Population ecology and functioning of Enchytraeidae in some arable farming systems

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Wim Didden

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Cover photograph: Wim van Hof

1. Het belang van potwormen voor nutriëntenstromen in (agro)oecosystemen wordt niet alleen bepaald door biomassa en turnover van de populaties, maar tevens door hun verticale verdeling over het profiel en temporele dynamiek.

    Dit proefschrift

2. De indirecte effecten van potwormen op de nutriëntenmobilisatie kunnen aanzienlijk zijn als gevolg van de vermoedelijk lage selectiviteit bij de voedselopname en de hoge selectiviteit waarmee voedsel wordt geassimileerd.

    Abrahamsen, G., 1990 - Biol. Fertil. Soils 9:159-162
    Dit proefschrift

3. Potwormen dragen aanmerkelijk bij aan de dynamiek van de bodemstructuur en kunnen zodoende een belangrijke rol spelen bij de lucht- en vochthuishouding van de bodem.

    Dit proefschrift

4. De fysisch-chemische parameters die in de meeste oecologische studies gemeten worden, zijn voor het voorspellen van de aan te treffen hoeveelheden potwormen van geringe waarde.

    Dit proefschrift

5. Laboratoriumgegevens over de levenscyclus van dieren zijn slechts dan bruikbaar voor voorspellingen van de veldsituatie, wanneer ze tevens bepaald zijn onder daar optredende extreme omstandigheden en wanneer veldmetingen op de relevante schaal worden verricht.

    Dit proefschrift

6. Ruimtelijke heterogeniteit op micro- en macroschaal vormt de basis voor het functioneren van het bodemoecosysteem en tegelijkertijd een van de belangrijkste hinderpalen voor bodembiologisch onderzoek.

7. Het gebruik van functionele groepen in een oecologische analyse, zonder soort-gericht oecologisch onderzoek naar de in deze groepen geplaatste organismen, leidt onvoldoende tot inzicht in het functioneren van oecosystemen.

    Hunt, H.W. et al., 1987 - Biol. Fertil. Soils 3:57-68

8. Het feit dat oecologisch onderzoek aan potwormen slechts relatief laat is aangepakt, ondanks het zeer talrijk voorkomen van deze dieren, doet vermoeden dat de ontwikkeling van de wetenschap mede wordt bepaald door angst voor het onbekende.

9. De huidige praktijk van voornamelijk kortlopende contracten voor wetenschappelijk onderzoek bevordert zowel de produktiviteit als de verschraling van dat onderzoek.

10. 'No-nonsense beleid' wijst niet alleen op een povere beheersing van de Nederlandse taal, maar ook op een duidelijke minachting voor afwijkende meningen.

11. Veel bodembiologisch onderzoek blijft aan de oppervlakte.

Abstract

The population ecology of Enchytraeidae, and their functioning, were studied in some arable farming systems and in laboratory experiments. The systems studied consisted of a 'conventional' (high input of energy and matter) and several 'integrated' (reduced input of energy and matter) systems. Emphasis was given to population dynamics and the role of Enchytraeidae in nutrient cycling and soil structure evolution.

Mean yearly enchytraeid abundance and biomass in the systems studied ranged from 11000 ind/m^2 to 43000 ind/m^2, and from 0.08 g C/m^2 to 0.42 g C/m^2, respectively. It was calculated that 0.5-3.7% of the yearly organic carbon input was respired by the enchytraeid populations. Yearly nitrogen flux from the populations (through storage in enchytraeid tissue) ranged from 0.19 to 0.60 g/m^2.

There were no significant differences between the systems studied as regards population dynamical and production ecological parameters. However, vertical distribution of enchytraeid populations differed markedly between the conventional field and the integrated fields, probably related with differences in soil tillage and the resulting distribution of organic fertilizer and plant residues. These differences in vertical distribution may have consequences for the risk of nutrients leaching from the systems.

The impact of enchytraeid activity on soil structure evolution was studied in a field experiment with artificial soil cores, in combination with field observations. It was found that enchytraeid activity produced measurable effects on air permeability, pore size distribution, and distribution of aggregate sizes, probably through selective burrowing and transport of organic besides mineral material.

Life-history parameters of *Enchytraeus buchholzi*, the dominant species at the research site, were determined in a laboratory experiment, and predictions based on the laboratory trials were compared with data on population development under more natural conditions. There were significant discrepancies, indicating an influence of the physiological condition of the experimental animals on the length of the life-cycle in this species.

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Woord vooraf

Toen ik in 1986 begon met het bestuderen van de oecologie van potwormen, wist ik nauwelijks wat potwormen waren en welke vragen op dit terrein liggen. Nu, vijf jaar later, ben ik er mij daar in ieder geval beter van bewust. Dit proefschrift vormt de neerslag van dit leerproces.

Hoewel slechts bij één hoofdstuk van dit proefschrift anderen zijn genoemd als mede-auteur, houdt dat geenszins in dat alles op eigen kracht is gedaan. Zonder de steun, aanmoediging en kritiek van velen, zou dit proefschrift er waarschijnlijk niet zijn geweest.

Op de eerste plaats wil ik hier mijn ouders bedanken, die mij steeds hebben aangemoedigd om mijn interesses te volgen, en speciaal mijn vader, die mij al vroeg in contact bracht met de natuur en mij leerde kijken en luisteren. Helaas heeft hij niet meer mogen meemaken wat daaruit is voortgekomen.

Lijbert Brussaard heeft, door de vele stimulerende gesprekken en discussies over het onderzoek zelf en het beschrijven ervan, een heel belangrijke rol gespeeld bij de totstandkoming van dit proefschrift. Leen Pons, hoewel niet vaak aanwezig, heeft door zijn onbevangen kijk op de problematiek mij deze soms vanuit een ander perspectief laten zien.

Twee mensen in mijn directe werkomgeving zijn steeds heel belangrijk, en vaak onmisbaar geweest gedurende de afgelopen jaren. Joke Marinissen heeft, in onze talloze discussies over ons beider onderzoek, een zeer belangrijke positieve rol gespeeld, en Rijndert de Fluiter heeft met veel geduld en inzet talloze klussen geklaard, van het tellen van potwormeieren tot het in weer en wind bemonsteren op de Lovinkhoeve. Joke en Rijndert, bedankt!

De medewerkers in het Lovinkhoeve-project, met name Peter de Ruiter, Gerrit Lebbink, Lucas Bouwman en Rieks van Faassen, en té veel anderen om hier op te kunnen noemen, wil ik bedanken voor de collegiale samenwerking en de soms hevige, maar altijd vruchtbare discussies. Op de Lovinkhoeve zelf waren de heren Koning en Daniëls degenen die er voor zorgden dat het onderzoek überhaupt mogelijk was, waarvoor op deze plaats mijn dank.

Dankzij Jos Kroesbergen konden de grote hoeveelheden kunstmatige bodems die voor de experimenten nodig waren, worden geproduceerd. Bovendien speelde hij een belangrijke rol bij de ontwikkeling van de methode voor het vervaardigen van deze bodems en was hij ook degene die mij enig begrip voor bodemfysische bepalingen wist bij te brengen.

Zonder de hulp van Maja Kooistra zou ik niet in staat zijn geweest om een begin te maken met het bestuderen van de polijstblokken, en ook haar inbreng in de discussies over de invloed van potwormen op structuurontwikkeling is voor mij belangrijk geweest.

