August is the month of egg laying and first instar.)

As shown by Table 20, for the Cumbrian area, the estimated density of leatherjackets in 1979 was 892,000/ha. (A.D.A.S.), nearly twice as great compared to the Durham area. This result was attributed by A.D.A.S. to the wetter climate in Cumbria. In 1976 (a 'good year') rainfall totals for the same month were 29 mm in Cumbria and 18.4 mm in Durham, corresponding to average Tipula densities of 174,000/ha. and 540,000/ha., a reduction of 80% in Cumbrian density levels, although Durham's increased by 10%.

TABLE 20: Estimated leatherjacket population for the counties of Durham and Cumbria from 1973 to 1979 (Source: A.D.A.S.)

Year	1973	1974	1975	1976	1977	1978	1979
Durham	328	556	925	540	2046	1100	485
Cumbria	452	193	220	174	995	724	892

Figures = 000's/ha. Nov. sampling.

(ii) Effect of treatments

Contrary to the results found by Coulson (1959) where the larvae of T. paludosa were restricted to alluvial soils, here the greatest density levels of this species were on some of the peat soils. Obviously the treatments undertaken by Mr Carrick have caused this result, the peat of the improved fields no longer possesses its former physico-chemical characteristics as shown by the analyses carried out. By contrast no Tipula larvae were found on the control site.

The newly reseeded pastures form an oasis of palatable green matter within a desert of rough hill grazing and blanket bog. Although the females when fully gravid are unable to fly, they deposit 50% of their eggs within 7 hours of completion of mating and 90% within 17 hours. (Coulson 1962). They would then be able to fly to new areas, the remaining eggs acting as a colonisation source. Once in the field and sufficiently established they are able to survive the extreme winter conditions. A thick snow cover would act as an insulating blanket and keep soil temperatures above the lethal limit. Vertical migrations have been reported in order to overwinter and in this condition they can still feed. A.D.A.S. reports that the least decline in numbers are in upland areas with very deep snow cover, the highest declines are in areas where deep snow is absent and consequently the soil is severely frozen.

c) Damaging population levels

The favourable weather conditions therefore lead to excessive numbers due to survival of a large number of the young produced, enhanced by the new ready supply of nutritious food. A.D.A.S. assigns a population level of 50,000/ha. for the threshold of economic damage necessitating control, which as shown by Table 19 was far below that of FI ($\times 10^4$ = nos./ha.).

Observations in North West Germany by Lange (1964) state that damage to grassland is likely if autumn and early winter infestations exceed 988,000/ha., nearly double the British threshold, severe damage occurring with populations about 3 m/ha. These figures seem excessively high when only about 3% of all farms sampled by A.D.A.S. are in the range of $>$ 250,000/ha.

These figures are also for autumn sampling whereas those for my sites are spring sampling estimates which therefore accounts for winter mortality. This is usually about 30 - 50% but can be far higher in bad winters.

Taking Tow Law (an upland pasture in County Durham) as an example, in November 1978 populations were 3527,000/ha. By March 1979 a massive 72% reduction had occurred, which brought the levels down to 980,000/ha. (A.D.A.S.).

Therefore corrections must be applied to autumn sampling figures in order to predict population levels and possible loss of yield in spring. This requires reliable data on weather conditions together with the salient site features important for survival of larvae.

The plants own intrinsic response mechanisms must also be accounted for. One reason why frequent attacks are noted in reseeded upland pastures may be because the prevailing site and weather conditions do not favour rapid germination or growth. In a field survey in N.E. Scotland, where the normal time between sowing and germination is 10-14 days, extending this period from 16-21 days due to poor weather lead to attack by larvae and failure of part of the oat crop, the proportion lost ranging from 1/10 - 1/3 (Rennie 1917). A cold late spring which may delay primary growth constitutes an important climatic condition making the plant susceptible to attack. Although the grass varieties are specifically bred for conditions in the uplands, temperature thresholds still vary markedly, ranging from 2.9°C for 50% germination in Italian ryegrass, 4.9°C for Huia and $>$ 7.5°C for Timothy (H.F.R.O.). Complications also occur in plant growth due to the nature of the peat substrate. It therefore becomes necessary to add lime and the major nutrients to counteract such deficiencies. Again difficult access and usually steep, rocky terrain precludes the necessary treatments, and although the theory has been adequately tested, such practical difficulties are usually overriding.

d) Loss in yield due to leatherjackets

Control of leatherjacket populations at 1 m/ac (equivalent to the level found on FI), has been shown to increase dry matter production by 171% of the early bite (see glossary) and 70% of the hay yield (French 1969). Grennan (1966) obtained increases of 25% and 73% in production when 1 and 2 million leatherjackets/ac. respectively, were eliminated on a ley sown on a virgin bog.

French (1969) has estimated that a population of 1 m/ac lead to yield losses of 6 cwt. dry matter/ac. (d.m./ac.) on a field 40 acs. (the size of FI), this means a loss of 240 cwt. d.m. Comparing this estimate to what has been found technically feasible to produce in Wales (at Pant - y - dŵr, 305 m) using 500 units of nitrogen on a rye grass/white clover sward, equals 1000 lb d.m./ac. Although this is probably an overestimate due to the very high output obtained through use of excessive nitrogen quantities, the loss can still be quite substantial, important when the grass is intended for increasing sheep condition and density.

e) Control measures advocated at this site

The damage to this year's pasture has already occurred but to prevent a recurrence it seems that some form of control is necessary.

French (1969) has shown that additions of nitrogen can counteract the damage up to a certain level if Tipula populations are $<$ 1 m/ac. in spring and maximum nitrogen quantities are not being used. It is then cheaper to apply extra amounts of nitrogen than to use an insecticide. On Mr Carrick's land nitrogen applications are classed as low ($<$ 36 units/ac.). He should therefore benefit by extra nitrogen treatment.

This increase in amount of nitrogen is justifiable economically and ecologically as the alternative is to use DDT. Other chemicals such as chlorpyrifos (trade name Dursban) and Triazophos (Hostathion) are not suitable as they give variable control on peaty soils and are mainly used for treating isolated patches, whereas the distribution of larvae on FI was quite widespread.

A reduction in moisture content may prove inimical to the leatherjackets, but FI is already open drained, albeit at distances of 20 m, but the inherent difficulties of draining peat successfully have been mentioned already.

Some cultural control including rolling, which inhibits the larvae movement and allows better root/soil contact of the plant might help.

Disturbance of the ground, although not possible when in pasture, but necessary in order to reseed, which would be necessary here, would bring the larvae to the surface where possibly they would be heavily preyed upon. Starlings (Sturnus vulgaris L.) are their main enemies, flocks of which occur at the site, together with a variety of shore birds using the area to feed, such as Lapwings (Vanellus vanellus L.) and Golden Plovers (Pluvialis apricaria L.). Such a situation occurred after rotavating FII prior to reseeding, dense flocks of feeding birds picked off the larvae.

f) Influence of site position

The Tipula larvae benefit from the greater rainfall totals experienced in Cumbria on Mr Carrick's fields. About 95% of their weight increase is due to water intake (Meats 1967). The larval density levels may also be influenced by site position. Mr Scott's fields in County Durham are not as physically handicapped as those in Cumbria. He has greater accessibility to his land, roads being well kept (obviously enhanced by its position next to the Teesdale N.R.) and the fields situated on moderately flat land. This facilitates a more intensive programme of improvements, as general cultivations such as rolling can almost eliminate populations, as shown by the near disappearance of the species on FII within the space of 2 years, after cultivations had been carried out prior to the second reseed in 1979. No doubt this field's general location in respect to the house was significant in its treatment (borne out by the negative correlation for distance to the farm in the regression r = -0.4955).

g) Summary of results

(i) The density estimate of Tipula larvae was found to be excessively high on FI, one of the newly reclaimed fields. The level of 2,460,000/ha. (1 m/ac.) is nearly 50 times the recommended threshold density above which economic damage occurs and control is advocated.

(ii) The estimate on all the other sites sampled were not significantly different from one another.

(iii) Multiple regression failed to indicate significant factors which would explain this distribution, but using the single correlations plus data on its life cycle, the most likely factors were moisture and the treatments.

(iv) Various suggestions were advanced which would reduce this high density level.

4) Survival and effects of earthworms and leatherjackets on yield of grass sown in three soil types

Four treatments were replicated in three soil types. The treatments were inclusion of two individuals each of L. rubellus and L. castaneus, an equal number and weight of dead worms, 14 T. paludosa larvae/pot and a control. The soil types used were the recently improved field soil, FI and FII, a 'normal' mineral soil and the control peat soil. These were all sown with the upland grass mixture containing ryegrass, timothy and white clover.

Originally this experiment was designed to test the survival rates of the earthworm species chosen in the newly improved field soil, together with any attendant effects on the plant yield compared to those of the larvae. But during the course of the experiment, the mesh netting which was used to prevent the animals escape had to be removed due to the extent of the grass growth. A few worms may have escaped but the pots also attracted worms from the surrounding area, even though they were situated on a bed of gravel and the nearest mineral soil source was about 4m. away over a 40cm. wooden ridge.

Because of this the results were interpreted differently, the intended treatments were no longer distinct from one another. Therefore, each replicate within a treatment was grouped together and the treatments bulked into the 3 separate soil classes. Replicates containing larvae were excluded from this bulking of the yield data as although the pots acquired a significant number of earthworms the effect of the larvae on the yield may still be apparent. Thus comparisons have been made between the three soil types only.

Although disappointing to lose this data, the error in removing the netting enabled other interesting aspects of the project and particularly earthworm behaviour to emerge.

a) Earthworms and yield in 3 soil types

The dry weight yield of green shoot matter from the 3 soil types all proved highly significantly different (Table 21) compared by student 't' tests, the largest value was obtained in the improved peat soil, the lowest in the pure natural peat.

TABLE 21 - Yield d.w.g^{-1} of vegetation in the 3 soil types with the level of significance in the matrix, where * donates the 1% level

Soil Type

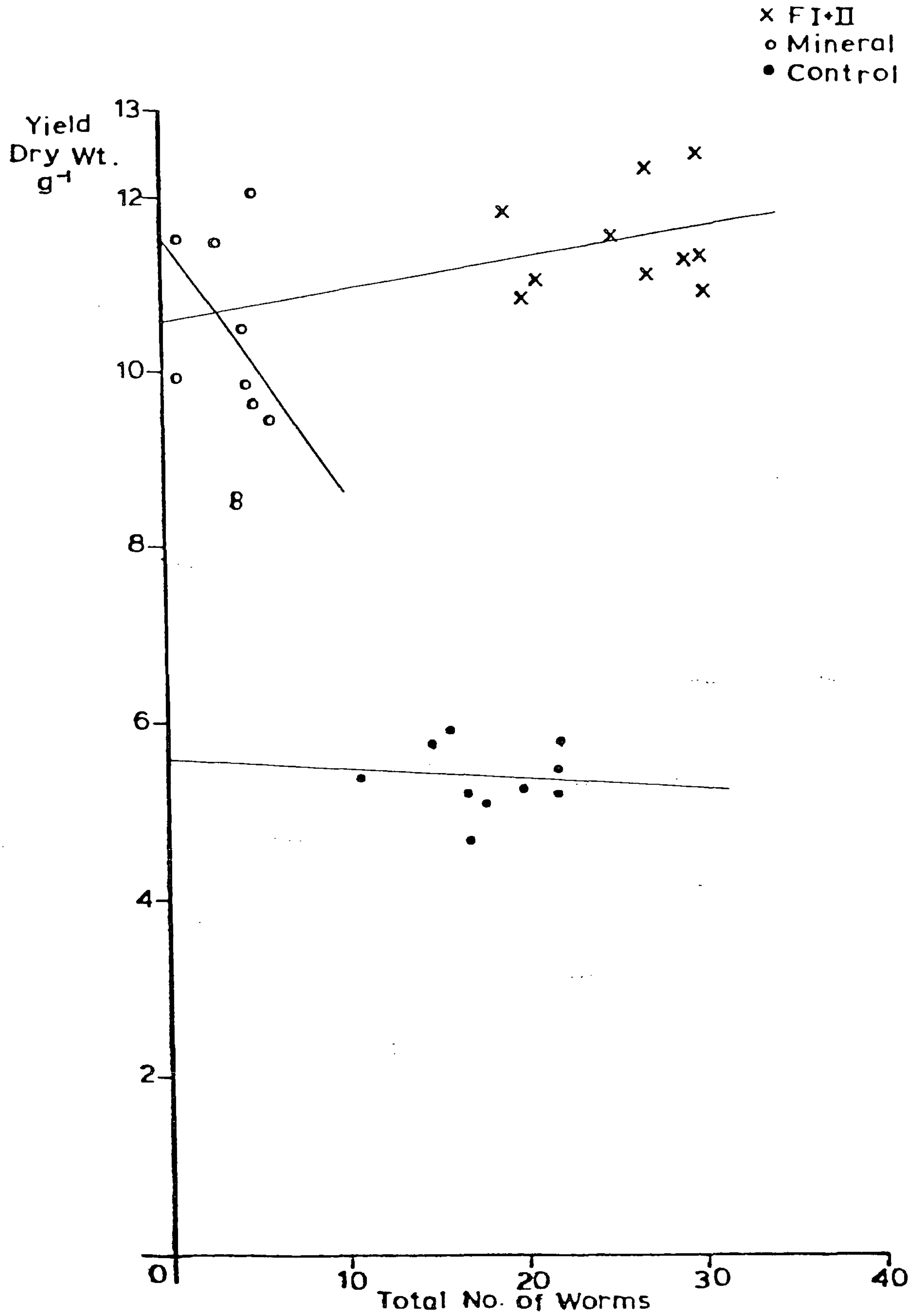
	FI + FII		MINERAL		CONTROL	
n	$\bar{x}$	so	$\bar{x}$	so	$\bar{x}$	so
10	11.23	0.23	10.08	0.62	5.36	0.12

	F	M	C
F		S	S*
M			S*
C			

When the number of worms in each pot is plotted against its corresponding yield (graph 8 & 9), the positive influence on improved soils is shown, compared to little or no effect in the other two soil types. The presence of earthworms seems to influence the wet weight yield more than the dry weight, closer correlations were obtained in the former.

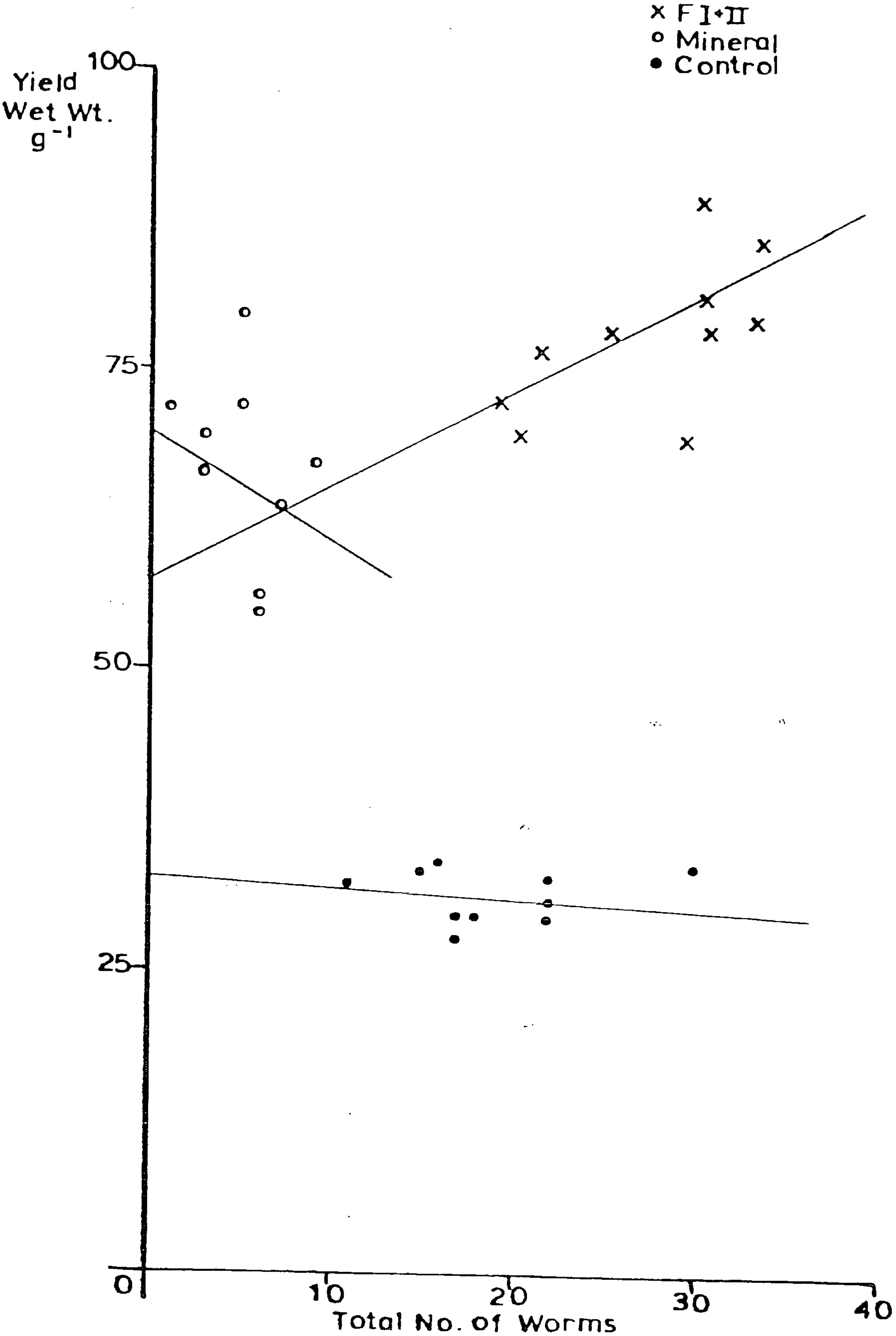
It is difficult to attribute the increased yields in the improved peat directly to the influence of earthworms. The species of grass used were specially selected for use on such substrate and would therefore be expected to have superior growth, although the extra available nutrients in the mineral soil may offset this to some degree. The grasses are primarily selected for their ability to utilise the short growing season and complete development rapidly, this was not a consideration of the climate at the science site. Within the mineral soil, increased numbers of earthworms seem to decrease yields, an effect contrary to those of most workers.

That soil effects must be taken into consideration was shown by the low yields obtained in the control soil, even though these had comparable earthworm numbers. Obviously the low pH (4.1) is critical to growth, clover has optimum levels at 6.0 and most grass species at a pH >5.0 (HFRO).



GRAPH 8: Relationship between total number of worms in each pot and dry matter yield of grass in the 3 soil types

x	FI + FII	$y = 0.017x + 11.0$	$r = 0.14$
o	Mineral	$y = -0.28x + 11.6$	$r = -0.53$
●	Control	$y = -0.0036x + 5.45$	$r = -0.035$



GRAPH 9: Relationship between total number of worms in each pot and wet weight yield of grass in the 3 soil types

x	FI + FII	y = 0.7797	+ 55.776	r = 0.571
o	Mineral	y = -1.21	+ 72.60	r = -0.377
•	Control	y = -0.077	+ 32.73	r = -0.132

Soil structure also influences the yield. Natural peat soil is compacted and this effectively limits the zone available for root penetration and nutrient uptake.

b) Conclusions

The results do show that yield increases of the actual varieties were obtained within this improved soil and yield was also related to the numbers of earthworms. The situation, albeit artificial and within the influence of the Durham City climate, may still have direct applications to the field situation; the number of worms found were not unrealistically high compared to those found on normal pasture fields. It is significant that out of all the 3 soil types, yield was greatest in the improved peat, but as mentioned previously, physico-chemical conditions were possibly unfavourable in the control soil although favourable in the mineral soil. However, in the mineral soil, the number of worms was low and a definite negative trend between numbers and yield was produced instead.

c) Summary of results

i) A greater yield was obtained on the improved peat soil for a clover/ryegrass sward,least on blanket bog peat with mineral soil intermediate.

ii) Earthworms significantly affected this yield in a positive manner on the field soil, but had a slightly negative effect on the other two soil types. This affect was more pronounced in wet weight yields rather than in dry weight yields.