1. General introduction

Although man in Western Europe has worked the soil for thousands of years, soil itself, and the processes responsible for its fertility, have, till fairly recently, always been treated as a black box. Management practices therefore seldom included conscious manipulation of soil processes or biota as a means of increasing production. Thus, although measures like tillage, crop rotation and manuring proved successful, the underlying mechanisms remained unknown. It was not until the 19th century, that scientific knowledge of soil chemistry and, to a lesser extent, soil biology started to develop, with the discovery of chemical fertilization (Von Liebig, 1840) and the work of Darwin (1881) on earthworms. The use of inorganic fertilizers permitted intensification and expansion of agricultural practice, a process which was stimulated by the increased use of chemical pesticides since World War II. For some time, agronomists generally believed that a combination of mechanical and chemical management practices enabled a continuing expansion, with the maintenance of soil fertility and structure, and control of pests and diseases. In most types of agriculture, soil biota (microorganisms and especially animals, with the exception of earthworms) were largely ignored, unless they were suspected of being injurious to crops or animals. Economically speaking, this has been a successful approach.

In recent years, however, the price that was paid for the economic success of this type of agriculture became increasingly clear, from problems with soil fertility and the environment. Urgent problems in this respect are:
- Pollution of groundwater, surface water and atmosphere, caused by the intensive and inefficient use of inorganic fertilizers and manures leading to leaching and/or volatilization of excess amounts. Part of the 'acid rain' problem originates from these processes.
- Environmental side-effects of pesticides, that are being used abundantly and at high costs (both financially and publicly).
- Deterioration of soil structure in many agricultural soils, caused by a decrease in soil organic matter through crop rotations including more root crops, and by the use of heavy machinery under too wet conditions. As consequences, problems with water infiltration, workability and trafficability may occur in many soils, leading to the need for even more intensive tillage. Moreover, through deterioration of soil structure and enlargement of agricultural fields, erosion problems may occur.

These problems stimulated the interest in ecologically sound forms of land use, in which management practices are tuned to environmental and economical objectives. Such forms of 'integrated' land use imply reductions of mechanical and chemical inputs

to the system, any yield reduction to be balanced by the reduction of costs. An important condition in this respect is, that the use efficiency of exogenous inputs will be increased by making use of naturally occurring, internal processes of soil structure evolution and of storage and transformation of plant nutrients. A thorough knowledge of these mechanisms not only requires an understanding of physical and chemical processes occurring in the soil, but also of the biological processes, as microbial and faunal activities become more important with reduction of human inputs.

Soil structure is being biologically affected through microbial and biochemical processes that contribute to the formation of soil aggregates and influence their stability (Oades, 1984). On a different, but not less important scale, soil structure is affected through the construction and disruption of more or less stable channels and voids by the activity of roots and soil animals, and by the mixing of organic and mineral material by faunal activity (Tischler, 1965; Wallwork, 1976; Coleman, 1985).
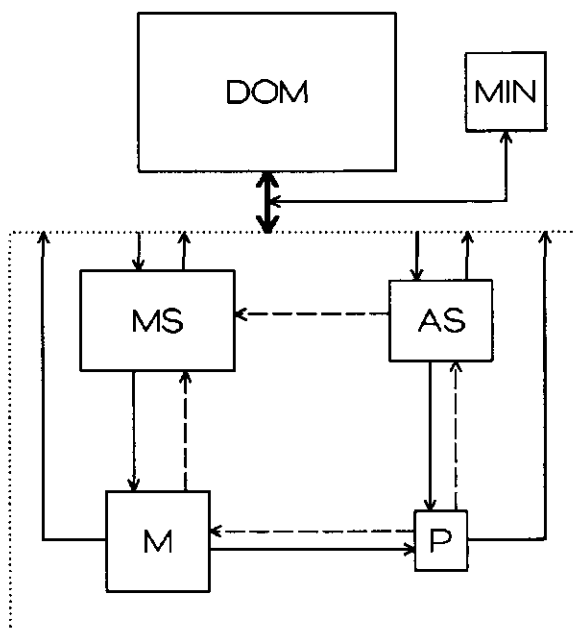
Figure 1.1: Schematic diagram of the flows of matter in the decomposition subsystem, and major regulatory interactions. Boxes represent pools of nutrients. Solid arrows represent flows of matter, dashed arrows regulatory interactions. DOM = Dead organic matter; MS = Microbial saprovores; AS = Animal saprovores; M = Microbivores; P = Predators; MIN = Mineralized nutrients pool.

Soil fertility is very clearly biologically affected, as decomposition of organic material, both of upper- and underground origin, is for the larger part a biological process, in which micro-organisms, and meso- and macrofauna are intimately involved, in ways that are only gradually being disclosed. Figure 1.1 is a schematic diagram of the decomposition subsystem, representing the overall processes taking place in the decomposition of organic material. Solid arrows in the diagram represent flows of matter, dashed arrows important regulatory mechanisms. Partly decomposed material and dead microbial and animal tissue returns to the pool of dead organic matter (DOM), and may be processed over and over again before it is completely respired or otherwise mineralized, or transformed to relatively stable humus. This recycling of matter distinguishes the decomposition subsystem from the herbivore subsystem, where the remains of organisms, once dead or consumed, leave the subsystem as dead organic material, thereby entering the decomposition subsystem (Heal & MacLean, 1975).

The decomposition of a particular piece of dead organic matter starts with the colonization by microbial saprovores (MS), rapidly decomposing easily degradable organic compounds (mostly the simpler carbohydrates). This process is enhanced by saprovorous animals (AS) comminuting the material and thereby enlarging the surfaces that are capable of being colonized, and by effects of grazing by microbivorous animals (M) on micro-organisms. Grazing, though reducing microbial biomass, may also stimulate microbial activity, prevent ageing of colonies and, if selective, may influence the microbial community structure. Faunal activity may also be important in that animals may act as vectors in the propagation of micro-organisms. In these ways mobilization of nutrients may be increased or reduced by the activities of the soil fauna (Moore et al., 1988). Later stages of decomposition are characterized by a slowing down of the processes, when the proportion of more recalcitrant compounds increases.

This relatively simple picture of the decomposition process is in reality much more complex, as a consequence of a variety of factors:
- The soil community has a structure with several trophic positions, in which each group of organisms is being influenced by several others.
- It is not unusual that one species belongs to several trophic positions at the same time, exhibiting different degrees of omnivory, or shows a temporal shift in feeding habits, as with predators that in some periods may change their habits to saprovory or herbivory. Directly related to organic matter decomposition is the fact that many soil animals may be regarded as saprovores as well as microbivores, because virtually all organic matter that is consumed in soil contains microbial colonies.
- Normally, all stages of decomposition occur together in the decomposer subsystem, and the number and types of stages will differ per type of substrate. Hence, the soil system is characterized by the spatial and temporal coexistence of numerous types of microhabitats, differing in intensity of the decomposition processes

occurring. Moreover, the size of microhabitats as experienced by soil organisms will be related with their own size and activity.

It will be clear, that in many cases it is difficult to assess the role that an organism, or a group of organisms, plays in this complex system. These difficulties are the greater since most decomposition processes occur in microsites in soil, that are generally not accessible to direct observations. Yet, for an increasing number of organisms, their part is gradually becoming clearer, as more, and more coordinated research is being devoted to their study, and better methods of research and analysis are being developed.

For a long time Enchytraeidae (potworms) have largely been ignored in this type of research, both in natural and agricultural systems, for a variety of reasons. As regards agroecosystems, the reason for neglecting enchytraeids was the same as for other soil organisms and especially soil fauna: they were simply deemed unimportant. One of the first occasions they attracted attention in agricultural respect, was when they were thought to be possibly injurious to sugar beet (Vejdovský, 1892; Stoklasa, 1897). The most important reasons for not conducting research on potworms, however, were of a more practical nature: difficulties with their extraction from soil, and especially systematic and taxonomic difficulties. Since O'Connor (1955) developed a relatively simple and reliable extraction method, and the taxonomy of Enchytraeidae was revised by Nielsen & Christensen (1959, 1961, 1963), an increasing amount of studies have been carried out, notably in natural habitats, and knowledge on the ecology of these animals is growing. It has repeatedly been demonstrated since then, that enchytraeids may constitute a major element of the soil faunal community in a variety of habitats, also in arable fields, in temperate regions.
As still relatively little is known about the functioning of enchytraeids in ecosystems, and most knowledge originates from more or less natural habitats, an agriculturally oriented research project addressing this field has to deal with a variety of fundamental questions. These issues include population dynamics, species composition, energetical significance, reproductive potential, ecological efficiencies, food preferences, reactions to xenobiotic substances, behaviour in soil etc.

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1.1. Outline of this thesis

From the very beginning, the research reported in this thesis was embedded in the Dutch Programme on Soil Ecology of Arable Farming Systems, an integrated multidisciplinary research programme which focusses on the functioning of differently managed agroecosystems. A general outline of this programme was presented by Brussaard et al. (1988). The main objective is to generate scientific knowledge relevant for the practice of sustainable ('integrated') arable farming. Research is being carried out on the experimental farm 'Dr. H.J. Lovinkhoeve' in the Noordoostpolder, reclaimed from the sea in 1942. Here, experimental fields have been laid out, that have conventional and various types of integrated management. In concordance with the general problems in agriculture mentioned above, the main research themes are:
1. The flows of carbon and nitrogen in the systems and the mechanisms involved.
2. The interactions between soil organisms and soil structure.

The research on Enchytraeidae started out with two derived questions:
1. What do enchytraeids contribute to soil structure evolution in agricultural fields?
2. What is the significance of enchytraeid populations in agricultural fields concerning decomposition of organic matter and nutrient dynamics?

From the beginning, it was clear that to understand the part played by enchytraeids in the fields under study in any quantitative way, it was necessary to conduct a population dynamical study. In view of the relatively scarce ecological knowledge on potworms (chapter 2), it was decided not to rely on the few available data on enchytraeid populations in arable fields, but to carry out a detailed sampling programme. This study yielded data on numbers and biomass of enchytraeids, and their seasonal dynamics, and on species composition, phenology of the populations, and depth distributions (chapter 3).

The results of the population dynamical study were used to calculate production biological parameters such as respiration, production and consumption of the enchytraeids, and to estimate the amount of nitrogen transformed directly by enchytraeids (chapter 3).

The reproductive potential of a species is an important fundamental aspect of enchytraeid biology that has to be understood to be able to predict population development, and to include knowledge of enchytraeid population biology in simulation models. In a series of laboratory experiments, the life-history of *Enchytraeus buchholzi*, the dominant species at the Lovinkhoeve experimental site, was studied. The results of these experiments were used to predict population development under field conditions, and these predictions were compared with actual population development. These experiments are described in chapter 4.

Chapter 5 deals with the development of a method to construct artificial soil cores, used in experiments on the interactions of potworms and soil structure. Such artificial soils were considered a prerequisite for a meaningful study of interactions, as they combine a reproducible soil structure with a near-natural environment for the experimental animals.

In the experiments on the interactions between enchytraeids and soil structure, not the effects of soil structure on potworms, but only the effects of potworms on soil structure evolution were studied, as this was considered the most interesting problem in the fields under study. An experiment was carried out in which artificial soil cores, with and without potworms, and with and without added organic material, were brought into the field. After retrieval the cores were analyzed in various ways to quantify enchytraeid effects on soil structure (chapter 6).

The thesis is concluded with a synthesis (chapter 7).

2. Ecology of terrestrial Enchytraeidae

Abstract

Thus far, little is known about the part enchytraeids play in ecosystems, both natural and managed. In this review of the ecological literature it is shown, that, although it is clear that enchytraeids must constitute an important faunal group in the soil of many terrestrial ecosystems, their part is difficult to quantify because of scanty knowledge of the factors influencing population dynamics and activity. This is because most studies have not been carried out at the species level, while it is clear that there exist appreciable interspecific differences as regards biology and response to environmental factors.

2.1. Introduction

Nowadays, much ecological research is aimed at the revealment of structures and processes occurring within ecosystems, in terms of pools and flows of energy and matter. Notably in research projects aimed at the development of sustainable agriculture, the need for such information is clearly felt (Andrén, 1988; Brussaard et al., 1988). In this type of research, increasing use is being made of simulation modelling, that may help to understand, and eventually intervene intelligently in the functioning of ecosystems. In most simulation models that incorporate faunal elements, parameters like data on the life-history of species, their food preferences, and reactions to abiotic factors play an important part. Particularly in the case of soil fauna, however, it often appears to be difficult to obtain reliable estimates of such parameters. Especially as regards Enchytraeidae, available data are scarce and often hard to find. The purpose of the present review is to gather the available knowledge in this area, and to identify topics where more study is needed. Besides, it is attempted to give an impression of the relative importance of enchytraeids in terrestrial ecosystems. The scope of this review will therefore comprise the ecological aspects of enchytraeid biology and the dynamics and functioning of enchytraeid populations. Extra attention will be given to man-induced influences and to the functioning of Enchytraeidae in terrestrial ecosystems.

In two earlier reviews, O'Connor (1967, 1971) summarized the available knowledge on the ecology of terrestrial Enchytraeidae. Due to an increasing interest in their important role in soil processes, including nutrient cycling, many more studies have been carried out since then. Kasprzak (1982) examined more recent literature on enchytraeid ecology, restricted to agroecosystems. In the two surveys by Dash (1983, 1990) on enchytraeid

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biology, the scope was too broad to cover enchytraeid ecology in any detail. In view of the increased quantity of data, a review of recent advances in enchytraeid ecology would therefore seem appropriate.

It would be too far-reaching to include systematics and taxonomy in the present review. Much in these fields has changed since the work of Nielsen & Christensen (1959, 1961, 1963), and it is clear that in view of the vital importance of systematics and taxonomy for most ecological studies, of the many new species described, and of newly developing insights and methodologies, there is a need for a review of the advances in these fields, too.

2.2. Factors influencing population sizes of Enchytraeidae

2.2.1. Introduction

Terrestrial Enchytraeidae have been recorded from all continents. The habitats they populate range from glaciers to tropical rain forests and from savannas to moors.

Although numerous authors reported on the occurrence of enchytraeids, most records originate from incidental samples or faunistic surveys (e.g. Backlund, 1945; Nurminen, 1965a; 1965b; 1967b; 1970; 1973a,b,c,d,e; Healy, 1979; 1980a,b). Such data, though often worthwhile also from an ecological point of view, typically are obtained from few samples per locality, taken during a restricted time, and, more often than not, using qualitative extraction methods. Density estimates found in this way can not be used to characterize enchytraeid abundances in various habitats, since the estimates are not reliable and the effect of population dynamics are not taken into account. For this, more scarcely gathered census data are needed, based on year-round sampling in well documented sites, and using reliable quantitative extraction methods like those described by Nielsen (1953; 1955a), O'Connor (1955, 1962) and Schauermann (1983). Application of these criteria to the available literature data excludes some otherwise valuable studies like those of Abrahamsen (1972), Solhøy (1975) and Parmelee (1987), but a fairly large number of data remains, recorded in Table 2.1. In this table, the mean abundance of enchytraeids, calculated on the basis of regular samplings, is listed for a number of sites, together with some abiotic characteristics. The depth of sampling varied between the various studies in this table, but as the sampling depth generally was in accordance with the vertical distribution of the populations, these density estimates may be compared.

In Figure 2.1 the abundance data from Table 2.1 are plotted against the environmental variables. Generally, no correlation seems to exist between enchytraeid densities on the one hand, and mean annual precipitation, mean annual temperature, and acidity of the soil on the other. Largest populations have been found in cold to temperate, moist habitats, but this may also be related with the greater amount of data from this region of the world, especially from Europe.

With the exception of the data from Yeates (1968) and this thesis, all sites listed in Table 2.1 have a pH value below 7. This suggests that enchytraeids are mainly found in neutral to acid soils; however, Healy (1980a), among others, has recorded substantial populations of potworms from more alkaline sites, but there are no data on population dynamics in these habitats.