5) Colonisation of earthworms into 3 soil types

a) Total Abundance

That earthworms are active, industrious creatures must be borne out by the total number occurring in each soil type (Table 22).

TABLE 22: The total numbers of earthworms occurring in each soil type with level of significance

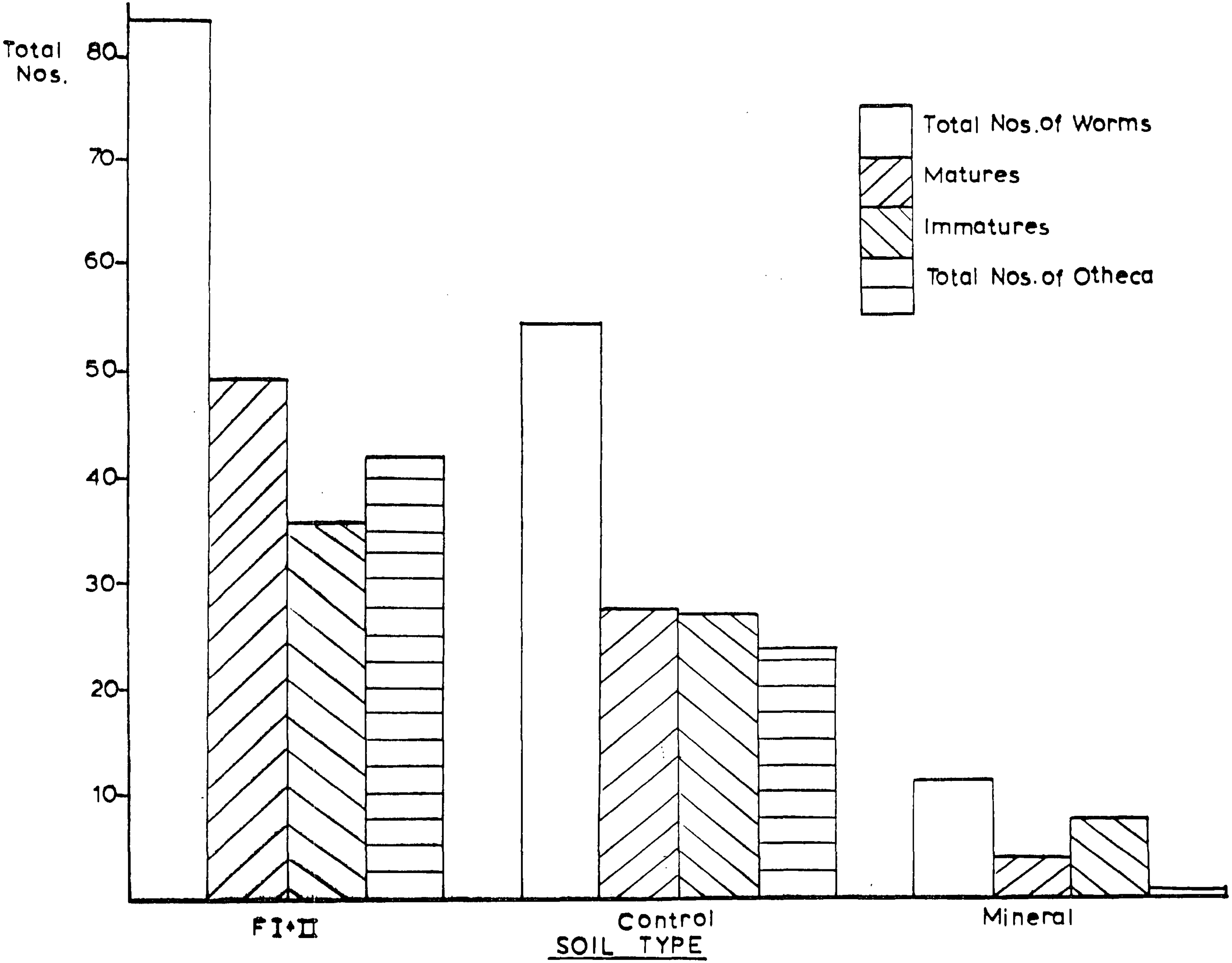
	Soil type					
	FI + FII		Control		Mineral	
+N	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
14	83.5	9.25	54.2	8.26	11.25	3.4

	F	C	M
F		S*	S*
C			S*
M			

+ N.B. The pots containing the larvae were also used for this data, their presence was thought not to affect colonisation by earthworms to any significant extent.

The differences are also highly significant ($p < 0.01$) the largest number occurred within the improved soil, the least in the mineral soil. Expressed graphically (Graph 10) it can be seen that the numbers in the former dominate the other 2 types, both for total numbers and also when divided into its components of matures, immatures and ootheca.

The large number which occurred in the improved peat is significant in that conditions cannot have been totally inimical to their survival or reproduction, in fact seemingly quite the opposite. What the major attraction was to this soil is difficult to say, as numbers are very low in the mineral soil, which was expected to be the most favourable medium, but nearly comparable in the pure peat soil, which was expected to be the least favourable to



GRAPH 10: Total abundance of earthworms and ootheca in each soil type after immigration

earthworms. The large numbers, the majority being mature, together with the fact that the soil was sorted and sieved before use, precludes their existence within the mediums prior to the netting being put on. As the pots stood 23 cm. vertically off the ground, their knowledge of its contents would be unknown. Positioning of the pots may have influenced the results, but no trends were discernible with respect to the external mineral environment.

Tests of significance using the students 't', were carried out for each component of the population between each soil type. They revealed significant differences in all except for the immature population and ootheca number, between the field and control soil. It seems therefore that although differences occur in the total number colonising, once established, they can reproduce equally well in either of the two mediums.

b) Relative dominance

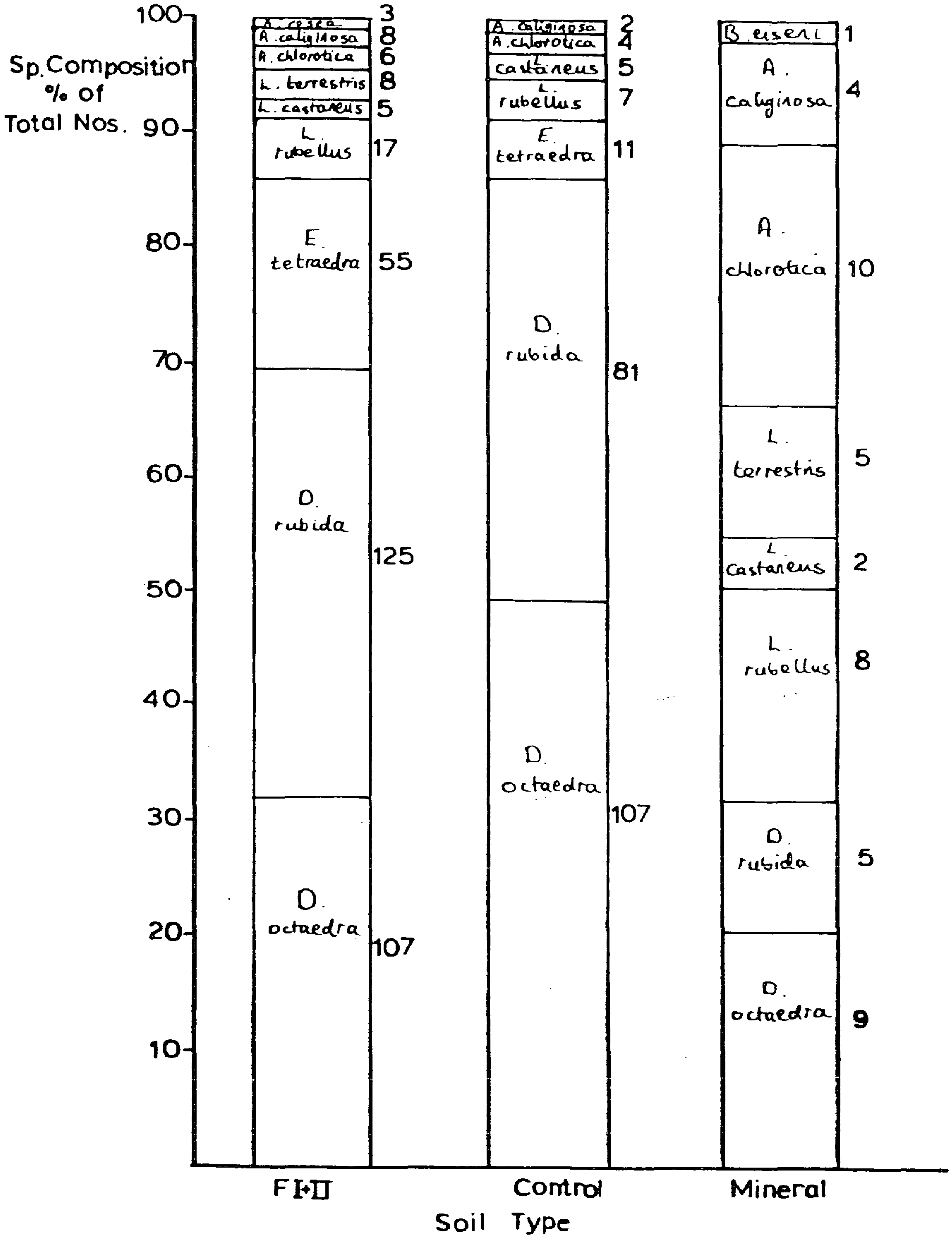
(i) Total numbers (Table 23, Graph 11)

The high densities of worms which immigrated into the pots and the fact that they aggregated in the field soil, may be partly explained when their species composition is determined. Table 23 outlines this, together with the proportional abundance (Pi) and rank (Rk) of each species within each soil type.

The dominant species within the field soil is *D. rubida* closely followed by *D. octaedra*, together accounting for nearly 70% of the total numbers (Graph 11). Within the control soil, their relative positions of dominance are reversed, but they constitute a greater percentage of the total number of species occurring within this soil type (86.6%). In the mineral soil *D. octaedra* again dominates *D. rubida* but together they no longer occupy the dominant positions, *A. chlorotica* ranked first with the lumbricids following.

TABLE 23: The total numbers of earthworms, their proportional abundance and rank in the 3 soil types after immigration

	FI + FII			Control			Mineral		
Species	Tot No.	Pi	Rk	Tot No.	Pi		Tot No.	Pi	Rk
D. rub.	125	0.374	1	81	0.373	2	5	0.113	4
D. oct.	107	0.320	2	107	0.493	1	9	0.204	2
E. tet.	55	0.160	3	11	0.050	3	0	-	9=
L. rub.	17	0.050	4	7	0.032	4	8	0.181	3
L. terr.	8	0.024	5	0	-	8=	5	0.113	4=
A. calig.	8	0.024	6	2	0.0009	7	4	0.090	6
A. chl.	6	0.018	7	4	0.018	6	10	0.227	1
L. cast.	5	0.015	8	5	0.023	5	2	0.045	7
A. rosea	3	0.009	9	0	-	8=	0	-	9=
B. eisini	0	-	10	0	-	8=	1	0.023	8
Tot. number:	334			217			44		



GRAPH 11: Species composition as a percentage of total numbers in each of the 3 soil types after immigration

Their positions of rank for each species are quite similar within the two peaty soils, but in the mineral soil this situation changes completely. As shown by Table 23 and Graph 11, a more even distribution occurs, no one or two species predominating over the others. The majority found in this soil are associated with pastures or mull type soils. The decrease in proportional abundance of the Dendrobaena species, appears consistent with the results of Evans (1948a) who found that as the number of pasture species increase with soil fertility Dendrobaena decrease.

Nordstöm and Rundgren (1973 and 1974) have hypothesised that the number of Dendrobaena species are reduced due to interspecific competition with other surface active species in all habitats. L. castaneus was the surface competitor in their case. Here, no one species appears to be causing the decline. Piearce (1972b) found that the diet of Dendrobaena species, mainly consisted of organic matter at various stages of decomposition, the mineral soil used, contained little humic material. L. rubellus and L. castaneus both feed on organic material (Piearce 1972b) their numbers may be sufficient to actively compete with these smaller species within the mineral soil here.

The greater importance of the Allobophora species here compared to the two peaty soils, again fits in with the results of Piearce (1972b), in that they are primarily mineral feeders. Satchell (1955) classed them as intolerant of acid conditions and their very low numbers on the control soil confirmed this. The pH value was only just above the value at which he found they wouldn't burrow into the soil.

The only anomaly that appears within the mineral soil type is B. eiseni, usually associated with highly eutrophic conditions being classed as acid tolerant and not found in well established field populations. Its low proportional abundance indicates that its presence within the mineral soil is due to chance.

That the physico-chemical conditions of the pure peat soil are less favourable to earthworms, is emphasised by the division into species composition. The number of species able to tolerate such conditions is small. The degree of acidity seems to be the determining factor, as this would act directly and immediately, rather than through the substrate type which indirectly controls the quality of food. Compared to the Dendrobaena species, the total numbers of other species occurring in peat were insignificant, reflecting the restricted species range and their numbers decline progressively, related to their acidity tolerances.

The altered conditions within the field soil allowed colonisation by the greatest number of different species, still proportionately dominated by the Dendrobaena species, but with a significant number of the pasture forms included. The decline in rank, again seems to reflect the level of soil acidity and their tolerance to it, although this soil had the maximum pH value. This seems to suggest that it is the nature of the substrate and the quality of material available for food, which exerts an effect on species composition, rather than pH alone.

The very large numbers of both D. octaedra and D. rubida in the two peat soils is a combined effect of their rapid migration rate and their tolerance to the prevailing conditions. Both species are small with high surface activity indices (Standen 1979), and are known to be rapid colonisers. They were put into the pioneering phase by Boyd (1957a). D. rubida appears to be less tolerant of the more acidic conditions of the control soil, consistent with the recent results found by Hågvar and Abrahamsen (1980), who also found a positive reaction to liming a raw humus soil, equivalent to the field soil in this situation. Svendsen (1955a) also found D. rubida dominant on the richer alluvial soils at M.H.N.N.R. whereas D. octaedra was more numerous on mixed moor areas consisting of Calluna, Eriophorum and mosses. Here it appears not to be influenced by the conditions on either site and maintained equal numbers in both.

The occurrence of E. tetraedra within the peat soils and their absence from the mineral soil, demonstrates the high water retaining capacity of these materials; this species is usually associated with water saturated soils and aquatic habitats (Gerard 1964).

Although not possible to determine the actual percentage survival of the introduced L. rubellus and L. castaneus, it can be seen from Table 23 and Graph 11 that L. rubellus increased over 8 times in the field soil and 4 times in the other two types. Its relative position of dominance was quite stable over all the mediums. For L. castaneus, numbers were not as great, but still more than doubled in the two peat soils, the actual introduced numbers being maintained in the mineral soil. Both these results are relevant in indicating that survival in the field is possible.

(ii) Total numbers of matures (Table 24, Graph 12)

TABLE 24: Total number of mature earthworms, their proportional abundance and rank in the 3 soil types after colonisation

	FI & FII			Control			Mineral		
Species	Mats	Pi	Rk	Mats	Pi	Rk	Mats	Pi	Rk
D. rub.	48	0.246	2	15	0.137	2	3	0.200	2=
D. oct.	84	0.430	1	84	0.770	1	3	0.200	2=
E. tet.	35	0.179	3	1	0.009	5=	0	-	7=
L. rub.	13	0.066	4	4	0.036	3	6	0.400	1
L. terr.	2	0.010	9	0	-	8=	0	-	7=
A. calig.	3	0.015	6=	1	0.009	5=	0	-	7=
A. chl.	4	0.020	5	1	0.009	5=	1	0.066	4=
L. cast.	3	0.015	6=	3	0.027	4	1	0.066	4=
A. rosea	3	0.015	6=	0	-	8=	0	-	7=
B. eiseni	0	-	10	0	-	8=	1	0.066	4=
Tot. No.:	195			109			15		

When separated into matures and immatures, mature D. octaedra are again uninfluenced by the different conditions represented by the two peat soils, whereas numbers of D. rubida decline by over 2/3. Within the field soil, D. octaedra becomes dominant over D. rubida, a reversal compared to the total numbers, but they account for nearly 70% of all matures within this soil type. The relative positions of the other species do not alter greatly from those of the total numbers, again 4 species dominate numerically, the rest not being significantly different from one another in their proportional abundances.

A similar situation occurred in the control soil. There was little change in ranking position compared to total numbers. The Dendrobaena species still numerically dominate over all the others, accounting for over 90% of the total species.

Lack of dominance by any one species is again shown in the mineral soil and both the Dendrobaena species are much lower in numbers compared to the peat soils. L. rubellus is proportionately the most abundant, which may indicate some kind of interspecific competition for available food. Bengston et al (1975) found a similar reduction of Dendrobaena when L. rubellus was present in the moss and litter layer in Iceland.