The large variability of the data is conspicuous. While the largest mean abundances have been recorded from moors (Peachey, 1963), moist coniferous forests (Kitazawa, 1977) and dune grassland (Yeates, 1968), lowest densities also were found in moist, temperate habitats (Dash & Cragg, 1972a; Nakamura, 1980). This considerable variability suggests that the species composition of enchytraeid communities, and the physiological and behavioral adaptations of the various species may be important aspects. Unfortunately, in the majority of population dynamical studies on

Table 2.1:Average abundance and environmental correlates of Enchytraeidae in various habitats. Sample depths assumed sufficient to yield the major part of the populations.

Biotope	Country	Precipitation (mm/year)	Air temperature (Ann. mean, °C)	pH	Abundance (Number/m²)	Author
Grassland						
Onobrychido-Brometum	Germany (GDR)	550	8.0		13500	Dunger, 1978
idem, forma typicum	Germany (GDR)	550	8.0		10700	
Epipactis-Seslerietum	Germany (GDR)	550	8.0		2700	
Festuca rubra	Germany (FRG)	1045	6.6		40000	Ellenberg et al., 1986
Dryas site	Norway	850	-1.4		3400	Klungland, 1981
on limestone	England	780	5.6	5.0-5.8	80000	Coulson & Whittaker, 1978
Nardus	England	780	5.6	4.8-5.0	120000	
Ammophila arenaria dune	New Zealand			7.5-8.6	130000	Yeates, 1968
raised beach	Canada	185	-14.9	7.8	9000	Ryan, 1977
sedge-moss meadow	Canada	185	-14.9	6.5	27500	
sedge meadows	Alaska	170	-12.2	4.9-5.4	46100	MacLean, 1980
alpine herbfield	Australia	2160	3.3	4.3-4.9	3250	Wood, 1971
tropical	India	1150	29.8	6.6	3800	Thambi & Dash, 1973
natural	Canada	341	3.6	7.5	30000	Willard, 1974a
irrigated	Canada	341	3.6	7.5	39000	
unused hay-land	Germany (GDR)	710	9.1	4.5	49000	Brockmann, 1984
abandoned field	Sweden	518	5.4	5.8-6.5	23800	Persson & Lohm, 1977
grazed, 10 sheep/ha	Australia	750	14.3	5.6	6000	King & Hutchinson, 1976
grazed, 20 sheep/ha	Australia	750	14.3	5.5	2600	
grazed, 30 sheep/ha	Australia	750	14.3	5.6	2300	
grazed	Japan	1200	7.8		1650	Nakamura, 1980
grazed	Japan	1470	12.5		1400	
cut, fertilized	Japan	1470	12.5		2800	
ley	Sweden	520	5.4	6.3	5500	Lagerlöf et al., 1989
meadow	Poland	533	8.0	6.1-6.5	17000	Ryl, 1977
ryegrass-clover sward	New Zealand	971		5.7-6.2	13800	McColl, 1984
Moor						
fen	Canada	580	2.5	6.4	5600	Dash & Cragg, 1972a
Juncus peat	England	780	5.6	4.4-4.7	145000	Peachey, 1963
Nardus	England	780	5.6	4.8-5.0	71000	
blanket bog	England	780	5.6	4.4-5.0	40000	Standen, 1973
Carex nigra mire	Norway	850	-1.4		22000	Klungland, 1981

Table 2.1, continued

Biotope	Country	Precipitation (mm/year)	Air temperature (Ann. mean, °C)	pH	Abundance (Number/m²)	Author
Forest						
deciduous, moist	Finland	596	3.8	5.1	5700	Kairesalo, 1978
deciduous, dry	Finland	596	3.8	5.4	8000	
deciduous	Canada	580	2.5	6.4-6.7	10000	Dash & Cragg, 1972a
deciduous	Japan	2000	7.0		22000	Kitazawa, 1971
deciduous, beech	Germany (FRG)	1045	6.6	3.3-4.0	108000	Ellenberg et al., 1986
deciduous, beech	Germany (FRG)	1017	8.3	3.8-4.7	46000	Römbke, 1988
deciduous, beech	Germany (FRG)	613	8.7	5.4-6.4	12000	Mellin, 1988
deciduous, beech	Germany (FRG)	700	7.0	6.8-4.3	22300	Schaefer, 1990
deciduous, oak	Hungary	627	11.1		18000	Dózsa-Farkas, 1973b
deciduous, oak-hornbeam	Hungary	643	9.9		22000	Dózsa-Farkas, 1978c
deciduous, oak-hazel	Sweden	570	5.5	5.0-7.0	3800	Axelsson et al., 1984
deciduous, ash-alder	Poland			5.5	29500	Makulec, 1983
deciduous, oak-hornbeam	Poland			4.0	38600	
mixed, pine-oak	Poland			4.1	39500	
coniferous, pine	Poland			3.9	35600	
coniferous, pine	Germany (FRG)	1045	6.6	3.3-4.5	134000	Ellenberg et al., 1986
coniferous	Sweden	600	3.8	4.0-4.6	17000	Lundkvist, 1982
coniferous	S. Finland	620	4.3		12300	Nurminen, 1967a;
coniferous	C. Finland	630	2.4		10400	Huhta et al., 1967
coniferous	Canada	1174	9.0	5.7	5700	Marshall, 1974
coniferous, subalpine	Japan	943	4.2	3.4-5.0	138000	Kitazawa, 1977
coniferous, subalpine	Japan	2000	4.0		10000	Kitazawa, 1971
subtropical rainforest	Japan	2000	15.0		10000	
tropical rainforest	Malaysia	2000	26.5	4.3-4.8	8900	Chiba et al., 1976; Kira, 1976
Liriodendron forest	USA	1265	13.3		6250	Reichle et al., 1975
dry sclerophyll	Australia	889	8.2		250	Wood, 1971
wet sclerophyll	Australia	1144	6.8		1075	
Arable land						
rye	Poland	533	8.0	6.1-6.5	9800	Ryl, 1977
potato	Poland	533	8.0	6.1-6.5	13000	
lucerne	Poland	533	8.0	6.1-6.5	5700	
sugar beet	Poland	533	8.0	6.1-6.5	9600	
sugar beet	The Netherlands	725	8.4	7.5	30000	this thesis
winter wheat	The Netherlands	725	8.4	7.5	12000	
wheat	Canada	341	3.6	7.5	4650	Willard, 1974a
Barley	Sweden	520	5.4	6.3	8100	Lagerlöf et al., 1989

Enchytraeidae no information on species composition and the dynamics of the various species was recorded. As a consequence, species related differences, that might serve as an explanation for the large variability observed, are not known. Inferences can therefore only be drawn for enchytraeids as a group. Given this situation, the data suggest that only extreme values of abiotic parameters may influence the size of populations, and that any threshold values of these parameters will largely be species dependent. Other parameters may also play an important role in the determination of enchytraeid population sizes, such as the amount and quality of primary production (Abrahamsen, 1972; MacLean et al., 1977), the proportion of it entering the soil system as dead organic material, the abundance and activity of the soil microflora, and the incidence and quantitative importance of competition, predation and parasitism.
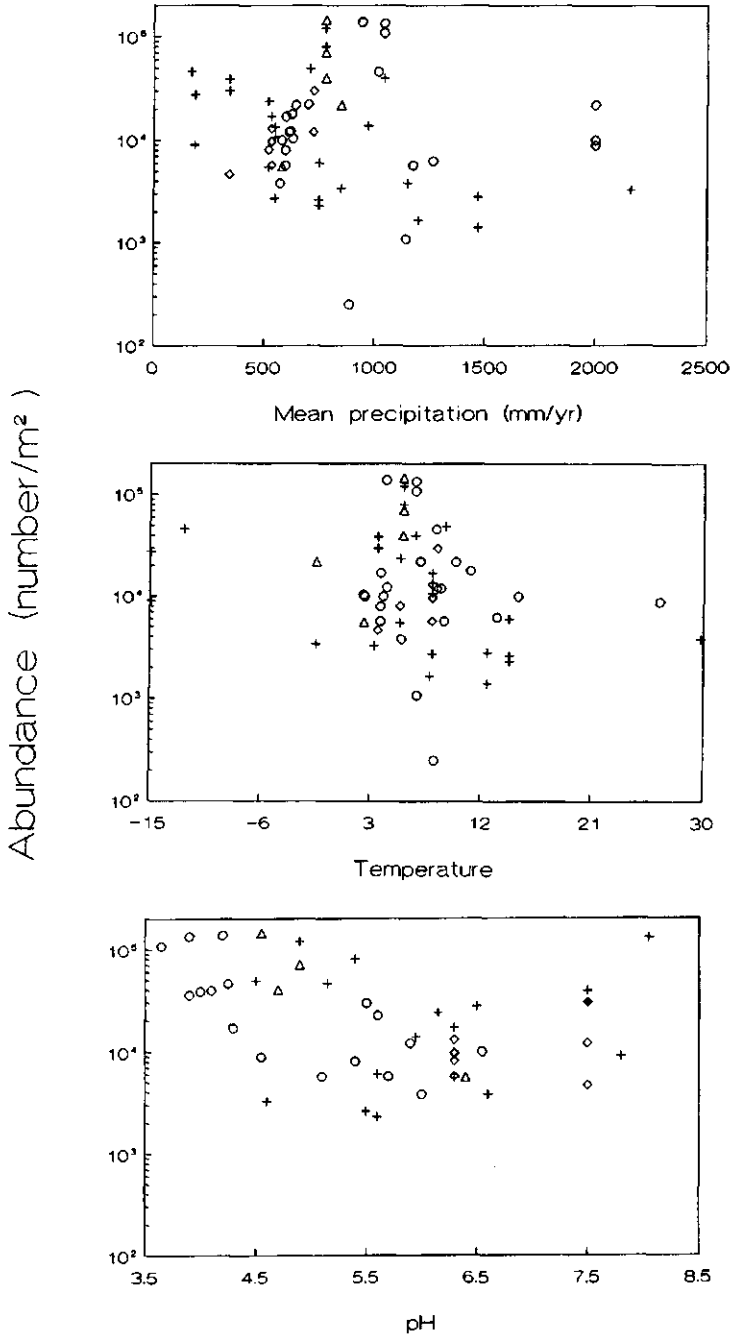
Figure 2.1: Abundance data (y-axes) of enchytraeids from various habitat types plotted against
mean precipitation, temperature, and pH.   +: grassland;   △: moor;   O: forest;   ◇:arable land

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2.2.2. Abiotic factors

2.2.2.1. Moisture

As the enchytraeid epidermis is permeable to water and no protection mechanisms against evaporation are known, it is generally assumed that they are vulnerable to drought and therefore confined to moist habitats. Indeed, large numbers and biomass are found in wet places, and a number of species are restricted to aquatic or very wet terrestrial habitats. Healy (1987) even reported the frequent occurrence of several species (*Marionina riparia*, *Cognettia glandulosa* and *Cernosvitoviella spp.*) in the deep, anaerobic zone of a quaking marsh. Yet, enchytraeids also occur in drier habitats, which may be facilitated by the fact that even in dry soils moist microhabitats may exist, as a consequence of the spatial heterogeneity of the soil. Potworms may actively move to such places, as demonstrated by vertical migration in dry periods (Peachey, 1963; Dash & Cragg, 1972a; Springett et al., 1970; Markkula, 1981, 1982).

There are also indications that at least some species are adapted to survive in drier habitats, like *Fridericia galba* (Dózsa-Farkas, 1977), *Enchytraeus buchholzi* (Trappmann, 1952; Healy, 1980a), *Henlea perpusilla* (Klungland, 1981), *Henlea ventriculosa* (Healy, 1980a), several *Achaeta* species (Healy, 1980b) and the "Ice worm", *Mesenchytraeus solifugus* (Goodman & Parrish, 1971). Abrahamsen (1971) showed that *Cognettia sphagnetorum* was able to survive in rather arid conditions (water potential slightly beneath -1 MPa), provided that the temperature was not above 12°C. Dózsa-Farkas (1977) obtained comparable results with *Fridericia galba*. Willard (1974a,b) reported rather high numbers of enchytraeids from prairie soils in Canada, where potworms represented one of the major groups of invertebrates. As this area was characterized by very dry summers and severe winters, these populations must have been very well adapted to arid conditions. The fairly high densities and number of species Healy (1980b) found during a drought period in France and Spain, and the high numbers reported by Yeates (1967, 1968) from New Zealand dune habitats also suggest the existence of adaptations to dry conditions.

In an investigation of enchytraeid population dynamics in two types of Scots pine stands, Gröngröft & Miehlich (1983) found a significant positive correlation between population densities and the water potential in the moister type of pine stand, whereas in the dryer stand populations increased while the water potential decreased to −0.8 MPa. In both types the same species, *Cognettia sphagnetorum*, dominated, suggesting intraspecific physiological adaptations.

Thus, it would seem that influences of moisture conditions on enchytraeid population sizes depend on several factors, notably species composition and temperature conditions. Enchytraeids may be able to tolerate extremes in moisture conditions by

physiological or behavioral adaptations at the species level, or even intraspecific adaptations. Besides, factors like soil organic matter content and soil structure will undoubtedly be of importance, as these may determine the occurrence of favourable microhabitats in otherwise unfavourable conditions. Predictions of the influence of changes in soil moisture on the development of enchytraeid populations must therefore take these factors in account, and their interactions certainly deserve further study.

2.2.2.2. Temperature

As can be inferred from Table 2.1, Enchytraeidae are found at a wide range of mean annual air temperatures. For some species, notably from the genera *Enchytraeus* and *Lumbricillus*, which can be cultured easily and some of which are being cultured commercially, optimum temperatures for reproduction have been found ranging from 8°C to 28°C (Trappmann, 1952; Ivleva, 1969; Learner, 1972; this thesis). The range of temperatures at which reproduction is possible is still much wider. Trappmann (1952) reported a lower limit of 0.5°C and an upper limit of 37°C for *Enchytraeus buchholzi* and Ivleva (1969) mentioned as limits for good reproductive success in *E. albidus* 8 and 25°C, respectively.

There exist appreciable differences in the reaction of different enchytraeid species to temperature regimes. Klungland (1981) reported a sharp reduction in numbers of *Henlea perpusilla* with decreasing temperatures, while numbers of *Bryodrilus ehlersi* remained unaffected. Healy (1980b) found a high proportion of sexually mature individuals in France and Spain during a dry and warm (temperatures up to 38°C) period. Dózsa-Farkas (1973a) was able to prove experimentally that *Stercutus niveus* was able to survive periods of frost, while *Fridericia*-species were not and had to retreat to deeper soil layers to survive. Some species are adapted to very low temperatures, like the subarctic *Henlea cf. udei* (Smith et al., 1990) and the Alaskan "Ice worm", *Mesenchytraeus solifugus* (Goodman & Parrish, 1971), which lives in the snow cover of glaciers. The nature of such adaptations remains to be investigated, but may be of a biochemical, rather than a structural, origin (Goodman & Parrish, 1971).

It would seem, therefore, that temperature regimes hardly would be a limiting factor for enchytraeid populations to get established. Generally, temperature may be regarded as influencing species composition and population density, rather than presence or absence of potworms.

2.2.2.3. pH

Largest numbers of potworms have generally been found in neutral to acid (pH ±4) habitats. But also in more alkaline (to pH above 8) habitats large populations may be found, as appears from the data of Yeates (1967; 1968) on the enchytraeid fauna of dune grasslands in New Zealand and of Healy (1980a), in an extensive survey of Irish enchytraeids.