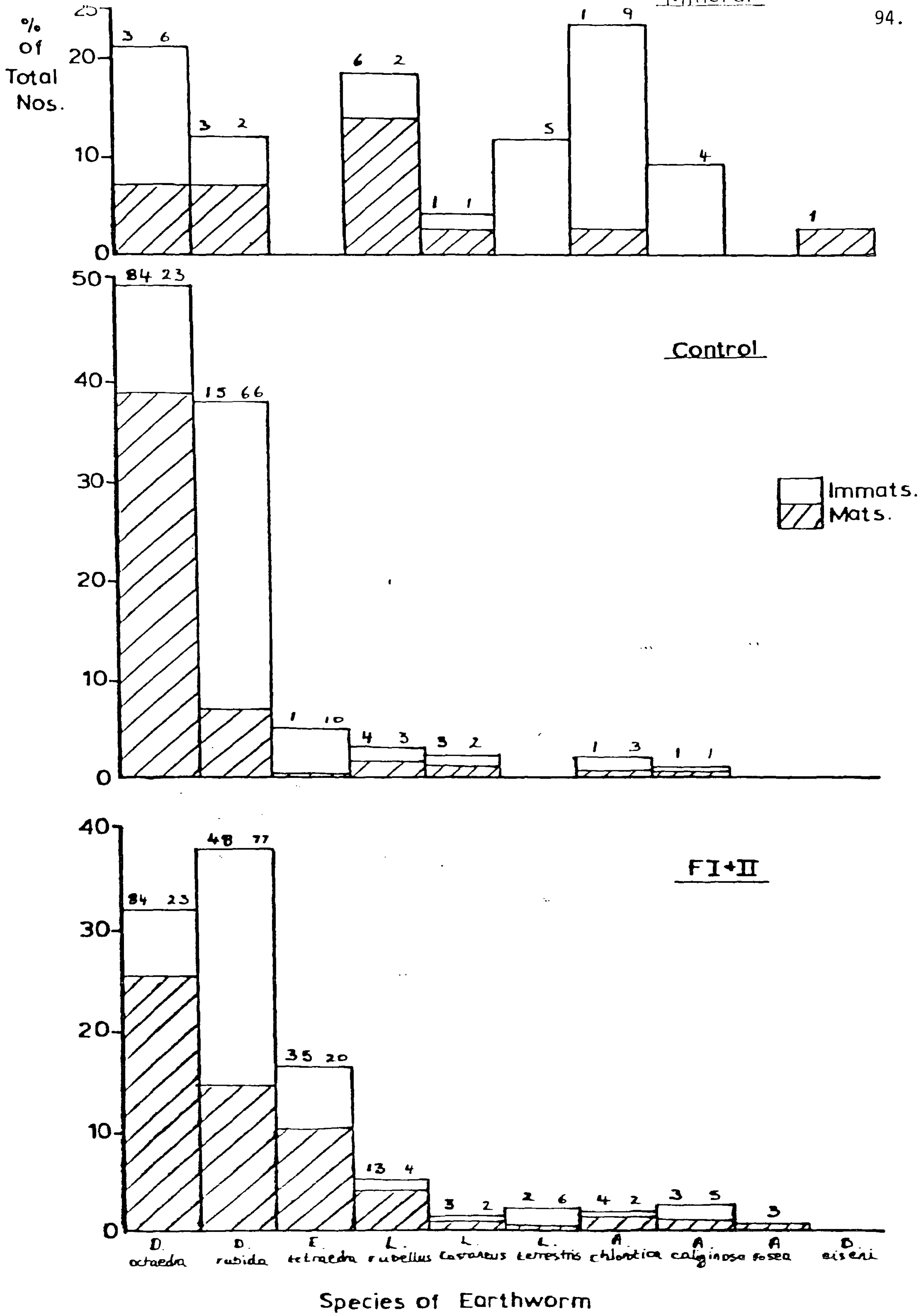
(iii) Total number of immatures (Table 25, Graph 12)

TABLE 25: Total numbers of immature earthworms, their proportional abundance and rank in the 3 soil types after colonisation

Species	Imms	Pi	Rk	Imms	Pi	Rk	Imms	Pi	Rk
D. rub.	77	0.553	1	66	0.611	2	2	0.068	5=
D. oct.	23	0.165	2	23	0.212	2	6	0.206	2
E. tet.	20	0.143	3	10	0.092	3	0	-	8=
L. rub.	4	0.028	6	3	0.027	4=	2	0.068	5=
L. terr.	6	0.043	4	0	-	8=	5	0.172	3
A. calig.	5	0.036	5	1	0.009	7	4	0.137	4
A. chl.	2	0.014	7=	3	0.027	4=	9	0.310	1
L. cast.	2	0.014	7=	2	0.018	6	1	0.034	7
A. rosea	0	-	9=	0	-	8=	0	-	8=
B. eiseni	0	-	9=	0	-	8=	0	-	8=
Tot. No.:	139			108			29		

Divided into immatures D. rubida again assumed dominance in the field soil, numbers were greater than for matures of the same species. Numerically three species dominated, accounting for over 80% of the total numbers. Positioning and proportional abundance of species below this was very close, the numbers were not significantly different from one another. The soil still contained 8 of the 9 original species, which is significant in that juveniles are usually more susceptible to various mortality factors, and indicates that survival of the younger stages is possible. Numerically though, the numbers of immatures was about 30% below that of the matures.

Within the control soil, the immatures of D. rubida predominated over D. octaedra, opposite to the trends found for total numbers and mature worms. The ranking in this respect parallels that of the field soil. Both the matures and immatures of D. octaedra had equal numbers in both soil types, displaying their high level of tolerance to the markedly different soil acidities and structures. Although



GRAPH 12: Percentage of mature and immature worms in the 3 soil types after immigration

Thicker numbers on the left refer to the total number of mature worms of each species, those on the right refer to the total number of immature worms far lower in numbers than the two dominant species, the ranking positions are very close to that obtained for total numbers, the species composition was identical, and total numbers of immatures equal those for matures.

Within the mineral soil the number of immatures was twice that of the matures, and there was an increase in species composition. A marked reorganisation of ranking positions was evident compared to the matures, indicating the chance occurrence of most species from the outside colonisation source, the majority of immatures being near adults.

(iv) Total number of ootheca (Table 26, Graph 13)

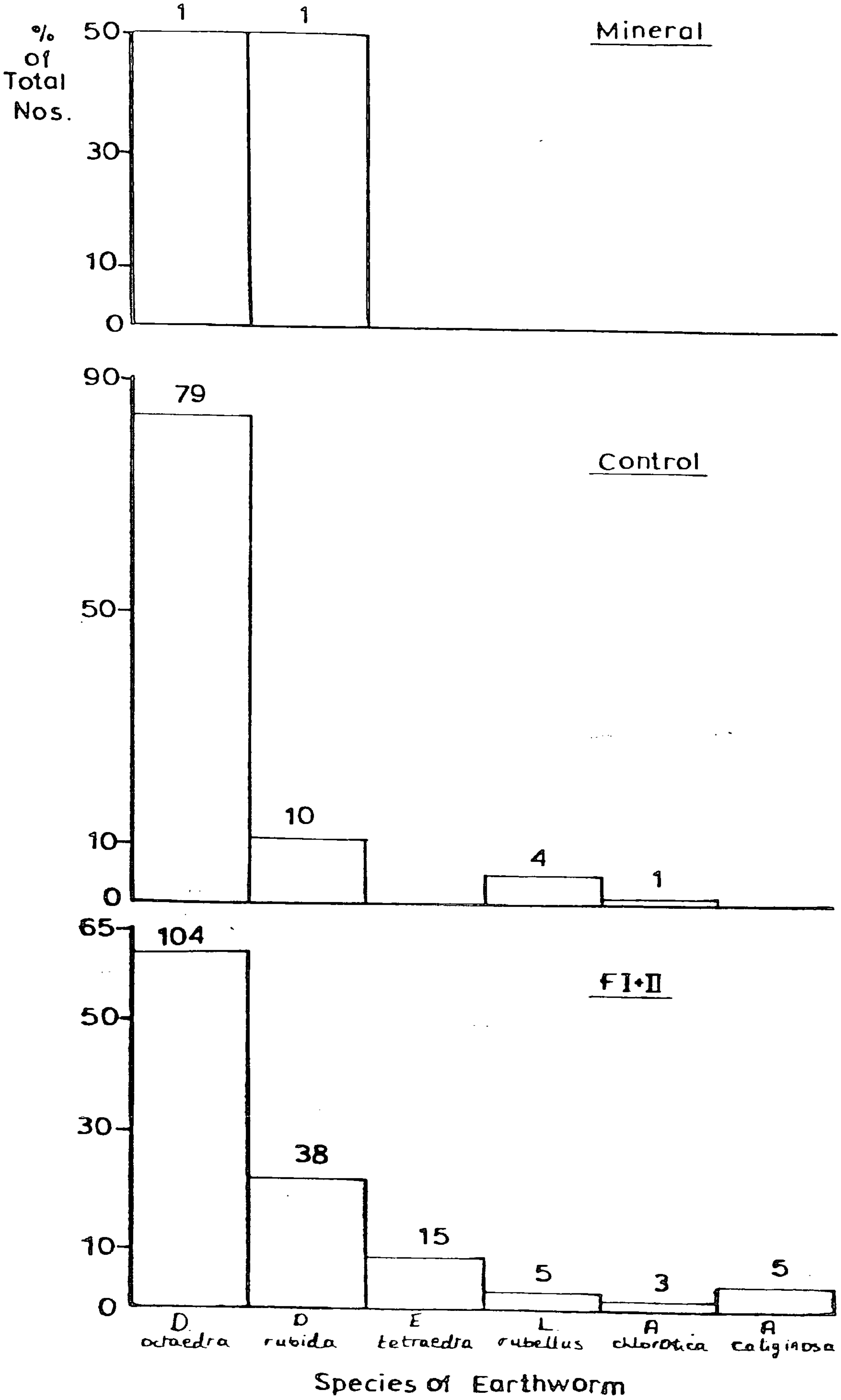
TABLE 26: Total numbers of ootheca, their proportional abundance and rank in the 3 soil types after colonisation

Species	Ooth No.	Pi	Rk	Ooth No.	Pi	Rk	Ooth No.	Pi	Rk
D. oct.	104	0.611	1	79	0.840	1	1	0.500	1=
D. rub.	38	0.223	2	10	0.106	2	1	0.500	1=
E. tet.	15	0.088	3	0	-				
L. rub.	5=	0.029	4=	4	0.042	3			
A. calig.	5=	0.029	4=	0	-				
A. chl.	3	0.017	6	1	0.010	4			
Total No.:	170			94			2		

Species with no ootheca

L. terr.
L. cast.
A. rosea
B. eiseni

The number of ootheca found in each soil type again demonstrates the numerical dominance of the Dendrobaena species and of D. octaedra especially. The graph shows that the field soil supports the largest number of different cocoon types, together with the largest total number produced. This is in keeping with the wide species range present.



GRAPH 13: Percentage of total number of ootheca of each species found in the 3 soil types after immigration

Although the number of species in the mineral soil able to produce cocoons is the lowest, when compared to the other two mediums, it cannot account for the drastically low numbers found. Some factor, present either in the soil, or due to the biology of the matures occurring here, seems to be inhibiting production of cocoons completely.

The number of species able to produce cocoons on the control soil is also restricted, though to a far less extent, the differences between the actual numbers present here and those in the field soil were not significantly different from one another. D. octaedra proportionately dominates accounting for 84% of the total number of ootheca found.

(v) Conclusions

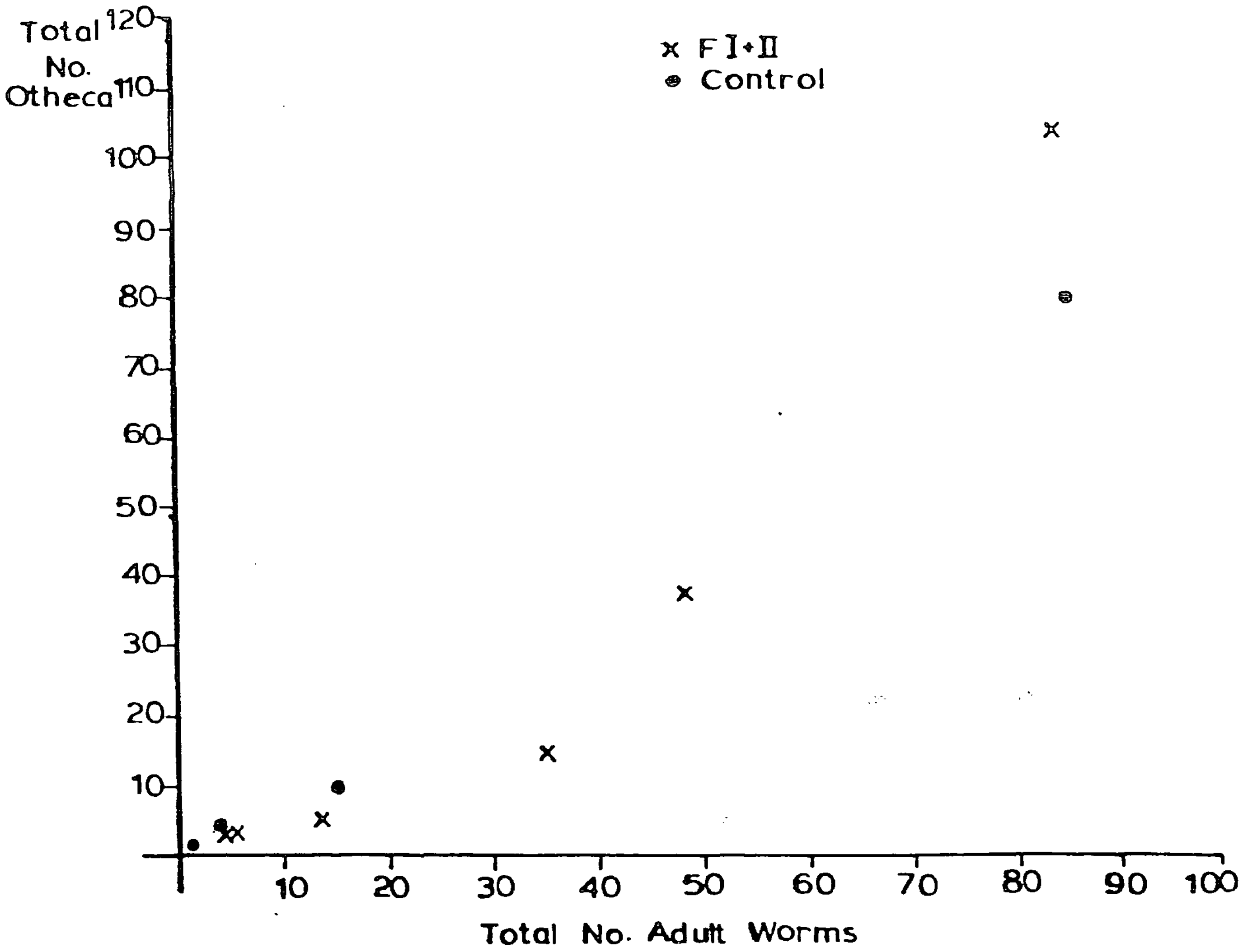
The number of animals within a sample is a combined result of the migration to and from the surrounding soil and birth and death within that sample. The rate of migration is important at first and this is reflected here in the large numbers of Dendrobaena species which are favoured by their high activity and are therefore able to colonise an area in a shorter time, establishing a significant population before other species have appeared. This may account for their rapid multiplication in favourable situations. Their subsequent decline is possible due to interspecific competition as suggested by Nordström and Rundgren (1973, 1974), once a more cosmopolitan range of species have invaded.

In this situation, they maintained their dominance in the peat soils which have conditions suitable for their survival, and time precluded a large build up of other species. In the mineral soil, conditions did not match their ecological requirements, and this was reflected in their low numbers, and an increase in abundance of the Allobophora - Lumbricus association. This can be illustrated by the rise in number and proportional dominance of L. terrestris. Being a deep burrower and primarily a pasture species, it is absent on the control and low in numbers on the field soil, acidity plus substrate type probably exerted an influence. Only on the mineral soil does it become relatively more dominant compared to the other two mediums.

No information is available of the reproductive rates of these two particular *Dendrobaena* species, but within the same genus, Evans and Guild (1948c) state a maximum of 42 cocoons produced p.a. for *D. subrundicunda*, with a short incubation period of 8½ weeks. The length of time over which this experiment was conducted was about 9 weeks. From the numbers of cocoons, it could be postulated that *D. rubida* has a shorter incubation than *D. octaedra* because their numbers were lower, while the number of very small immatures of *D. rubida* were markedly higher in comparison. In this situation, given that colonisation proceeded from the same starting point and that there was no difference in the stage of reproductive cycle in the adults, hatching must have occurred sooner for *D. rubida*. These stipulations though are hardly likely to be equal.

The low numbers of cocoons and immatures of other species, can be explained through these differences in migration rates. After the *Dendrobaena* species, *L. rubellus* has a high activity index, noted by van Rhee (1969b) as the first to colonise natural polder soils in Holland, becoming dominant in the very early stages of worm establishment. *L. castaneus* with an index higher than *L. rubellus* (Standen 1979) does not show such numerical dominance indicating that it is not only migration rates that are important but also the actual conditions within the medium. *L. castaneus* is not noted as having such a large tolerance range as *L. rubellus*.

The migration rates account for the numbers of different species present, the total numbers of these reflecting cocoon production, as shown by Graph 14, the larger the number of adults present, the greater the number of cocoons produced. But length of incubation period must also be considered in accounting for the number of immatures present, the shortest time for species found here after



GRAPH 14: Scattergraph showing the number of ootheca increasing linearly with the total number of adult worms

the Dendrobaena species is A. chlorotica at 12½ weeks (Evans and Guild 1948c) which is outside the duration of this experient.

Colonisation by the immatures must be from external sources, which again reflects the differences in migration rates, and emphasises the rapidity of colonisation by the small Dendrobaena species. The actual size of immatures supports this fact.

(vi) A note on the reproduction of the introduced species

Survival, was demonstrated as possible for the introduced L. rubellus and L. castaneus but this is not sufficient if they cannot reproduce, continue their life cycle and perpetuate their existence within the medium. Table 26 and Graph 13 shows that L. rubellus produced cocoons in both the peat soils, but none were reclaimed for L. castaneus. Whether this reflects their inability to produce cocoons here, or other factors operating cannot be deduced from this experiment. Lumbricus cocoons are darkly coloured, often with adhering soil and vegetation, mitigating against their detection in an amorphous humic peat or brown mineral soil. The identification of the cocoons within the genus is not clearly differentiated, sizes, shapes and colour overlap in range between the different species. These factors could account for the lack of L. castaneus cocoons, although those of L. rubellus were found.

(vii) Summary of Results

(1) The greatest number of earthworms at all stages in the life cycle were found on the improved peat soil, least in the mineral soil.

(2) The field soil contained 9 different species, the Dendrobaena genus was numerically dominant accounting for 70% of total numbers. Out of total numbers D. rubida ranked first, D. octaedra second. This position was maintained for the juveniles, but for the matures D. octaedra ranked first with D. rubida second.

(3) The control soil contained 7 different species, the genus *Dendrobaena* was again dominant, 87% of the total numbers were accounted for by the two species. *D. octaedra* dominated the total numbers and matures but *D. rubida* immatures were ranked first with those of *D. octaedra* second.

(4) The mineral soil contained 8 different species, characterised by a lack of dominance by any one genus.

(5) Total numbers of ootheca found were greatest in the improved peat soil, cocoons of *D. octaedra* ranked first. This soil also contained the largest number of different cocoon types. The lowest number and types were found in the mineral soil.

(6) The number of cocoons found is related to the total number of matures present in the medium.