The species which, in recent years, was most intensively studied with respect to its response to changes in pH is *Cognettia sphagnetorum*. This is the dominating species in northern and temperate coniferous forests and moors, and the rather extensive literature on this subject originates from the 'acid rain' issue and questions concerning fertilization of forests. In several experiments the pH of forest plots was manipulated by acidification, liming or fertilization (Lohm et al., 1977; Abrahamsen & Thompson, 1979; Bååth et al., 1980a,b; Huhta et al., 1983; Persson et al., 1987). The general trend in these studies was that *C. sphagnetorum* reacted positively to slight acidification, after a temporary reduction in population size, and negatively to liming. Reaction of lumbricids, in this case *Dendrobaena octaedra*, was the reverse. These findings were corroborated in more controlled experiments by Hågvar & Abrahamsen (1980) on colonization of sterile soil samples with adjusted pH values. However, other enchytraeid species in their experiments showed no conclusive or the opposite reaction.

Heungens (1984) conducted a short term experiment with *C. sphagnetorum* and concluded that the effect of changes in pH was insignificant compared with the effect of changes in the electrical conductivity of the soil solution. This may well be an alternative explanation for the shock-effect observed in various field experiments on pH manipulation and fertilizer application.

Standen (1980b) reported a positive correlation between pH and numbers of some species of the genus *Fridericia* and *C. glandulosa*. In an other study Standen (1984) found a negative correlation between abundance of potworms and soil pH, which was largely accounted for by *C. sphagnetorum* and to a lesser extent by *Achaeta affinis*, *A. eiseni* and *C. glandulosa*. Other species showed no negative or even a slightly positive response, and diversity of the enchytraeid communities was positively related with soil pH. Yeates (1968) found large populations of *Hemifridericia* sp. and *Achaeta* sp. in neutral to alkaline (pH 7.5 to 8.6) soil. Healy & Bolger (1984) mentioned pH as one of the most important environmental factors for the distribution of enchytraeid species in Irish wetlands. More species appeared to be acid intolerant than acid tolerant in these habitats.

Thus, it may be concluded that some enchytraeid species, notably *C. sphagnetorum*, clearly are acidophilic or acid tolerant and, possibly because of the absence of competitors, may constitute the dominant mesofauna group in acid habitats. The majority of enchytraeid species, however, prefer slightly acid to alkaline habitats.

2.2.3. Biotic factors

2.2.3.1. Food and feeding

Data on the feeding mechanisms of terrestrial enchytraeids are scarce. A detailed account on the littoral species *Lumbricillus lineatus*, however, was presented by Gelder (1984). This species ingested mineral particles and organic debris with diameters less than 60 μm, an upper limit which was probably determined by the maximum mouth aperture. Small particles could be sucked up directly, but mostly ingestion took place protracting the pharyngeal pad, the surface of which was covered with adhesive secretions from the pharyngeal glands. In this way, the food mass entered the pharynx and was transported to the intestine by peristaltic movements and ciliary action. In truly terrestrial enchytraeids such observations are not known, but available data (Hrabě, 1934; Matschek, 1972) suggest a similar function of the pharyngeal pad in the ingestion of food. Head (1967) observed enchytraeids and nematodes feeding on decaying root cortex, thereby opening channels that allowed mites and collembola to enter.

To assess the impact of enchytraeid feeding on the functioning of the decomposer system, knowledge on the diet and feeding preferences of enchytraeid species is required. An important question in this respect is, wether enchytraeids should be classified as primary or as secondary decomposers, i.e. wether they are saprovores or microbivores.

One approach to this problem was followed by Gotthold et al. (1967) and Gotthold & Koch (1974), who investigated the nutritional requirements of *Enchytraeus fragmentosus* using axenic cultures established earlier (Dougherty & Solberg, 1960; 1961). From the fact that *E. fragmentosus* can be cultured in the absence of either bacteria or fungi, it may be concluded that this species is not an obligatory microbivore and may be capable of obtaining food from sources like dead organic material and root exudates. Also, Palka & Spaul (1970) found in an other species, *Lumbricillus rivalis* (according to Learner, 1972) the capability of digesting carbohydrates, fats and proteins.

To be able to decompose dead organic material, however, it would be necessary for enchytraeids to produce the right enzymes. Some information on this is found in Nielsen (1962) and Dash et al. (1981), who studied enzymes in various species of enchytraeids from Europe and India, respectively. From both studies it appeared that the species studied were capable of digesting di- and some polysaccharides, but that most complex plant substances would become available through microbial action. From feeding experiments with *Cognettia sphagnetorum* in normal and axenic cultures, Latter (1977) and Latter & Howson (1978) arrived at a similar conclusion, i.e. that this species utilized simple organic compounds, possibly through the action of enzymes and/or microorganisms. They found no indications of utilization of microorganisms

proper, but this could not be excluded either. Brockmeyer et al. (1990), using labeled methionine, demonstrated that *Enchytraeus cf. globuliferus* and *E. minutus* digested microorganisms, and that fresh plant material was assimilated distinctly less. Oat bran however (rich in carbohydrates, with deficient cell walls) was taken up to a greater extent than microorganisms.

Pokarzhevsky et al. (1989) pointed out, that in view of the amounts and forms of nitrogen and phosphorus required to maintain soil animal populations, microorganisms must play an important part as a food source. Again, based on $\beta^{13}C$ measurement of earthworm tissue, plant material and soil, Spain et al. (1990) argued that the glos-soscolecid earthworm *Pontoscolex corethrurus* derived much of its tissue carbon from rhizosphere products and microbial biomass. Consumption and digestion of fungi by several enchytraeid species was reported by Dash & Cragg (1972b) and Dash et al. (1980), so that assimilation of at least part of the cell contents of the fungi would seem a real possibility. In the gut contents of 2 out of 3 investigated species, O'Connor (1967) found significantly more fungal material than in the substrate. Dash & Cragg (1972b) also reported on high proportions of fungi in the gut contents of 4 species investigated, and selective feeding on fungal baits in a field experiment.

In an ultrastructural study of the gut contents of *Fridericia striata*, Toutain et al. (1982) found that ingested plant material underwent little change during passage through the gut, while associated bacteria and fungi were lysed soon after ingestion. Gelder (1984) also presumed the utilization of organic compounds and bacteria by *Lumbricillus lineatus*.

Dózsa-Farkas (1976; 1978a) studied the consumption of leaf litter by *Fridericia galba*, *F. hegemon* and *Henlea nasuta*. It appeared that leaves had to be decomposing to be consumed, the preference for degree of decomposition and tree species being not only dependent on species, but also on the season. For tubificid worms, digestion of (Gram negative) bacteria has also been supposed to be quantitatively important (Whitley & Seng, 1976).

Zachariae (1963) reported on enchytraeids consuming collembolan excrements, and Ponge (1984) found, besides plant remains and microorganisms, excrements of oribatid mites in the gut contents and suggested a relation with fungi growing on these excrements. Breakdown of plant material during the passage through the gut has not been observed in the studies mentioned above.

Various authors made a microscopical study of the gut contents of enchytraeids. In several of these studies considerable amounts of silica particles were reported (O'Connor, 1967; Babel, 1968; Matschek, 1972; Gelder, 1984; this thesis). From histo-physiological observations on *Lumbricillus lineatus* by Gelder (1984) it seems probable that such particles are being taken for the microorganisms and organic materials on their surface.

The above mentioned results point to the important part played by microorganisms and their activities in the feeding biology of enchytraeids. Obviously, enchytraeids are

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also capable to utilize easily digestible organic compounds that are produced by plants, or through the activity of microorganisms, but competition with the microflora might be limiting in this respect. As only a restricted number of species have been investigated so far, species related differences in feeding activities remain to be investigated.

In production ecological studies enchytraeids are often considered as being 50% saprovorous, 25% bacterivorous and 25% fungivorous (Persson et al., 1980; Lagerlöf et al., 1989). The available evidence suggests that in this way microbivory may be under-estimated, since at least some species of Enchytraeidae are well adapted to digest microbes, while no species have been found that produce enzymes needed to decom-pose complex vegetable compounds. The assumption of Whitfield (1977) and MacLean (1980), that enchytraeids are 80% microbivorous and 20% saprovorous, may be more realistic.