6) Growth rate of earthworms under controlled conditions

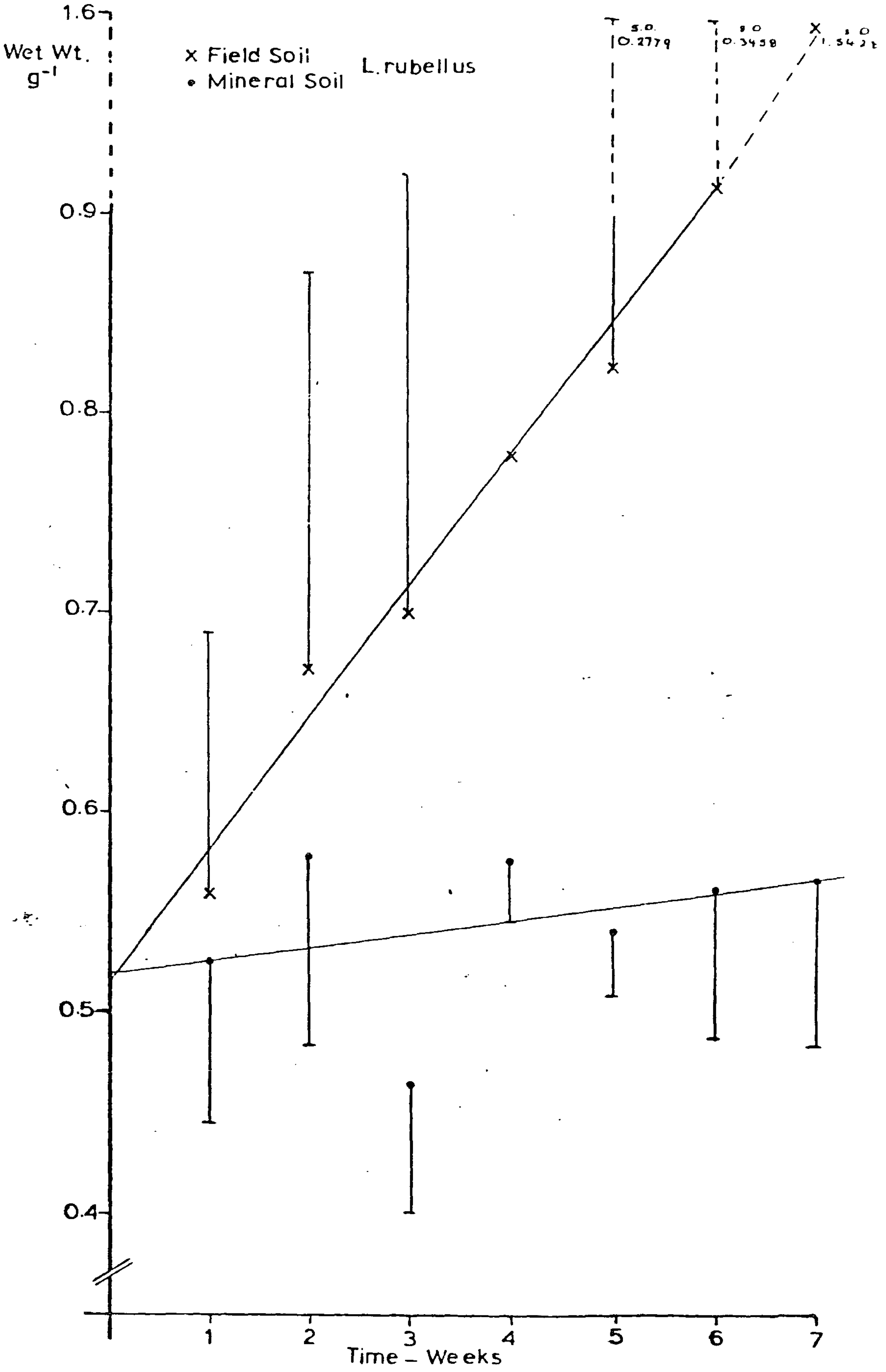
The growth rate of *L. rubellus* and *L. castaneus* was investigated under controlled conditions. They were kept individually in small earthenware pots within 2 soil types, a 'normal' mineral soil and the recently improved field soil for 6 weeks. These were situated in a constant temperature room held at 8^{0}C with a photoperiod normal for July/August.

a) Soil effects

It has been demonstrated that the introduced species of earthworm could survive and reproduce. In order for this to occur, growth must be possible within the medium. The duration of the experiment was 6 weeks, long enough for the worms to exhibit a decline in weight if feeding and therefore growth was inhibited.

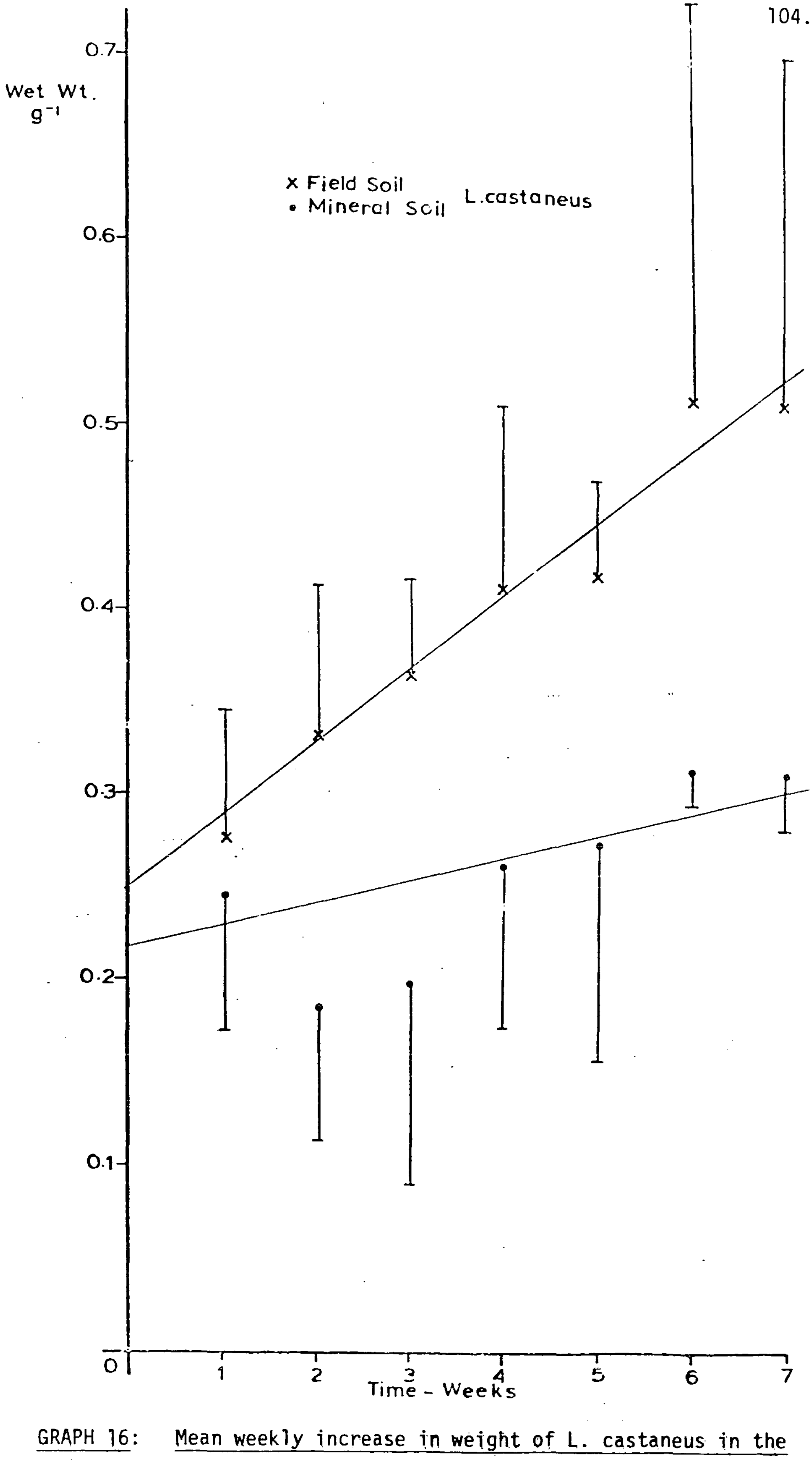
From the graphs 15-17 it can be seen that growth was always greater within the improved field soil compared to the mineral soil. When the slope of the regression lines are statistically analysed by use of a modified 't' test, only the growth of *L. rubellus* was significantly greater in the peat soil compared to the mineral ($p < 0.01$). That for *L. castaneus* and the immatures was not significant.

A steady increase in weight occurs for both species on the peat soil (graphs 15 and 16), high correlations were obtained, compared to the erratic fluctuations within the mineral soil, as shown by the much poorer agreement with the regression lines. The mean weekly increments occurred from the onset of the experiment in the peat soil compared to that in the mineral soil, where for the first 3 weeks, a general decline was noted (except for *L. rubellus* in the first week, Graph 15). This could be related to the moisture status of the soil, the peat retains water well, being moist from one week to the next, whereas the mineral soil was prone to drying out, although both were watered mid-week. As a greater part of a worms body constitutes water (Grant 1955), this would markedly affect their weight measurements, the value varying between wide limits in unsaturated soil.

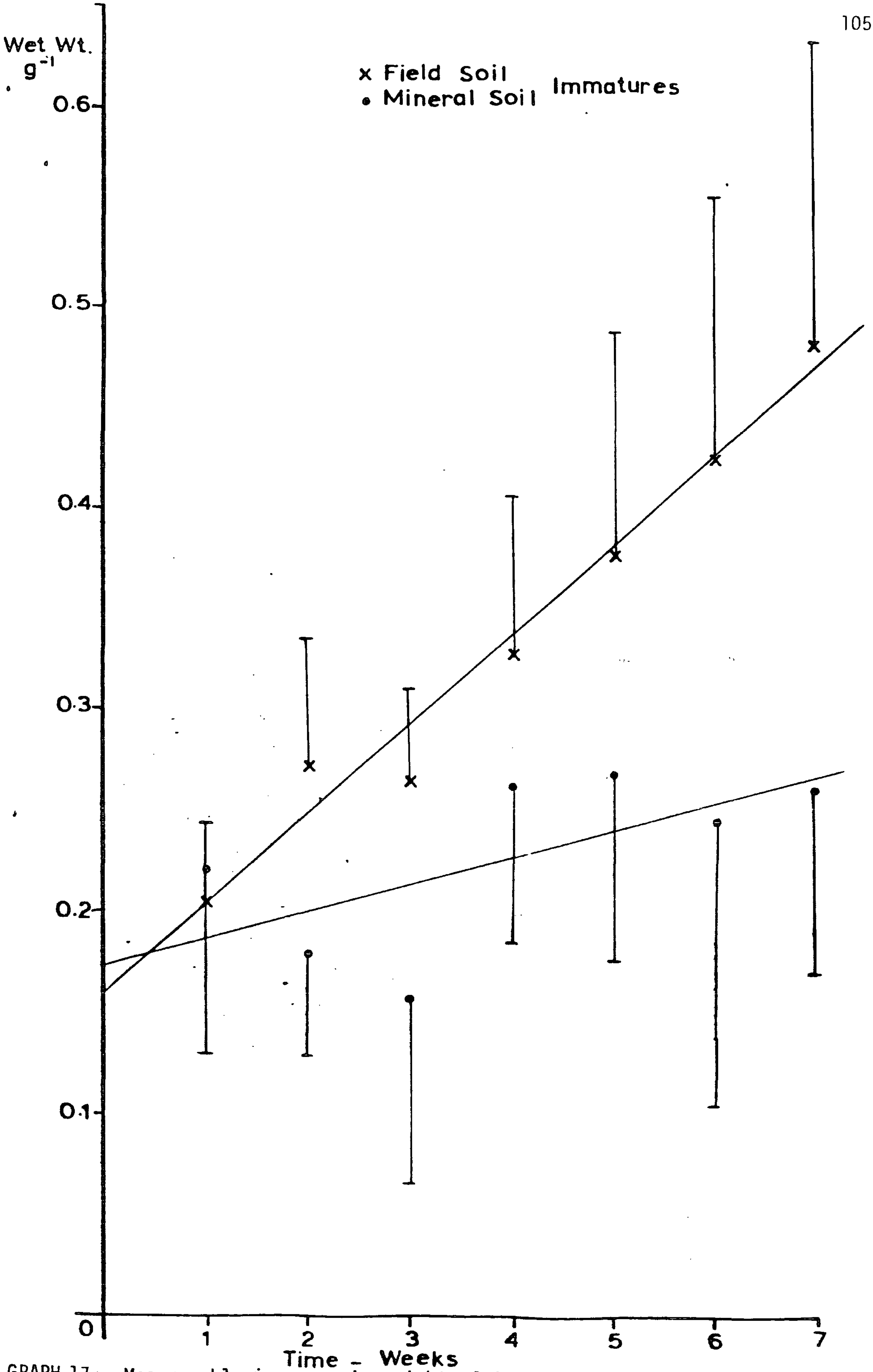


GRAPH 15: Mean weekly increase in weight of L. rubellus in the upland improved field soil and the normal mineral soil

X Field soil y = 0.0600 x _0.51 r = 0.99
o Mineral soil y = 0.0063 x +0.52 r = 0.34



GRAPH 16: Mean weekly increase in weight of L. castaneus in the upland improved field soil and the normal mineral soil



GRAPH 17: Mean weekly increase in weight of immature species of Lumbricus in the upland improved field soil and the normal mineral soil

x Field soil $y = 0.0449\,x + 0.1561$ $r = 0.98$
o Mineral soil $y = 0.0130\,x + 0.1743$ $r = 0.64$

The quantity of available organic matter supplying food could be limiting, leading to the decline in weight. Although the subsequent weight gains by about the 4th week and the overall total weight gain (Table 27) seems to indicate that food supply was adequate. This may therefore reflect the quality of material instead. The rapidity of the fluctuations in weight change point more to variations in moisture content, although when percentage change each week is calculated for each species in the mineral soil, the weight fluctuations fall within the 20% variation found by Edwards and Lofty (1977) for material held in the gut. The change in weight is therefore probably a combination of both water status and food quantity and quality. This applies also to the weight increases of worms in the field soil, but the fact that here increases were continuous and sustained indicates that feeding was actually taking place and that the increases were not solely due to the favourable moisture regime.

b) Species effects

From the table below and Graphs 15-17 it can be seen that L. rubellus exhibits the greatest increase in weight.

TABLE 27: Mean percentage weight increase after 6 weeks in the field and mineral soil

	soil type	
Species	Field	Mineral
L. rubellus	190	8
L. castaneus	80	21
Immatures	138	18

N = 3

It nearly trebled within the field soil, but showed the lowest weight increase over the 6 weeks in the mineral soil. L. castaneus nearly doubled its own weight in the field soil, but sustained a larger increase than L. rubellus in the mineral soil. The immatures showed similar trends and increased by nearly 250% in the former but only by 18% in the latter.

The weight increases can be partly related to the ecology of the species in question, L. castaneus sustained the largest increase relatively in the mineral soil due to a greater preference for such substrates. Although primarily a litter dweller within the Epigée category of Bouché, Phillipson et al (1976) noted its dependence on the textural composition of the lower horizons. In contrast, L. rubellus is often included amongst associations occurring in highly organic mediums (Bengston 1976) and Svendsen (1955a) noted a lack of dependence on soil type of L. rubellus, the dietary study of Piearce (1972b) supported this fact.

Earthworms display a great variability in growth rate which could invalidate the results, as the weight increases are only a mean of 3 individuals. Although they are statistically significant when individually compared by 't' tests and the grouped data within Table 27 by Chi squared ($\chi^2 = 20.5$ $P < 0.01$), this may still not indicate ecological significance. Satchell (1967) in his work on the growth rate of L. terrestris recommends using 60 specimens because of the large variation.

The temperature they were kept at may influence the result. Again, Satchell (1967), found that increases occurred almost entirely during the autumn and spring, with little if any weight gained during the winter and summer months, in fact decreases being noticed in some individuals. He found that after 3 years the average weight declined, possibly due to weight being lost before death. In this case, although all mature specimens, there is no way of knowing how long they had been mature or how close to to death they were. The immatures growth rate should overcome the subjectivity of this to some extent, rapid increases usually occurring before sexual maturity. If the last weeks weight gain of L. rubellus in the field soil is ignored (Graph 15), as this sudden increase seems atypical, the immatures do show the greatest growth rate. This increased by 108% over their initial weight at the 5th week compared to adult L. rubellus which showed only a 64% increase. This is more in agreement with the results of Bolton (1969) who found that worms weighing from 0.1 - 0.18 g produced the highest monthly growth rates, and Michon (1954) who studied the growth and development of D. subrundicunda in culture.

c) Conclusions

The weight increments of both species within the field soil seems to indicate that it can be utilised as a food source to maintain growth over a certain limited period. The development of the younger stages doesn't seem to be significantly inhibited either, suggesting that this particular peat soil is of adequate quality to sustain development to maturity. The fact that L. rubellus exhibited a faster growth rate within the field soil compared to the mineral soil also supports the fact that peat can be utilised even when the very last large growth increment was excluded.

d) Summary of Results

(i) Growth of L. rubellus, L. castaneus, and the immatures was always superior in the field soil, although only the growth rate of L. rubellus proved significant ($P < 0.01$).

(ii) Steady increases in weight were maintained in the field soil compared to erratic fluctuations in the mineral soil for all groups.

(iii) L. rubellus displayed the largest growth rate over the 6 weeks in the field soil, but the lowest in the mineral soil.

(iv) L. castaneus exhibited the largest weight increase in the mineral soil, the least in the field soil.

7) The effects of earthworms and leatherjackets on germination and the subsequent yield

Five individuals of L. rubellus and T. paludosa each, were introduced into small earthenware pots containing a 'normal' mineral soil, in order to compare their effects on plant germination with a control. The plant species used was the upland grass mixture, containing perennial rye grass, timothy and clover.

a) Effects on germination

(i) Effects on germination of both animals

Before the plant has even time to establish itself, it appears that it is susceptible both to attack and enhancement in its germination (Table 28).

TABLE 28: The percentage germination of grass and clover within each of the 3 treatments in mineral soil

Treatment	Grass		Clover		Total	
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Control	22.36	7.30	14.26	3.56	36.68	10.87
Earthworm	24.60	4.20	16.86	6.52	41.50	10.08
Tipulid	17.50	6.20	8.80	3.80	26.30	9.31

n = 5 in each treatment

't' test matrices for percentage germination of clover, grass and the total within the 3 treatments in mineral soil

Treatments	C	E	T
C		NS	NS
E			S
T			

Total

	C	E	T
C		NS	S
E			S
T			

Clover

	C	E	T
C		NS	NS
E			NS
T			

Grass

C = Control
E = Earthworm
T = Tipulid
S = Significant $p < 0.05$
NS = Not significant

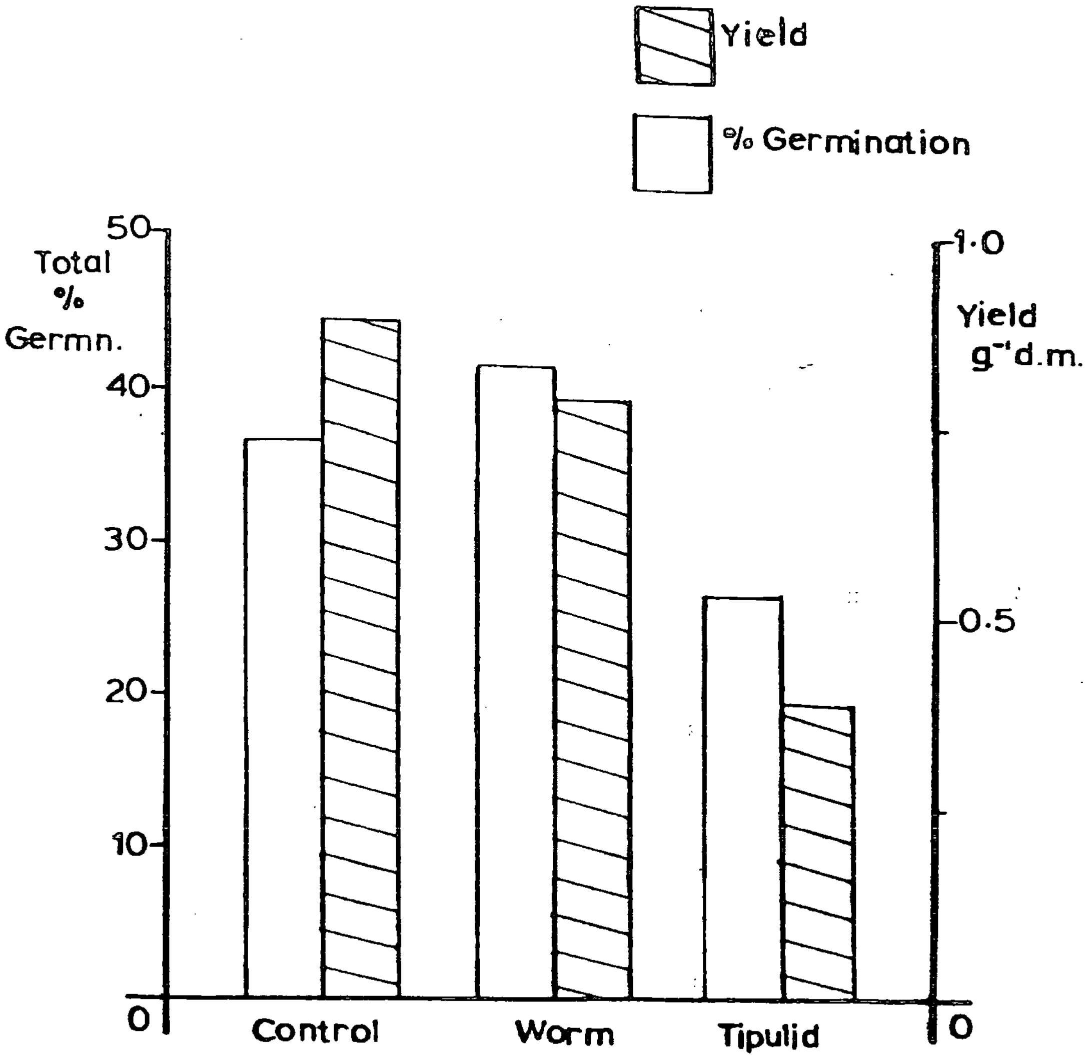
A reduction of germination occurred in those trials containing Tipula larvae, both on total germination and on germination of grass and clover separately (Graphs 18 and 19). The latter appears to be more susceptible, although grass germination is still reduced, it is not significantly so, compared to the control.