2.2.3.2. Competition

Little is known about competitive interactions between Enchytraeidae and other soil organisms. Healy (1980a) believed that the abundance of enchytraeids is related to competition, notably with earthworms, for food, and that high densities of potworms are found in cases where almost no competition occurs, as in extremely acid environ-ments. Some species, like Cognettia sphagnetorum, are very well adapted to such environments, and reach high densities there. Competition for food may also occur between enchytraeids and microarthropods, as suggested by Way & Scopes (1968), who found a significant increase in enchytraeid numbers after application of insecti-cides and the resulting severe reduction of microarthropod numbers. From experi-ments by Alejnikova et al. (1975) and Lagerlöf & Andrén (1985), with decomposing manure and barley straw, respectively, it appears that potworms mainly participate in the early phases of decomposition, and are followed by microarthropods. To what extent competition plays a role in this process is unclear as these results may also indicate differences in food preference between both groups.

Several authors have suggested an antagonistic relationship between enchytraeids and earthworms. Nielsen (1955c) believed the ecological status of both groups to be completely different, and their abundances to be negatively correlated. This view is partly corroborated by Górny (1984), who in Dutch polder soil found less potworms in plots inoculated with earthworms, as opposed to control plots. The an-tagonistic effect seemed to be interspecific however, rather than to exist between the two groups. The author supposed that secretions or excrements might play a part in this process.

In a breeding experiment with Eisenia fetida and Enchytraeus albidus, Haukka (1987) observed impeded growth of E. fetida at high temperatures, but faster growth at lower temperatures when E. albidus was present. Moreover, in the presence of

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E. albidus mortality of *E. fetida* increased. As both species showed optimal population development at different moisture levels, it appeared likely, however, that in natural situations they occupy somewhat different niches.

Positive relations between earthworms and enchytraeids have also been observed. Zachariae (1967), for instance, mentioned that potworms consumed the excrements of lumbricids, thereby promoting decomposition of enclosed litter, that could be consumed once more by earthworms. Bhatti (1967) reported associations of enchytraeids with the earthworms *Bimastos parvus* and *Pheretima posthuma*, and with Collembola. Dózsa-Farkas (1978c) found significantly more enchytraeids, notably *Fridericia galba* and *Stercutus niveus*, in earthworm burrows that were filled with litter. The author assumed that the litter in these burrows was attractive for the enchytraeids because its state of decomposition was favourable.

It may be concluded therefore, that some species of Enchytraeidae may have the same requirements as earthworms, but are better adapted to extreme (notably acid) situations, and are not able to compete with earthworms in other situations. The majority of enchytraeid species, however, have more complex relations with earthworms, and thus occupy at least partly different niches. Thus far, no conclusive evidence has been presented for competition between enchytraeid species and other members of the soil fauna.

2.2.3.3. Predators and parasites

The numerous occurrence of Enchytraeidae and the apparent lack of protective mechanisms make them an obvious prey for predatory soil animals. Yet, few studies mention predators of enchytraeids, and no quantitative data on the subject exist. In a review on predatory soil nematodes, Small (1987) listed a number of taxa, notably larger Dorylaimida and Mononchida, that were found to feed on potworms. For most of the species listed, however, it is not clear whether live or dead enchytraeids were consumed. Direct observations of predation on enchytraeids were reported only in the species *Anatonchus amicae* (Coomans & Lima, 1965), *Prionchulus punctatus* (Small, 1987), *Nygolaimus vulgaris* (Thorne, 1930), *Sectonema ventralis* (Thorne, 1930) and *Butlerius degrissei* (Grootaert et al., 1977). Yeates (1968) demonstrated a positive correlation between the abundance of several predatory nematodes and enchytraeids.

Sergeeva (1987) analyzed the gut content of several predatory soil invertebrates with serological methods. It was found that the larvae of the rhagionid flies *Ragio scolopaceus* and *R. tringarius*, especially the smaller ones, probably fed to a large extent on enchytraeids. In the gut contents of small and medium-sized individuals of the centipede *Monotarsobius curtipes* and larvae of the elaterid beetle *Dolopius marginatus* also enchytraeid material was established. The adults of several species of carabid beetles, notably *Abax ater* and *A. parallelus*, were reported by Loreau (1983) to

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prey on oligochaetes (enchytraeids and lumbricids) to a considerable extent. Nielsen (1955b), probably on the authority of Kühnelt (1950), mentions predation by the centipede *Schendyla nemorensis*, but considers its impact marginal. Some mesostigmatid mites may prey on potworms, as Singer & Kranz (1967) successfully used enchytraeids as a food source in cultures of the gamasid mites *Macrocheles superbus*, *M. robustulus* and *Glyptholaspis confusa*, and Heungens (1969) suggested that the gamasid mite *Parholaspulus alstoni* might be an influential predator on enchytraeids in Azalea cultures.

Parasitic organisms associated with potworms have been recorded from various taxa, of which Protozoa seem to be the most frequently occurring. Gelder (1984) reported the occurrence of Sporozoa in the alimentary canal of *Lumbricillus lineatus*. According to Purrini (1983, 1987), enchytraeids are frequently infected by microorganisms, especially in polluted areas, where infection rates may be as high as 70%. Pathogenic agents identified were virus-like organisms, Bacteria, Fungi and Protozoa. Infection could occur in various tissues, and frequently caused lethal diseases. Among the organisms identified, gregarinid Protozoa were the most abundant; these organisms were probably not parasitic, however, and lived as commensals in the gut lumen. Nielsen (1955b) also reported the incidence of Gregarinida in enchytraeids, and noted that the infection rate was at its maximum in the summer half of the year. Ciliates are reported to occur commonly in the gut of oligochaetes (Hartwig & Jelinek, 1974; Righi, 1974). Kunst (1954) reported on several parasitic Rotatoria from the genus *Balatro*, living in the gut of potworms. Taboga (1981) reported facultative parasitism on earthworm cocoons by the saprophytic nematode *Rhabditis terricola*. Although as yet not reported, it would seem only natural that productivity losses through such mechanisms also occur in the Enchytraeidae.

No quantitative data exist on the impact of predation and parasitism on enchytraeid populations. Yet, in view of the qualitative evidence, and notably the variety of predators and parasites reported, it seems obvious that substantial losses through these interactions may occur. Thus, it may be worthwhile to study these processes, that might influence enchytraeid population dynamics to a considerable degree.

2.2.4. Man induced factors

2.2.4.1. Physical habitat changes

Physical habitat changes clearly may influence enchytraeid communities, which specifically may be demonstrated in arable soils. Important factors that play a part in this respect are effects of changes in soil structure, the reduction in the amount of primary production reaching the soil as dead organic material, and the reduced diversity of plant species.

King & Hutchinson (1976, 1983) and Hutchinson & King (1980) studied the effects of sheep stocking intensity on invertebrate communities in Australian pastures. Enchytraeid numbers, biomass and activity were inversely related with the grazing pressure. The effects could mainly be attributed to a reduction in habitable pore space, changes in microclimatological regimes and a reduction in food supply. Brockmann et al. (1980) also reported a significant reduction of enchytraeid densities in a field experiment with soil compaction. A comparable effect of soil compaction was found by Dózsa-Farkas (1987a), who found a significant decrease in enchytraeid densities and diversity in Hungarian hiking trails. One species, *Fridericia conculcata*, however, seemed adapted to these compacted soils, and even showed higher incidence there.