In contrast earthworms appeared to enhance germination over both treatments for total germination as well as for each plant species. Using the control pots as a base of 100%, the relative effects can be clearly seen in Table 29, the results all showed the negative effects of the larvae compared to the positive ones of earthworms.

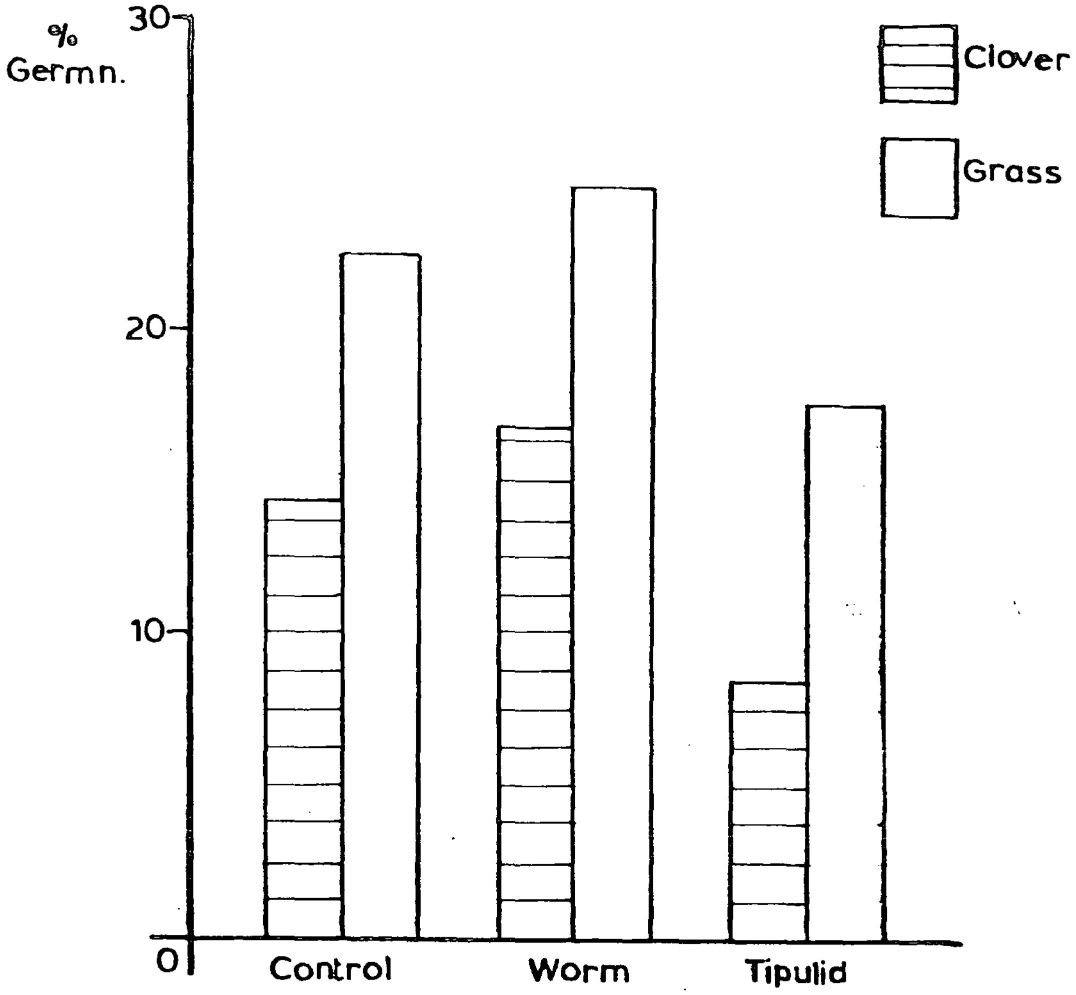
TABLE 29: The effects that each treatment has on percentage germination using the control as a base of 100%

Treatment	Grass	Clover	Total
Earthworm	+10	+17	+13
Tipulid	-22	-38	-28
$\frac{\text{Earthworm}}{\text{Tipulid}}$	+41	+92	+57

Although the trend is clear, none of the beneficial effects of earthworms on germination were significant in comparison to the control, but comparing earthworms to the larvae, total and clover germination were significant, but not grass ($p < 0.05$). All comparisons were made by use of students 't' test. Contrasting the two treatments containing animals clearly shows the beneficial effects of earthworms compared to the leatherjackets, clover germination increasing by nearly 100% and grass by just under 50%, together accounting for a 57% increase attributed to the worms over the tipulid larvae.



GRAPH 18: Effects of earthworms and leatherjackets on percentage germination and yield in mineral soil

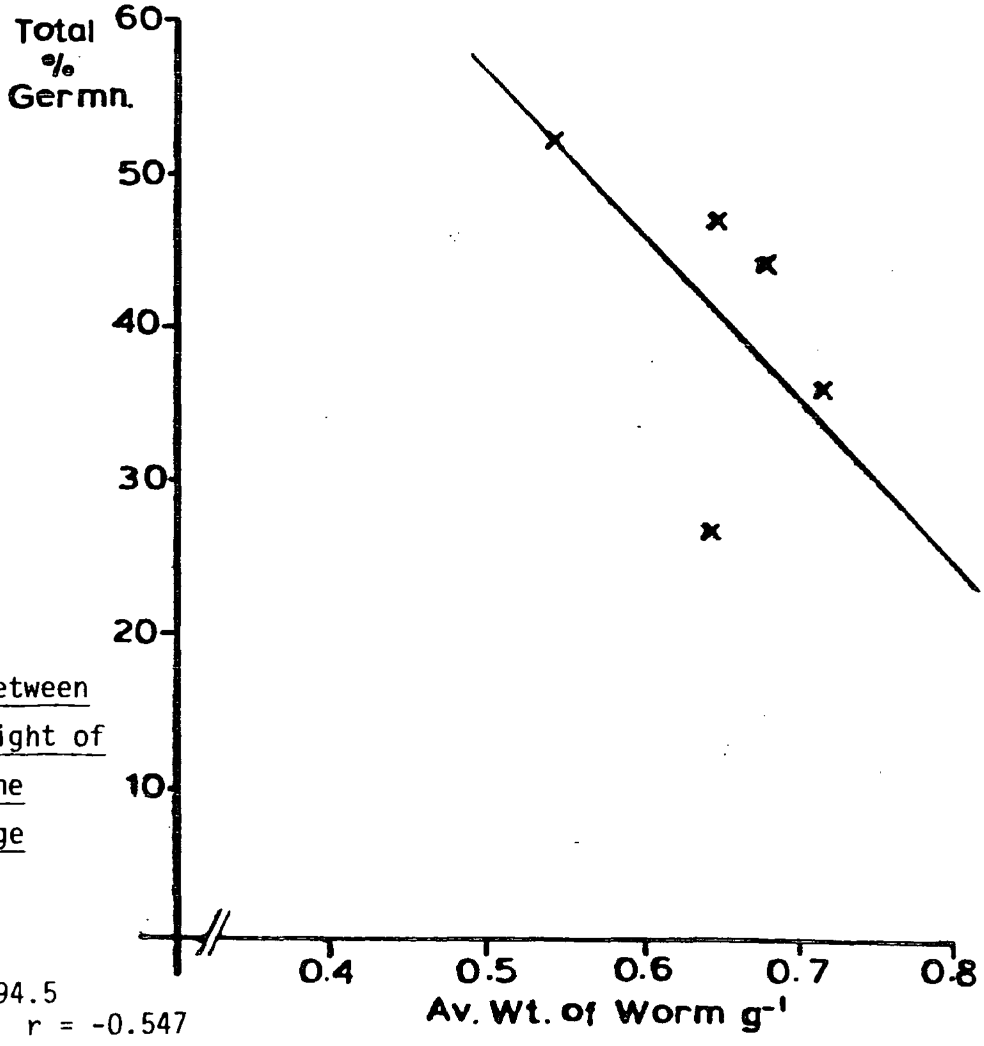


GRAPH 19: Percentage germination of grass and clover in the 3 treatments

(ii) Effects of earthworms

There have been suggestions that earthworms produce plant growth substances (Hopp and Slater 1949, Waters 1951). This could account for the improved germination, as the length of time over which the experiment lasted (39 days) would probably be insufficient to alter any physical properties of the soil, such as an improved tilth, which would produce a favourable seed bed.

Van Rhee (1965) attributed increases in yield of grass and wheat to better germination and later growth, due to the upper part of the soil being turned over into worm-casts by Allobophora species which effectively increased the seed/soil contact. But L. rubellus is not a casting species and is active within the upper soil layers. This, plus the confinement to a small pot may be detrimental, as shown by Graph 20, where reduction in total germination was related to increased average size of the worms introduced to each pot (r = -0.547).



GRAPH 20:

Relationship between the average weight of worm/pot and the total percentage germination

y = -81.84 x +94.5
r = -0.547

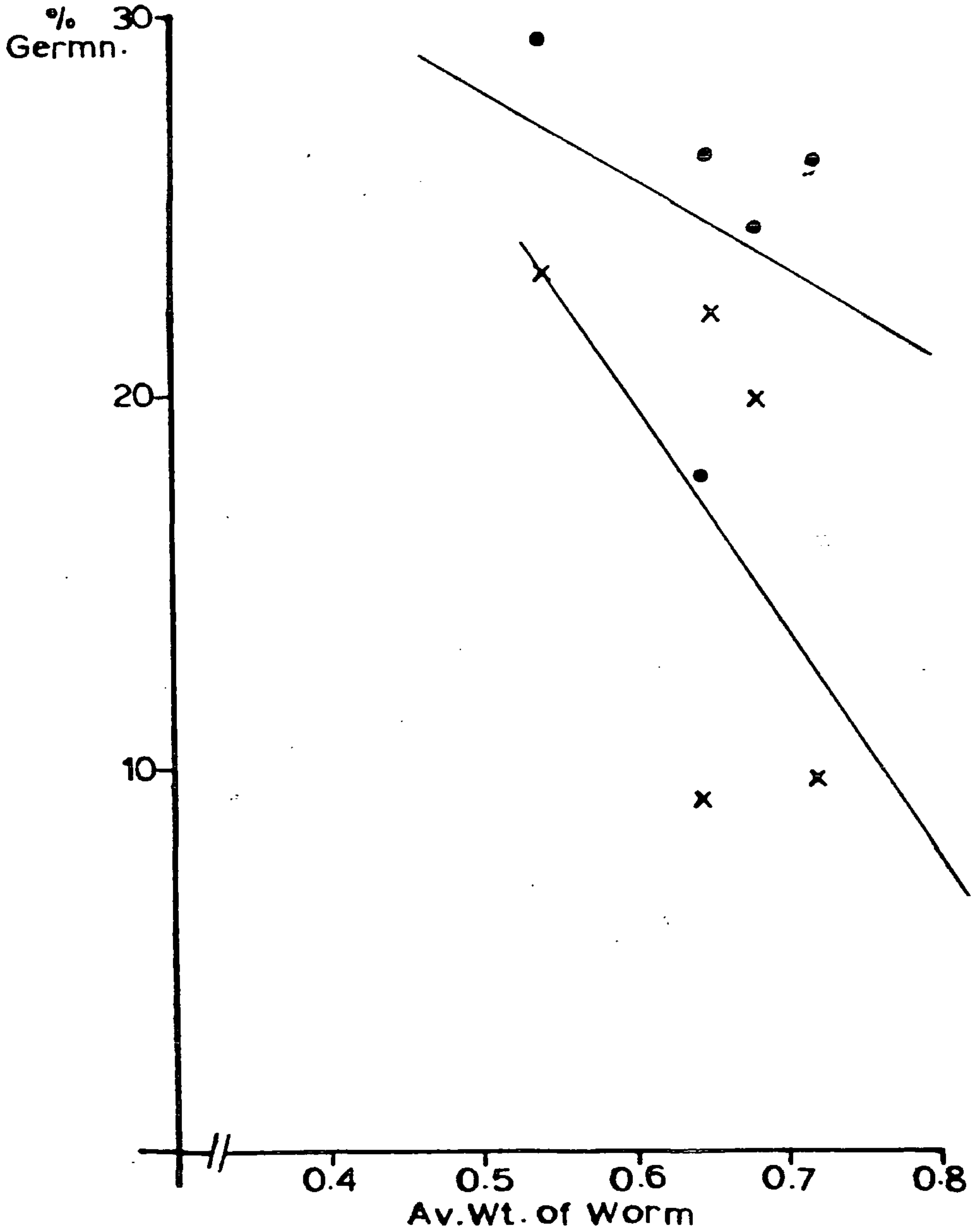
This result seems anomalous. One might expect their beneficial effects to increase linearly with their size. But this containment within a small pot will emphasise their activity - L. rubellus has been shown to be surface active by Standen (1979) and this was supported by their colonisation into open pots (Section 5). Active movement of larger individuals therefore within the upper layers in search of food, will disrupt the covering of seeds possibly leading to their burial below the surface, and lengthening the time taken for the seeds to germinate. The measurements were all taken at the same time, therefore buried seeds were not measured. The much improved germination due to the smaller worms, masked this effect when the mean figure is calculated for germination in the presence of both large and small worms, leading to the positive results.

The reduction in germination with increasing average size of the worm, was also negatively related to each of the components of total germination, (Graph 21), a clear correlation being obtained for clover, r = -0.59.

On the contrary, in the light of the results obtained in Tables 28 and 29, it is possible that worms eat the seeds, which pass unharmed through their guts, which may somehow stimulate their subsequent germination. No published work appears to have investigated this area.

(iii) Effects of Tipula larvae

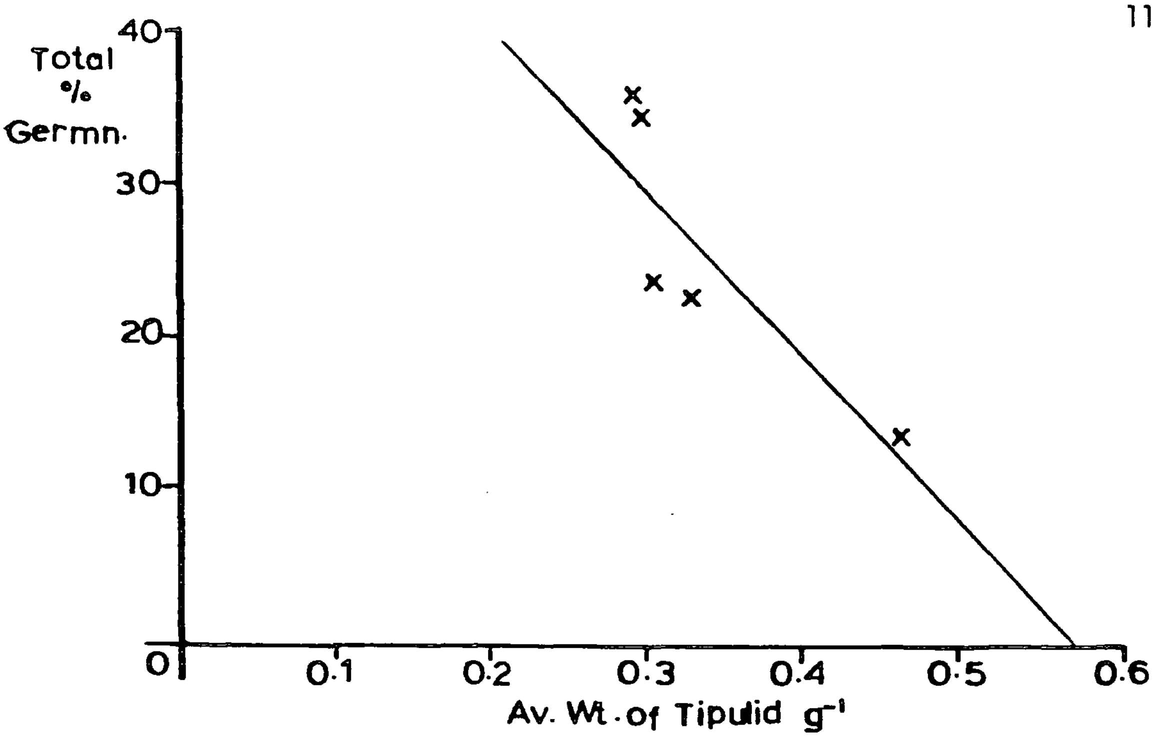
Quite conclusively, these results showed that leatherjackets inhibit germination. Their detrimental effects increased with their average weight; a high negative correlation was obtained (r = -0.84) (Graph 22). The component species of total germination reflected this trend, clover displayed a very close correlation which emphasised its susceptibility to attack (Graph 23). Although the larvae are not monophagous, when restricted to a limited range of vegetation, they will obviously eat the most palatable species, in this case the clover with a percentage organic matter digestibility of 75% compared to that of



GRAPH 21: Relationship between the average weight of worm/pot and percentage germination of clover and grass

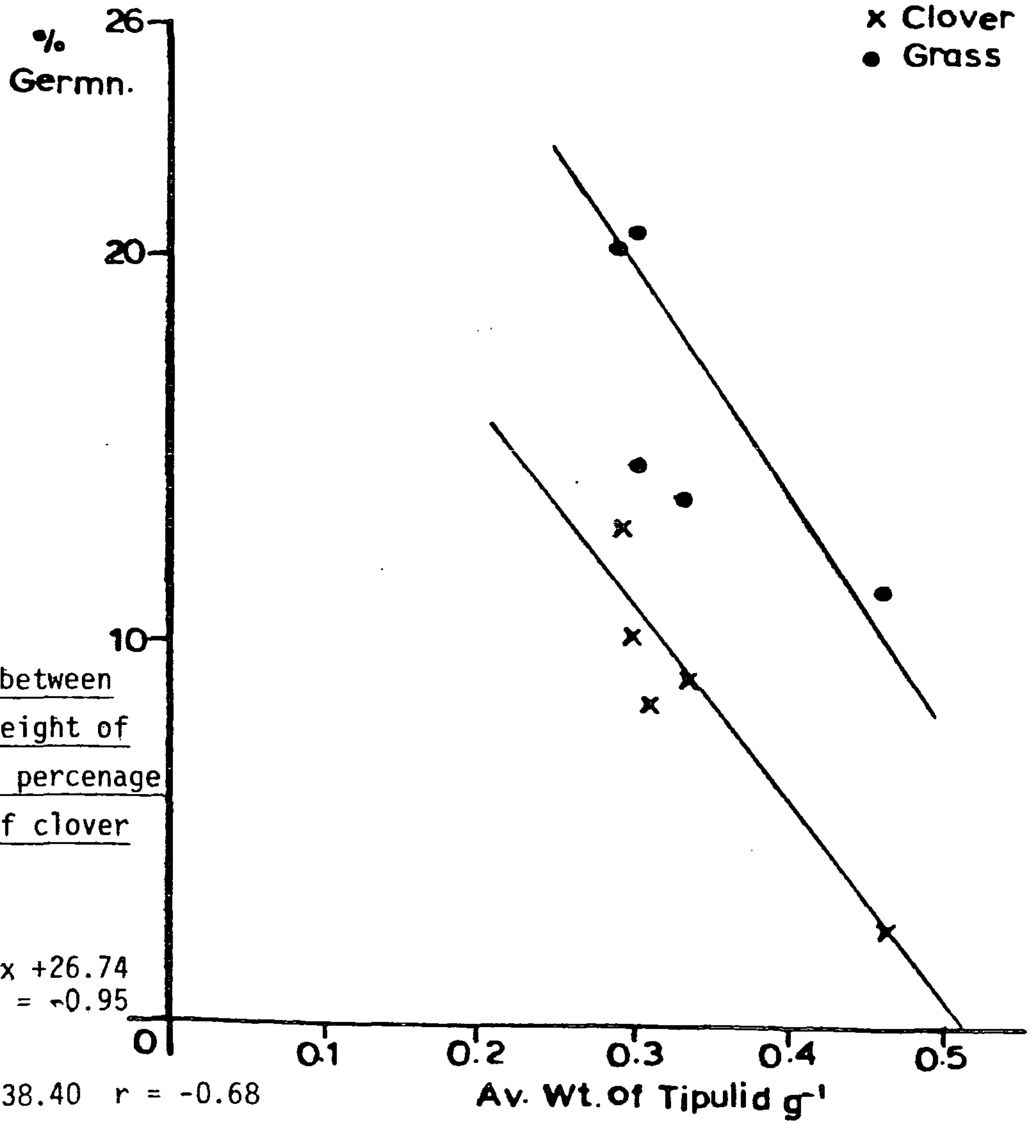
x = clover y = -60.33 x +55.97 r = -0.59

o = grass 6 = -21.90 x +38.80 r = -0.35



GRAPH 22: Relationship between the average weight of tipulid/pot and the percentage germination

$y = -113.1\ x + 65.25 \quad r = -0.84$



GRAPH 23: Relationship between the average weight of tipulid/pot & percenage germination of clover and grass

x clover
$y = -52.40\ x + 26.74$
$r = -0.95$

o grass
$y = -61\ x + 38.40 \quad r = -0.68$

the rye grass with 69% (Munro 1970). This would cause the reduction in clover germination.

Damage, or rather failure to germinate, in the pots containing Tipula larvae was 73.7%. In a similar study by Rennie (1917) using 25 larvae in cylinders 26.5 cm. in diameter, direct damage to oat plants was estimated at 63% after one week. Attack on the plumule accounted for most of the damage, but about 13% of the total estimation was due to direct attack on the seeds.

In this case, the damage was not accounted for specifically and therefore the poor germination cannot be attributed solely to larval attack - As shown by the result for the control pots 63% of the seeds failed to germinate uninfluenced by either the larvae or the worms (Table 28). The poor figures could be a result of the local weather experienced in late June, which consisted of hailstones, snow showers and torrential downpours, which may have delayed germination and flattened the shoots that had germinated, leading to browning and death. Clover, in this respect, may have been adversely affected to a greater extent when compared to the rye grass. The actions of the larvae and bad weather are synergistic in their effects on the plants growth, being difficult to separate without detailed knowledge of the factors influencing the growth of plants. Growth factors will obviously contribute to the differences in germination as each plant species possesses different abilities in their 'power of recovery' from attack. Most plants demonstrate some recovery if attacked, as long as the damage is not too great to overcome their recovery powers.

But conditions unfavourable for the plant may render it susceptible to Tipula larvae, as shown by the study in N.E. Scotland by Rennie (1917). A lengthening of the germination period increased the likelihood of damage. It is during the early days of growth from the time of sowing until the adventitious root system is established that attacks result in destruction of the individual plant. After this period the plant may be regarded as out of danger, although weakened. The weather, by extending this period increases the liability of loss of vegetation due to larval attack.

b) Effects on yield

(i) Effects of both animals on yield

Compared to the control, both treatments showed a reduction in dry matter yield averaged for each replicate, the earthworm treatment by 12%, the tipula larvae by 56%, although the only significant result was this latter treatment ($p < 0.01$) (Table 30, Graph 18).

TABLE 30: The resulting yield of g^{-1} d.w. of the total vegetation within the 3 treatments in mineral soil

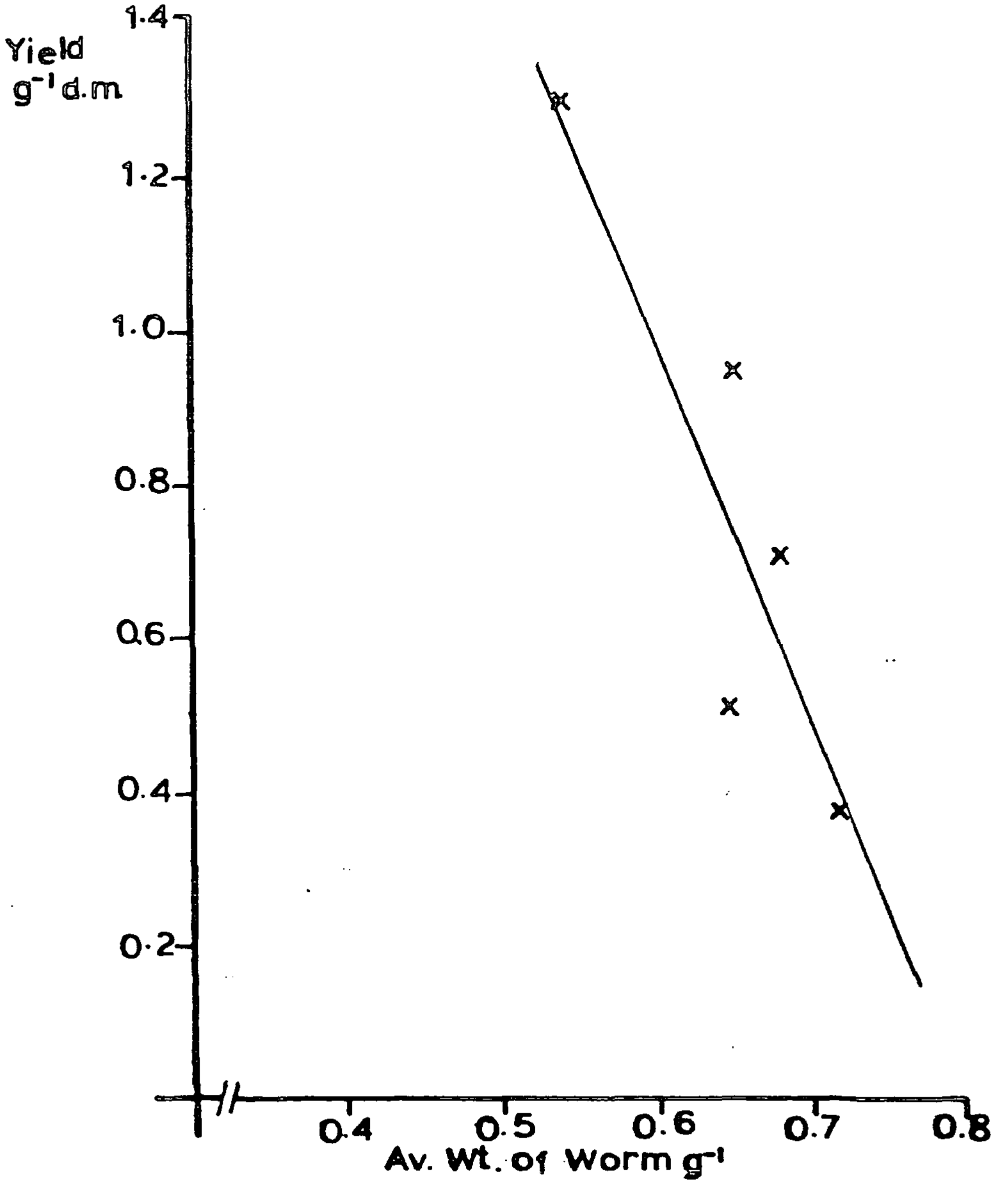
Treatment	Earthworm		Control		Tipulid	
	$\overline{X}$	SD	$\overline{X}$	SD	$\overline{X}$	SD
	0.78	0.37	0.89	0.28	0.39	0.16

(ii) Effects of earthworms

The result found here of the effects of earthworms on yield is in contrast to numerous other pot experiments, and agrees more with the negative results of Chadwick and Bradley (1948). Although not significant (statistically), the trend is still apparent.

A high negative correlation was also found when yield was plotted against average weight of the introduced worms (Graph 24) r = -0.88 - opposite to that found by Waters(1951).

Van Rhee (1965) concluded that there are wide differences between earthworm species and their effect in promoting the growth of different plant species, most workers used members of the genus Allobophora. Atlavinyte et al (1968)



GRAPH 24: Relationship between average weight of worm introduced into each pot and resulting dry matter yield

$y = -4.85\,x + 3.90 \quad r = -0.88$

used different species, amongst them L. rubellus and found that although L. rubellus produced increases in yield, these were lower than those due to A. caliginosa. Using numbers of 4, 8 and 16, introduced worms some replicates with the lower number produced no effect on plant yields.

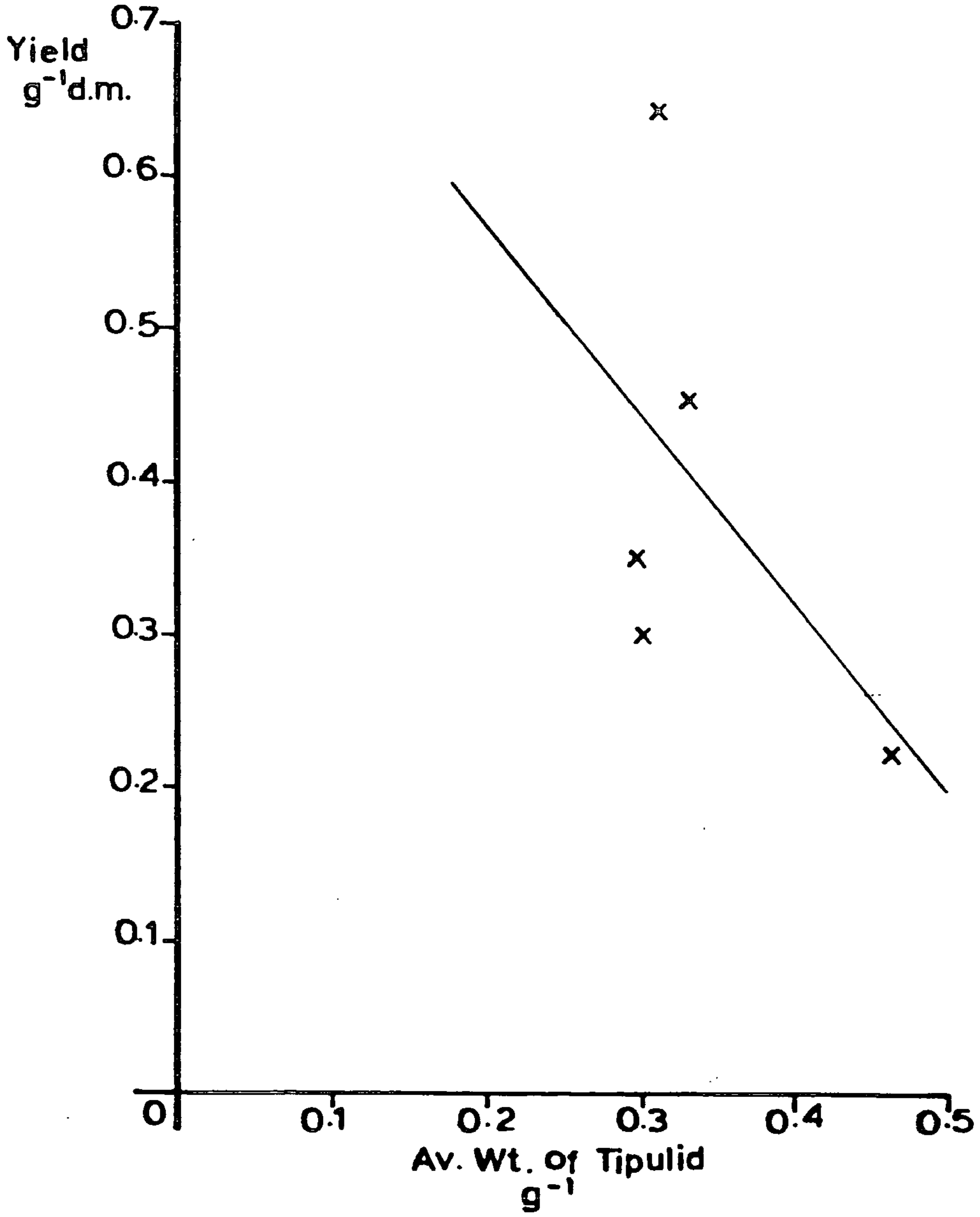
The changes earthworms cause in soil and their attendant effects on plant growth are more easily measured when few numbers are confined in small artificial cultures, but differences in species used, together with differences in crops and soils make comparisons difficult.

The anomalous result produced here, may be explained by a restriction of activity, mostly likely explained by the mineral soil being poor in organic material. The large worms would cause pressure on the delicate root systems which may have damaged them, causing the reduced yield compared to the control and the negative result obtained on Graph 35. It may also be postulated that larger worms could eat roots. This activity seems to offset any beneficial effects that have been claimed for the release of nutrients, either from their bodies or due to their role in decomposition of organic matter and subsequent release of nutrients.

Unfortunately separate yield data was not obtained for each species component, as Waters (1951) found a highly significant increase in rye grass yield but not of clover. Oddly, he found that the most profound effect of adding worms (in his case A. caliginosa was used), was to prevent clover suppressing the growth of rye grass.

(iii) Effects of tipula larvae

The larvae caused a significant reduction in plant yield. The larger Tipula introduced to each replicate caused a corresponding decrease in yield, as shown by Graph 25, r = -0.53. This suggests that the larger animals are consuming a greater proportion of vegetation (in contrast to the consumption experiments, Section 8). The range



GRAPH 25: Relationship between the average weight of larvae introduced to each pot and resulting dry matter yield

$y = -1.24\ x + 0.82 \quad r = -0.526$

of weights though is very small, the majority around 0.3 g. but still the weights are all significantly different from one another, even though only one mean weight for a replicate appears markedly so.

The average mean weight that they reach before pupation varies markedly from year to year, the females more so than the males (Laughlin 1967). In a field study on <u>T. paludosa</u> larvae collected from 16 fields in Northumberland and Cumberland over a span of 10 years, 1954-63, Laughlin (1967) found the mean peak weight ranged from 0.22 g. in 1961 to 0.51 g. in 1955. No reason could explain such a wide range, therefore these larvae could still have a significant weight increase, amounting to 40% of the largest mean figure found by Laughlin (1967).

As the tipulid larvae are very inefficient at utilising the consumed material (about 90% passes undigested through the gut, Coulson pers. comm.) this will have a drastic effect on resulting grass yield. Their position in their burrows at the soil surface and therefore close to the growing point of grasses, exaggerates their effects, and they cause damage far in excess of the amount they eat.

Although the results are quite marked, they cannot be directly related to the field situation for a variety of reasons, namely:-

(1) Larvae were confined to a limited amount of space and therefore restricted to the sown vegetation for food supplies.

(2) The relative absence of decaying or other vegetable matter in the soil used.

(3) The influence of the weather.

(4) The plant's own response.

No data is available as to which plant species was preferred, due to the lack of separation into species components at harvesting but work by White and French (1968) found that yield of white clover and Timothy were significantly reduced due to tipulid larvae but that of rye grass was not affected. Whether this is to do with palatability or the plant's own intrinsic defence mechanisms is unknown.

The effects of these two animals on germination were obvious. Although the yield was measured, stricter experimental design would be needed to validate these results completely.

(iv) Summary of Results

(1) Total germination was enhanced by earthworms of *L. rubellus*, as was that of the individual plant species compared to a control.

(2) The larvae of *T. paludosa* had a negative effect on all aspects of germination.

(3) The larger the average weight of introduced earthworm, the greater the decline in germination, more so for clover than for grass. The same result was obtained for the *Tipula* larvae.

(4) Addition of *L. rubellus* reduced total yield below that of a control, although the difference was not significant.

(5) A negative correlation between yield and average earthworm weight was obtained.

(6) *T. paludosa* larvae drastically reduced yield of clover and rye grass.

(7) The larger the average weight of the larvae (up to 0.46 g.) the greater was this effect.

8) The consumption of vegetation by the larvae of T. paludosa

The two size classes of tipulid larvae were fed on a known weight of vegetation for one week. Both the larvae and the plant material were weighed at the start of the experiment and at the end. The amount consumed by the larvae was converted into a dry weight figure, but larvae weights are wet weight estimates.

a) Shoots only (Table 31, Graph 26 and 27)

(i) Consumption (Graph 26)

Although the larger larvae consume a greater weight of green material, the smaller class eat a relatively far greater amount when expressed per gramme body weight.

In early June this effect is very clear, the smaller class consuming about 2½ times more than the larger class. Over the weeks, the amount consumed declined quite markedly until 2-3 weeks later when both size classes were eating < 10% of that eaten at the beginning of June. There is little difference in the amount consumed by the larvae over the time period 26/6 - 10/7 (Graph 26), in marked contrast to the experiment conducted over 3/6 - 10/6.

Although in the first week of July, consumption again increased slightly for both size classes (Graph 26), the larvae in experiment 3/7 - 10/7 were at lower initial starting weights compared to the week before, which accounted for the difference in consumption. Different sets of animals were used on each occasion.

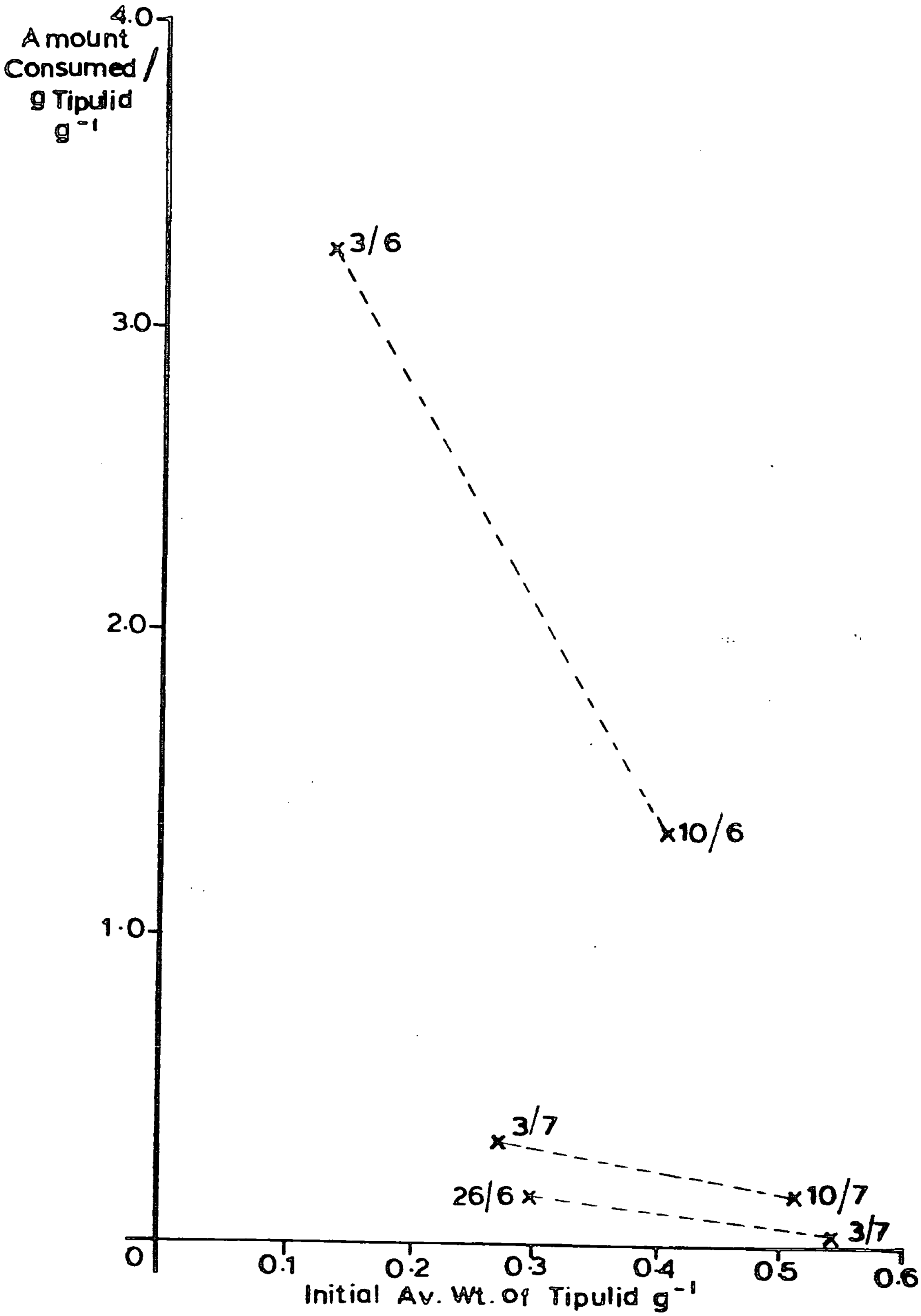
(ii) Growth of larvae (Graph 27)

Laughlin (1967) found that growth rate in the fourth instar was constant, reaching a peak where it remained for a few weeks and then fell as the larvae approached pupation. Peak weights are usually reached in mid-June for this species. The weight specific growth rate (Graph 27) showed that a decrease in weight did not occur until the end of June. But the timing of the decline varies according to the average weight of the

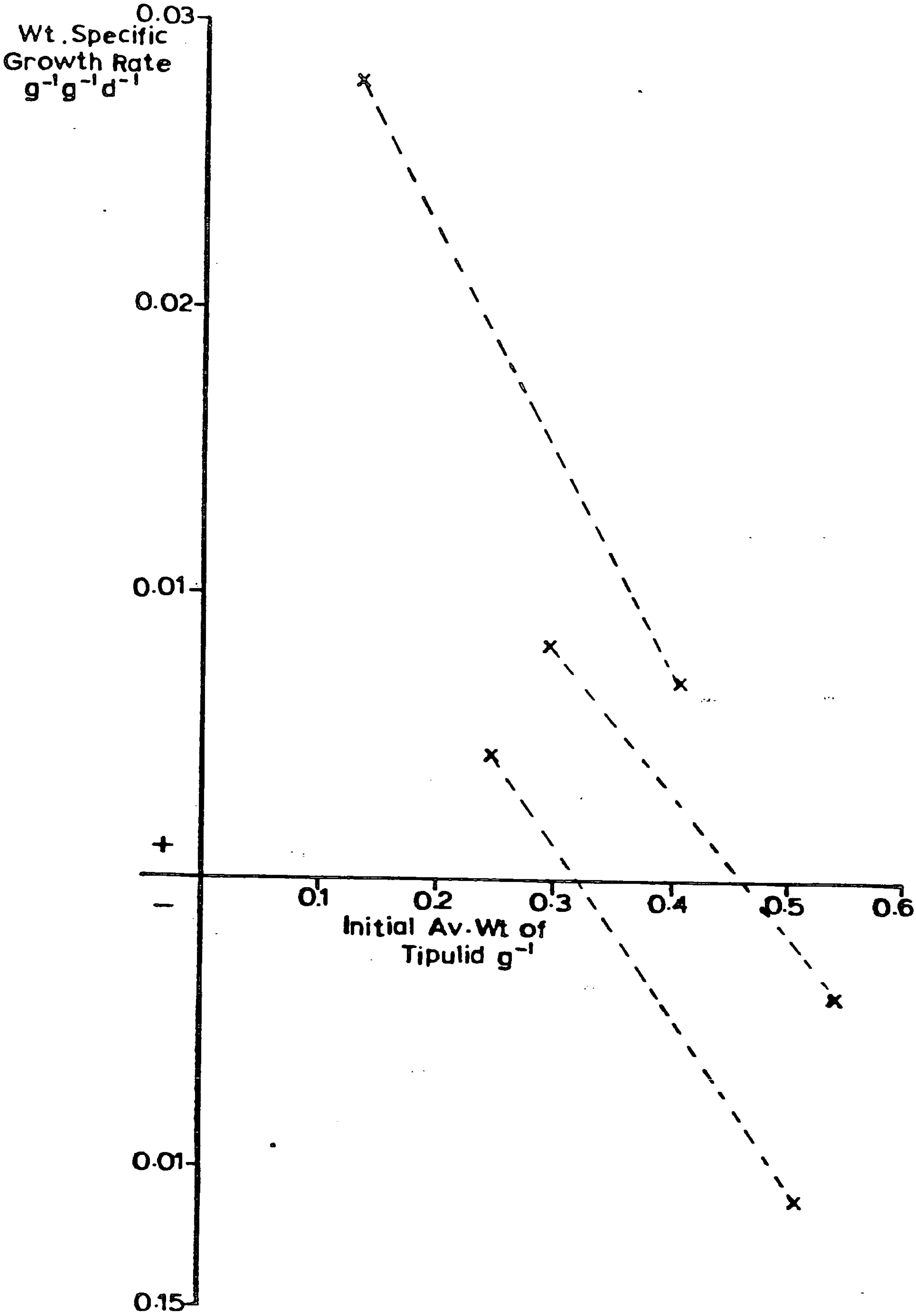
TABLE 3T: Consumption of grass shoots by larvae of Tipula paludosa

Date of experiment	Initial average weight of Tipulid g^{-1}	Average weight & shoot consumed	Average amount consumed/g Tipulid	Average change in initial body weight * g^{-1}	% change in initial body weight	Weight specific growth rate g^{-1} g^{-1} d^{-1}
3/6-10/6	N 5 $\bar{X}$ 0.1340 SD 0.0320	$\bar{X}$ 0.435 SD 0.444	3.250	$\bar{X}$ 0.0260 SD 0.0180	$\bar{X}$ 21.78 SD 7.72	0.0280
	N 5 $\bar{X}$ 0.4040 SD 0.0480	$\bar{X}$ 0.534 SD 0.540	1.320	$\bar{X}$ 0.0200 SD 0.0020	$\bar{X}$ 4.25 SD 10.32	0.0070
26/6-3/7	N 5 $\bar{X}$ 0.2973 SD 0.0770	$\bar{X}$ 0.047 SD 0.038	0.158	$\bar{X}$ 0.0170 SD 0.0013	$\bar{X}$ 5.92 SD 11.28	0.0082
	N 2 $\bar{X}$ 0.5407 SD 0.0570	$\bar{X}$ 0.025 SD 0.030	0.046	$\bar{X}$ -0.1440 SD 0.0015	$\bar{X}$ - 3.05 SD 5.05	-0.0040
3/7-10/7	N 4 $\bar{X}$ 0.2710 SD 0.0470	$\bar{X}$ 0.070 SD 0.047	0.260	$\bar{X}$ 0.0080 SD 0.0220	$\bar{X}$ 2.24 SD 7.45	0.0043
	N 4 $\bar{X}$ 0.5180 SD 0.0770	$\bar{X}$ 0.081 SD 0.009	0.156	$\bar{X}$ -0.0410 SD 0.0306	$\bar{X}$ - 7.92 SD 6.25	-0.0113

* Tipulids measures on a wet weight basis



GRAPH 26: Change-over time of amount of shoot material consumed/g tipulid for two differing size classes of Tipula paludosa larvae



GRAPH 27: Change-over time of weight specific growth rate for two size classes of T. paludosa larvae fed on shoots only for 1 week

larvae, the larger size class demonstrated a decline first, obviously having reached their peak weight quicker.

The trend is quite apparent as shown by Graphs 26 and 27, a reduction in the amount consumed occurred over time on a body weight basis, together with a corresponding decline in weight specific growth rate. The small size class exhibited the largest drop in growth rate. From an initial growth rate 4 times that of the larger class, within 3 weeks it had dropped to 15% of its original weight. This was to be expected as pupation period was approached and the smaller larvae showed a slowing down of their growth rate. The smaller ones still showed a positive weight gain, and as the size of the pupae is correlated with the fecundity of the resulting female (Laughlin 1967), it is important to achieve a certain minimum weight level.

Despite the fact that consumption was higher in the period 3/7 - 10/7 (Graph 26), this is not reflected in the growth rate (Graph 27), which seems to indicate that even while still feeding, positive increases do not necessarily occur in weight change.

b) Roots only (Table 32)

Unfortunately the results for consumption of roots comparable to experiments using only shoots, proved void for a variety of reasons. Only one set can therefore be used.

(i) Consumption

The larger size class ate over twice as much as the smaller one, on a body weight basis. But compared to consumption of shoots, the larger class ate only 1/3 of the weight of shoots on a weight specific basis. The smaller size class ate even less, at 8% of shoot consumption.

TABLE 32: Consumption of grass roots by larvae of Tipula paludosa

Date of experiment	Initial average weight of Tipulid g^{-1}	Average weight of root consumed	Average amount consumed/g Tipulid	Average change in initial body weight g^{-1}	% change in initial body weight	Weight specific growth rate g^{-1} g^{-1} d^{-1}
3/7-10/7	N 3 $\bar{X}$ 0.317 SD 0.038	$\bar{X}$ 0.0071 SD 0.0062	0.0224	$\bar{X}$ -0.00430 SD 0.39000	$\bar{X}$ 0.28 SD 12.48	-0.0019
	N 4 $\bar{X}$ 0.496 SD 0.047	$\bar{X}$ 0.0260 SD 0.0360	0.0524	$\bar{X}$ -0.00140 SD 0.00002	$\bar{X}$ - 2.80 SD 0.28	-0.0004

(ii) Growth of larvae

Comparisons between both size classes feeding on roots showed that the smaller ones sustained a greater weight loss, opposite of the results for those larvae fed on shoots. Whether this reflects a change in food preferences or nutrition is unknown, but it could indicate that those nearer to pupation can maintain adequate body weight on roots whereas those that are smaller and need to increase their weight still, find roots inadequate.

c) Roots and Shoots

(i) Over 1 week (Table 33, Graphs 28 and 29)

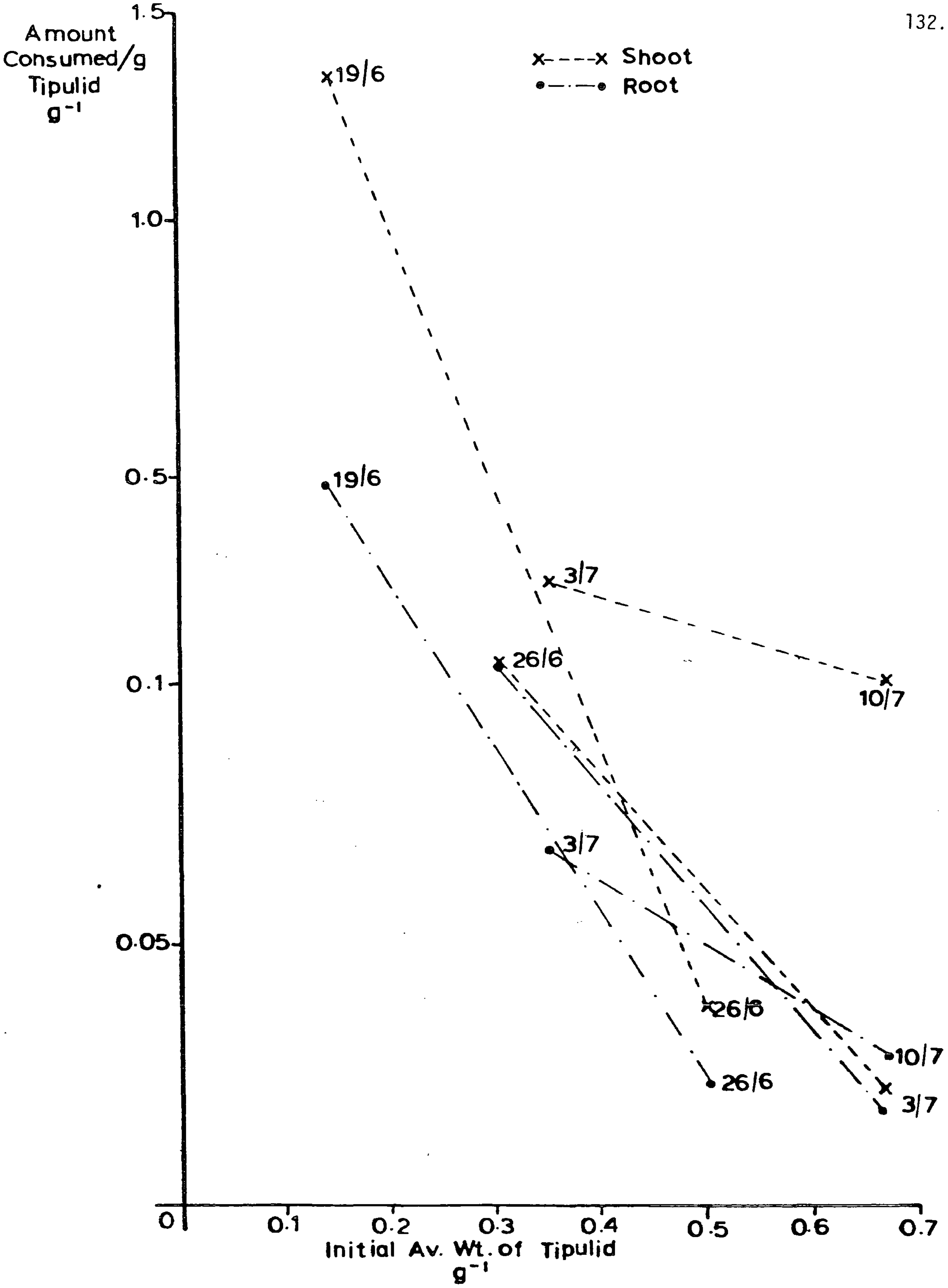
(1) Consumption

On all occasions a greater quantity of shoots were consumed compared to roots for both size classes, significant for all ($p < 0.01$) except in the second experiment.

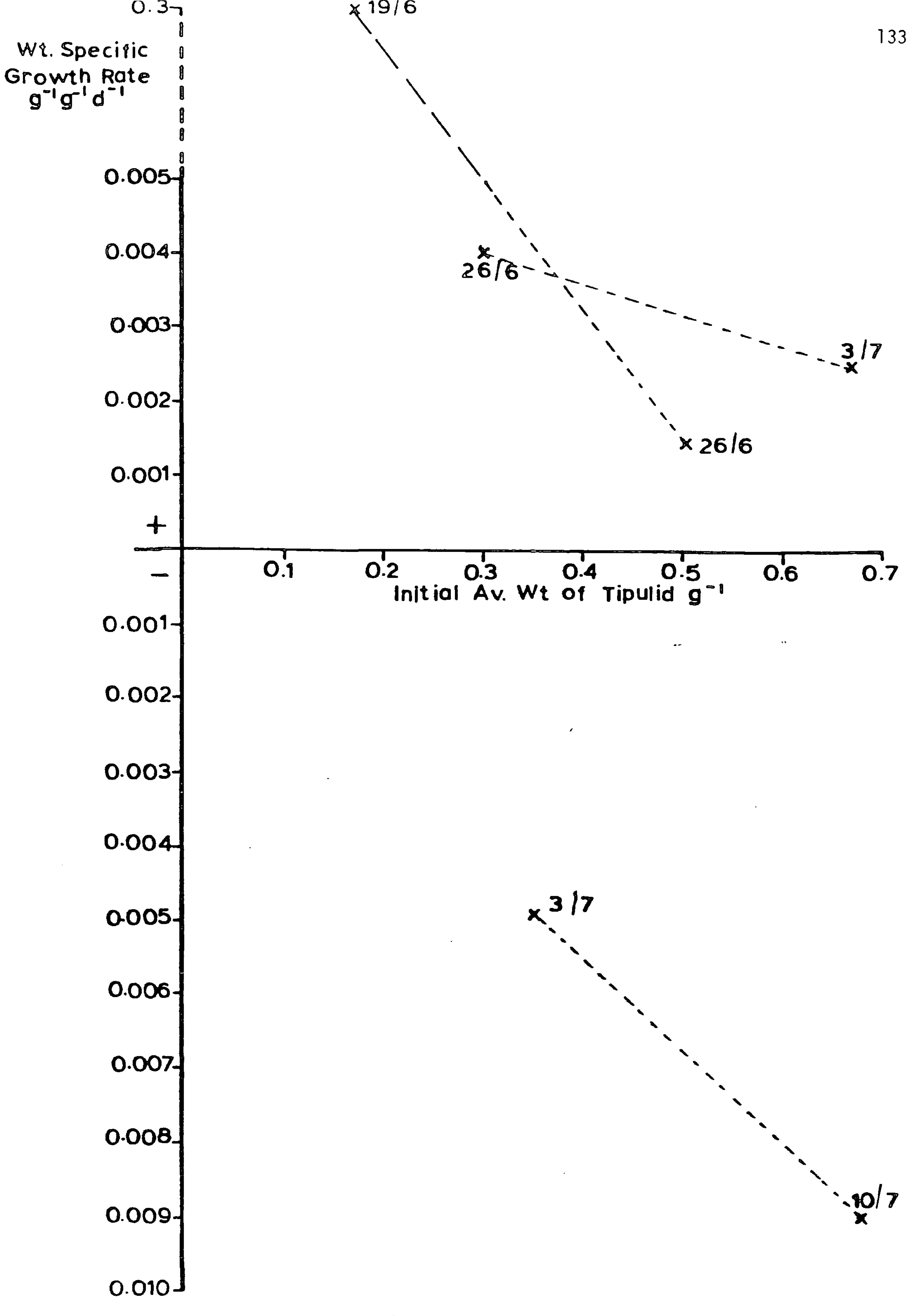
Taking each vegetation type separately, the consumption of shoots on a weight specific basis was erratic. As shown by Graph 28 consumption increased in the first week of July, even though the initial size of the larvae was greater than those in the experiment the week before, and was still greater than the larvae in the shoots only experiment. The difference in consumption cannot therefore be explained on different initial starting weights of the larvae. Despite this, within each time period, the smaller animals consumed a larger proportion of shoots than the heavier larvae on a weight specific basis. This difference dropped progressively over time, from a situation where the smaller ones consumed 33½ times as much shoots compared with the larger larvae, to the last date where they ate only 2½ times as much.

TABLE 33: Consumption of roots and shoots by larvae of Tipula paludosa

Date of experiment	INitial average weight of Tipulid g^{-1}	Average weight of material consumed Shoot	root	Average amount consumed/g Tipulid Shoot	root	Average change in initial body weight g^{-1}	% change in initial body weight	Weight specific growth rate g^{-1} g^{-1} d^{-1}
19/6-26/6	N 4 $\bar{X}$ 0.171 SD 0.500	$\bar{X}$ 0.2196 SD 0.0610	$\bar{X}$ 0.480 SD 0.0760	1.280	0.490	$\bar{X}$ 0.0360 SD 0.130	$\bar{X}$ 23.540 SD 14.209	0.3000
	N 4 $\bar{X}$ 0.508 SD 0.047	$\bar{X}$ 0.1960 SD 0.0260	$\bar{X}$ 0.1180 SD 0.0930	0.038	0.023	$\bar{X}$ -0.0049 SD 0.0101	$\bar{X}$ - 0.987 SD 1.949	0.0014
26/6-3/7	N 6 $\bar{X}$ 0.3103 SD 0.0770	$\bar{X}$ 0.0450 SD 0.1480	$\bar{X}$ 0.0430 SD 0.0410	0.145	0.138	$\bar{X}$ 0.0087 SD 0.0035	$\bar{X}$ 1.830 SD 5.890	0.0040
	N 2 $\bar{X}$ 0.6700 SD 0.0003	$\bar{X}$ 0.0148 SD 0.0056	$\bar{X}$ 0.0176 SD 0.0005	0.022	0.018	$\bar{X}$ 0.0125 SD 0.0210	$\bar{X}$ 2.460 SD 1.350	0.0026
3/7-10/7	N 4 $\bar{X}$ 0.03512 SD 0.3200	$\bar{X}$ 0.1047 SD 0.3600	$\bar{X}$ 0.0241 SD 0.0200	0.298	0.068	$\bar{X}$ 0.01212 SD 0.0197	$\bar{X}$ - 6.375 SD 2.080	-0.0049
	N 2 $\bar{X}$ 0.6741 SD 0.0240	$\bar{X}$ 0.0759 SD 0.0270	$\bar{X}$ 0.0190 SD 0.0050	0.113	0.028	$\bar{X}$ -0.0427 SD 0.0125	$\bar{X}$ - 6.375 SD 2.080	-0.0090



GRAPH 28: A comparison of the consumption of shoots and roots/g of tipulid for two size classes over 1 week



GRAPH 29: Comparison of the weight specific growth rate of two different size classes of tipulid larvae fed on roots and shoots over 1 week

Root consumption was less erratic and declined progressively over time for both size classes, except for the larger larvae in the last experiment, where a slight increase was noted, although not enough to offset the decline in growth rate (Graph 29). Again, the smaller larvae consumed a greater proportion of roots, although not quite such a marked difference in amounts, as for the shoots.

(2) Growth of larvae

When growth rates are plotted (Graph 29), within each experiment, the smaller animals have significantly higher rates. But overall they exhibit the steepest changes in weight reduction. An increase in growth rate occurs for the larger class within the week 26/6 - 3/7 compared to the growth rate of larvae within the other weeks, but this may be due to lack of replicates (n = 2).

It seems from this data that shoots are the preferred vegetation, even amongst the larger larvae. This conflicts with the results found for roots only (Table 32). However a greater growth rate was obtained on a combined diet. A decline in weight was not noticed on the combined diet until the first week in July, one week later than those on shoots.

(ii) Over 24 and 72 hours (Table 34)

Over a shorter time period the results were inconclusive. An opposite situation occurred compared to the experiment over one week, i.e. more roots than shoots were eaten for each individual over both short time periods (Table 34).

But the results were not significant. The results are inconclusive due to a number of reasons. Firstly, the larvae were not consuming to a great enough extent to offset the decline in vegetation weight loss due to bacterial decomposition. This is shown by the percent loss in the control, amounting to 4-5%. The late stage

TABLE 34: Consumption of roots and shoots by larvae of *Tipula paludosa* over 24 & 72 hrs.

Time period of experiment	Initial wt of individual used g^{-1}	Weight of material consumed		Amount consumed/g of Tipulid		Change in initial body wt. g^{-1}	% of total material eaten		% change in initial body wt.	Weight specific growth weight $g^{-1}\ g^{-1}\ d^{-1}$
		Shoots	Roots	Shoots	Roots		Shoots	Roots		
over 24 hrs	0.3508	0.0478	0.0955	0.1362	0.2722	-0.0300	7.83	13.82	-8.50	-0.0855
3/7-4/7	0.4161	0.0860	0.1067	0.2068	0.2564	0.0114	10.32	14.61	2.73	0.0011
	0.3935	0.0066	0.0156	0.0166	0.0396	0.0192	0.84	2.87	-4.87	-0.0488
	$\bar{X}$ 0.3868	$\bar{X}$ 0.0468	$\bar{X}$ 0.0726	$\bar{X}$ 0.1197	$\bar{X}$ 0.1894	$\bar{X}$ -0.0126	$\bar{X}$ 6.33	$\bar{X}$ 10.43	$\bar{X}$ -3.54	$\bar{X}$ -0.0444
	SD 0.0332	SD 0.0397	SD 0.0496	SD 0.0961	SD 0.1299	SD 0.0232	SD 4.91	SD 6.56	SD 6.25	SD 0.0536
	<u>Control</u>						<u>Lost</u> -4.7	<u>Lost</u> -5.4		
over 72 hrs	0.03240	0.0774	0.145	0.2388	0.4475	0.0015	17.40	19.00	0.463	0.0015
4/7-7/7	0.4351	0.0665	0.074	0.1528	0.1700	-0.0127	17.10	16.60	-2.918	-0.0097
	0.3705	0.0165	0.026	0.0445	0.0700	0.0195	3.80	6.00	5.263	0.0175
	$\bar{X}$ 0.3765	$\bar{X}$ 0.0534	$\bar{X}$ 0.082	$\bar{X}$ 0.1453	$\bar{X}$ 0.2291	$\bar{X}$ 0.0027	$\bar{X}$ 12.76	$\bar{X}$ 13.86	$\bar{X}$ 0.936	$\bar{X}$ 0.0031
	SD 0.0558	SD 0.0325	SD 0.059	SD 0.0974	SD 0.1955	SD 0.0163	SD 7.76	SD 6.91	SD 4.163	SD 0.0138
	<u>Control</u>						<u>Lost</u> 4.3	<u>Lost</u> 3.1		

in the larval's life cycle will also influence the amount eaten. Thirdly, lack of replication and differences in the initial starting size of larvae all mitigate against a conclusive result.

d) Clover and grass roots (Table 35)

No significant difference occurred in the consumption of grass and clover roots, although about 1½ times more grass roots were eaten on a weight specific basis. Animals fed on clover roots lost weight compared to the positive increase in weight for those eating grass roots, the difference was significant. It should be noted though, that the loss in weight for those on clover, were sustained by the two larger larvae, and that the three individuals fed on clover had a larger mean weight than the three larvae fed on roots. This weight difference was not statistically significant, but in the life cycle of larvae, a small difference in weight has important consequences. The deviation around the mean amount of clover consumed by the larvae is large. The impending onset of prepupal phase, more relevant for the larger larvae within the clover set and the lack of replicates, can account for the non-significant results.

e) Conclusions

The results support those of Freeman (1967) who suggests that tipulids are opportunistic and polyphagous in food preferences, able to eat both the shoots and roots of a wide variety of common grass species as shown here. The overall trend is apparent in that the smaller larvae are still gaining weight (although increases are not as large as time progresses), later in the season before their prepupal stage, when effectively they cease feeding. The larger larvae, enter the prepupal phase earlier and therefore show negative growth rates earlier on in the season. These would most likely be the first to emerge as adults. The range of emergence is enough to allow the smaller larvae to reach their peak weight and emerge in relative synchrony with the heavier larvae at the peak of emergence. It is unknown whether development is subject to a control, as in the related species T. subnodicornis and Molophilus ater. Here larval growth is temperature independent

TABLE 35: Comparison of consumptions of grass and clover roots by larvae of *Tipula paludosa*

Date of experiment	Initial wt of individual used g^{-1}	Weight of root consumed		Amount consumed/g Tipulid		Change in initial body wt. g^{-1}	% of total roots eaten		% change in initial body wt.	Weight specific growth rate $g^{-1}\ g^{-1}\ d^{-1}$
		Clover	Grass	Clover	Grass		Clover	Grass		
26/6-3/7	0.2002	0.1210		0.6050		0.0018	12.09		0.90	0.0013
	0.4049	0.1259		0.3108		-0.0332	12.57		-8.19	-0.0120
	0.3458	0.6910		0.1998		-0.0286	6.91		-8.27	-0.0120
	$\bar{X}$ 0.3169	$\bar{X}$ 0.3126		$\bar{X}$ 0.3719		$\bar{X}$ -0.0200	$\bar{X}$ 10.52		$\bar{X}$ -5.19	$\bar{X}$ -0.0075
	SD 0.1053	SD 0.3277		SD 0.2093		SD 0.0240	SD 3.14		SD 6.42	SD 0.0095
	0.3888		0.099		0.2546	0.0208		9.90	5.34	0.0076
	0.1665		0.1645		0.9879	0.0222		16.43	13.30	0.0190
	0.2426		0.1409		0.5808	-0.0036		14.08	-1.50	0.0022
	$\bar{X}$ 0.2659		$\bar{X}$ 0.1348		$\bar{X}$ 0.6077	$\bar{X}$ 0.0131		$\bar{X}$ 13.47	$\bar{X}$ 5.68	$\bar{X}$ 0.0096
	SD 0.1129		SD 0.0332		SD 0.3674	SD 0.0172		SD 3.30	SD 8.46	SD 0.0085

but the immediate prepupal and pupal stages are temperature dependent, causing synchronised emergence (Coulson et al 1967). A similar condition may exist in T. paludosa in order to regulate the life cycle.

The differences in larval growth as related to their weights, are important when damage to crops are considered. This damage primarily occurs in spring as a result of an early fourth instar burst of feeding, Dunnet (1955) found mean weight increases of 200-300% in 3 weeks in early spring, correlated with a rise in soil temperature. The same number of leatherjackets in a field therefore can cause marked differences in loss of yield depending on whether they were small or large at the time of increasing soil temperatures. This primarily depends on autumn growth, in 1-2 months they can increase their weight by 100 fold. Although Meats (1967) found that actual weight gain/unit area was faster the larger the larvae. Although these experiments missed the initial burst of weight increase, they did show the differences in consumption between the sizes, smaller ones eating a larger proportion of all vegetation (except for the one experiment on roots only) compared to the larger larvae. These results have obvious implications in the field situation.

As the size of the pupae is correlated with fecundity of the resulting female (Laughlin 1967), larval growth is important in attaining a certain minimum size, especially when the average number of eggs laid is between 250-350, although the range is between 48-487 (Dunnet 1955). Being univoltine with the generation time fixed at one year, the changes in population level are determined by fecundity and mortality, in these pre-reproductive stages. Laughlin (1967) though, considers mortality to be of much greater importance in affecting large changes in population levels from year to year.

Ideally therefore, the experiments should have been carried out earlier in the season, where more representative results, applicable to the field situation, could have been obtained.

The temperature of $8^{o}C$ at which they were kept, seems to have been sufficient in delaying development by up to 3 weeks (pupae did not start to emerge until late August), when in the field, emergence occurs in late July/early August (Coulson 1962). This seems to suggest that some temperature controlling effect influenced the larvae and prolonged their development in the larval stage.

The lack of replicates due to an inadequate supply of animals, caused some discrepancy in the results between those fed on roots and shoots. Although relatively similar sized larvae were chosen, this may not have overcome their basic differences in development, again the small number of replicates precluded any conclusive statements. Following the same animals over time may have overcome some of these difficulties.

The larvae were weighed on a wet weight basis and measurements were standardised, by rolling the larvae on filter paper before weighing, but obviously this is of variable accuracy. Meats (1967) has shown that growth rate appears to be related to the difficulty of extracting water from the soil, any weight gained comprising about 90% water, including that obtained in the food, plus that from the environment. The larvae in this case were kept on moistened soft paper, the size of the paper, amount of water absorbed and lost on drying may all have caused wide differences in the amount available to the larvae. This would consequently affect their weight changes, the larger surface area/volume ratio of the smaller larvae would enable greater water uptake and therefore a greater weight increase in a given period. Such difficulties in measurement are not easily overcome, even with a wet/dry conversion factor.

The experiments, although carried out in artifical situations indicate trends and general conclusions. Linked to a behaviour study in the field, analysing their faecal contents from larvae collected both during the day and night, could show actual vegetation consumed for a range of size classes. This would then indicate their preferences, so that these results, together with those obtained for their effects on plant germination and yield, could be verified.

The negative correlations obtained for the germination experiments with tipulid larvae, can be explained through these results. Although the larger larvae ate less per gramme body weight compared to the smaller animals, they eat in many cases a greater quantity of vegetation causing the decline in yield with increasing weight. A greater quantity of clover roots were eaten in these comparison experiments, which could account for the high negative correlation obtained with increasing larval weight in the germination experiments (Graph 23).

Through all these experiments though, it can be understood why this particular animal has earned the title of 'pest'.

Summary of results

(a) On shoots only

(i) Smaller larvae consumed a greater amount of shoot material per gramme of their own body weight compared to the larger larvae.

(ii) As prepupation period approached, less was eaten per gramme body weight, for both the 'large' and the 'small' larvae.

(iii) Weight specific growth rate declined over time once their peak weight has passed, the steepest reductions occurred in the smaller size range, although the larger class displayed this trend first.

(iv) Negative weight changes were sustained by the larger size class earlier than the smaller ones. When the latter did show a decline in weight, it was less than that for the larger larvae.

(b) On roots only

(i) The larger larvae consumed a greater amount of roots on a body weight basis compared to the smaller ones.

(ii) A greater reduction in weight specific growth rate was experienced by the smaller larvae in comparison.

These conclusions are based on one experiment only.

c) Shoots and roots

(i) Over 1 week

(1) A greater quantity of shoots were eaten per gramme of body weight compared to roots in all experiments.

(2) The smaller animals ate a greater amount on a body weight basis of both shoots and roots compared to the larger animals.

(3) The amount consumed of both vegetation types declined over time for both sets of larvae.

(4) Weight specific growth rate declined progressively over time, for both size classes, but the smaller ones exhibited largest change in weight measured.

(5) Both size classes showed negative weight changes at the same period, the larger class the greatest loss.

(ii) Over 24 and 72 hours

The results were non-significant, although more roots were eaten over both time periods compared to shoots, for a similar sized class of larvae. Various reasons mitigated against obtaining a conclusive result, amongst them, lack of significant consumption by the larvae to offset decline in vegetation weight loss, due to bacterial decomposition.

d) On clover and grass roots

(i) Grass roots were eaten in greater amounts per gramme body weight of larvae compared to clover roots, for a class of larvae not significantly different in size.

(ii) A slight negative weight change was shown by those larvae feeding on clover roots, compared to a positive weight gain for those on grass roots.

V GENERAL CONCLUSION

Through this study it was found that earthworms were absent from the two fields on Mr Carrick's land, one improved for 5 years the other for 3 years. By considering the environmental factors relevant to their survival it was concluded that existence of earthworms within this area is possible. The various improvement treatments carried out on FI and FII have altered the physico-chemical conditions sufficiently, in order to be able to support an earthworm population. It is suggested that the determining factor now in this situation is not the conditions within the peat, but its actual colonisation from an external source. The area is effectively isolated, the density of worms within the surrounding hills is very low, and colonisation by natural means is difficult. These factors preclude a substantial earthworm population from becoming established.

Study lower down the Tees Valley on Mr Scott's land, reveals large earthworm populations. His land still contains large quantities of organic material, is moderately wet, with the pH of the soil in many cases below that of Mr Carrick's two fields. The various improvement treatments Mr Scott has undertaken are basically very similar to Mr Carrick's except for the inclusion of farm yard manure. This material, together with a location that is more favourable to colonisation by earthworms, seems to have lead to a substantial build up of numbers, so much so that they are now comparable with lowland pastures in Britain.

The value of FYM is easily seen in arable cropping, large populations of earthworms are maintained where this is regularly applied, but low populations in its absence. The material actually introduces the cocoons of the worms together with those already hatched, which can develop within a favourable micro-climate produced by the FYM. This same material also serves as a favourable food source to the worms. Regular additions of this material would eventually lead to a significant earthworm population.

Whereas survival was demonstrated as possible for the two species of worm chosen i.e. L. rubellus and L. castaneus, FYM would introduce a range of species. Ecological tolerances differ widely for each one, but there seems no major reason to preclude the existence of other species on Mr Carrick's land. A varied range of earthworms occurred within the pots, thus survival and even reproduction was demonstrated as possible in the improved soils. The continuing treatments to FI and FII should reduce the peaty nature of the material, and the reseeded pastures should eventually contribute a more nutritious food supply than already present. Both will enhance earthworm survival.

The beneficial effects of earthworms are quite conclusive. Part of those effects have been shown in this study. In order that advantage can be taken of their benefits, for FI and FII, introduction of earthworms must occur and a good method would be the application of FYM. For FII this seems practical, as it is situated near to the farm and is within easy access of the lower pastures where cattle are grazed. But for FI, a higher altitude and a difficult trackway some distance from the farm, will mitigate against use of FYM.

The detrimental effects of Tipula paludosa larvae are well documented and substantiated by this study. The same permanent difficulties that are limiting earthworm colonisation, will also hamper the treatment to eradicate the larvae from FI. The theory behind their eradication is well known, but actually undertaking this step is more difficult. Preventing their return, once measures have been taken to treat this year's population, will entail more long term measures. A more efficient drainage of the peat soil should aid this process. But as long as lowland pasture grasses exist, the mature flies will be attracted to the area. Conditions therefore must be made unfavourable for the development of the eggs which would effectively curtail the destructive part of their life-cycle.

Although both farms are classed as upland, the study brings out the marked differences between the two areas. A distance of about 200 m. in altitude and only about 10 km. as the crow flies, separates the two locations. Yet this is enough to account for the greater proportion of permanent difficulties encountered on Mr Carrick's land. Although an attempt has been made to reduce some of the temporary limitations, actually trying to remove these will create further problems, such as economic difficulties and practical considerations in removing the larvae and introducing the earthworms.

GLOSSARY

Drouting	-	Confinement of the sheep stock to pens for separation prior to selling.
Early bite	-	The new season's grass growth in spring.
Gimmer	-	Female sheep from 1½ to 2½ years old. Most hill ewes are mated and lamb for the first time as gimmers.
Hogg	-	Sheep from 6 months to 1½ years old.
Inby land	-	Land close to the farm that has been improved and reseeded and is usually fenced.
Outby land	-	Rough, unimproved hill grazing, not enclosed by fences.
Tupping	-	Mating of the sheep.

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