Effects of soil tillage appear clearest when the top soil is inverted. Several investigators (Zimmermann, 1987; Lagerlöf et al., 1989; this thesis) have recorded a more even vertical distribution of Enchytraeidae in ploughed plots, or even a concentration in the deeper layers, where after ploughing the plant remains are to be found. Moreover, Tomlin & Miller (1987) recorded still an even vertical distribution of soil fauna (including enchytraeids) in a formerly ploughed plot at least 25 years after cultivation stopped. While much information exists on the detrimental effects on earthworms of most types of tillage, no indications have been found for such effects on potworms. Probably, this has to do with the smaller size of enchytraeids, rendering them less vulnerable to the tillage action, with relatively less disturbance of their microhabitats, and with their faster mode of reproduction. Less competition with the diminished earthworm populations may, however, also play a part.

2.2.4.2. Chemicals

In assessing the impact of the application of chemical substances (pesticides, fertilizers, pollution) on enchytraeid communities, it is important to discriminate between short-term and long-term effects. Short-term effects concern direct effects through toxicity of the substances applied or changes in the physical and chemical properties of the environment, and are found as long as the foreign substances are present. Long-term effects are manifested through more or less permanent changes in food supply, changes in composition of the soil community or the physical environment, or genetical adaptation within populations.

2.2.4.2.1. Pesticides

Direct toxic effects of the herbicide 2,4,5-T (2,4,5-Trichlorophenoxy acetic acid) on several enchytraeid species have been observed in laboratory experiments by Römbke (1988). It appeared, that the effect was species dependent, *Enchytraeus albidus* being less sensitive than *C. sphagnetorum*, *Marionina cambrensis* and *Achaeta cf. affinis*. Besides, kind and acidity of the substrate were important, the effect being greater in more acid substrates. In field experiments in a beech forest, where 2,4,5-T was bi-monthly applied for a period of two years, these results were only partly corroborated (Römbke, 1988): *C. sphagnetorum* appeared to be hardly influenced here. Enchytraeid abundance and biomass were almost unaffected at low, but reduced at high dosages. After the application had stopped, enchytraeid numbers temporarily were very high, returning to the control level after two years. Chalupský (1987, 1989) reported a similar effect after a single application of atrazine in an orchard, enchytraeid numbers being slightly lowered the first year after the application and higher the second year. In the same experiment continuous application of herbicides reduced enchytraeid densities significantly. The results obtained by Bäumler et al. (1978), with Paraquat and Simazin in forest sites, point in the same direction.

Andrén & Lagerlöf (1983) also reported a negative effect on enchytraeid populations of yearly applications of MCPA, Dinoseb, 2,4,5-T and 2,4-Dichlorophenoxy acetic acid (2,4-D) in pasture, but did not find an effect in arable fields. Again, Weber (1953) could detect no effect of a single application of 2,4-D in arable fields.

From the available data it would seem that a single application of a herbicide may result in initially lower enchytraeid numbers, probably through a direct effect, and followed by temporarily unusually high numbers, presumably through extra availability of dead plant material. These effects were also found in other soil fauna groups like nematodes, mites and collembola (Bäumler et al., 1978; Andrén & Lagerlöf, 1983).

Continuous application of herbicides will lead to a permanent decrease of enchytraeid densities and diversity, as a result of the reduction in weed production and plant species diversity.

Few studies address the effect of fungicides on potworms. Bethke-Beilfuß & Westheide (1987) demonstrated in laboratory experiments sublethal damage, notably reduced fertility and hatching success, caused by Benomyl in two *Enchytraeus*-species, although both species differed markedly in their sensitivity to this fungicide. Römbke (1988, 1989b) found considerable mortality in *E. albidus* at low dosages of Benomyl and PCP (Pentachlorophenol) in laboratory experiments, and even higher sensitivity to PCP with *C. sphagnetorum*, *M. cambrensis* and *A. cf. affinis*.

In field experiments with regular application of Benomyl (Niklas, 1980; Andrén & Lagerlöf, 1983) such effects have not been observed. Niklas (1980) even observed a slight increase in enchytraeid numbers in Benomyl treated plots, which supposedly was connected with a reduction in lumbricid numbers.

Field experiments with bimonthly application of PCP in a beech forest (Römbke, 1988), showed that this fungicide reduced enchytraeid abundance and biomass significantly, and that the populations recovered only slowly after the application had stopped. Not all species, however, reacted in the same way: *C. sphagnetorum*, *Mesenchytraeus glandulosus*, and *Achaeta* sp. were clearly negatively influenced, while others, like *Marionina clavata*, *M. cambrensis*, and *C. cognettii* appeared to be almost insensitive to this fungicide under field conditions.

Again, the fungicides TPN (Chlorothalonil), in a field experiment (Kitazawa & Kitazawa, 1980), and Trichlorotrinitrobenzene (TCTNB), in a pot experiment (Heungens, 1970), proved to reduce enchytraeid numbers considerably.

In view of the probable food relation between fungi and potworms discussed above, a negative indirect effect of fungicides on enchytraeid densities in the field might be expected. As such effect could not be demonstrated in all cases, this may indicate little food selectivity in the species concerned, or a shift in species composition towards less selective species.

Some insecticides and nematicides (Parathion, Carbofuran and Terbufos) have a short-term toxic effect on potworms under laboratory conditions (Bethke-Beilfuß & Westheide, 1987; Hagens & Westheide, 1987; Römbke, 1989b). However, of Nemagon, Aldrin and Lindane (hexachlorcyclohexane, BHC) no clear effects could be detected (Radu et al., 1970). As the test procedures between these investigators varied considerably, these results hardly can be compared.

The results of field observations on the effects of insecticides, acaricides and nematicides often seem inconclusive. Of organochlorine compounds neutral, positive as well as negative influences are reported. Richter (1953), sampling for one year after a single application of an organochlorine insecticide in pine forest, found no effect on

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oligochaete populations, and neither did Grigor'eva (1953), who sampled three months after application. Heungens (1969) also reported no effect of a single application of Aldrin after 12 weeks, and Edwards et al. (1967) detected no effects of Aldrin and DDT during one year in agricultural fields. The organochlorine compound Lindane was reported by Dormidontova (1973) to promote populations of Enchytraeidae in a pot experiment with compost, during two years after treatment. Kitazawa & Kitazawa (1980) also reported larger populations in agricultural plots treated with this insecticide during 4 to 6 months after application. Negative effects of organochlorine compounds on enchytraeid populations, lasting several weeks or months after treatment, were reported for Lindane by Weber (1953), in agricultural soil, and Huhta et al. (1967), in pine forest soil; for Dicofol by Heungens (1970), in a pot experiment; and for Toxaphene by Bäumler et al. (1978), in forest soil. Edwards & Arnold (1966) stated that Hexachlor was toxic to enchytraeids under field conditions.

Organophosphorus compounds are considered by Edwards & Arnold (1966) to have a short term negative influence on enchytraeid populations. Indeed, such short term effects were reported for Parathion by Weber (1953), in agricultural fields, and for Thionazin and Dimethoate by Heungens (1970), in a pot experiment. McColl (1984), on the other hand, sampling monthly for one year after a single application, detected no effects of the organophosphorus nematicide Phenamiphos, and Way & Scopes (1968) reported significantly more potworms several months after treatment of agricultural plots with the organophosphorus insecticide Phorate.

Edwards & Lofty (1971) mentioned a significant reduction in enchytraeid numbers during 8 weeks after application of the carbamate insecticide and nematicide Aldicarb, but no effect of the nematicide Methomyl. Heungens (1970), sampling 10 weeks after application in a pot experiment, found no effect of Aldicarb, and a negative effect of Propoxur; the same author (Heungens, 1969) also reported no effect of the carbamate insecticide Carbaryl 12 weeks after application. McColl (1984) also reported no effects of a single application of the carbamate nematicide Oxamyl during one year after application.

Didden (chapter 3, this thesis) found a significant depression of enchytraeid numbers after a single soil fumigation with the nematicide D-D (1,3-dichlorodipropene), an effect which was disappeared after two months, when densities had returned to the control value. The nematicide Dazomet was reported by Edwards & Lofty (1971) to cause a significant reduction of enchytraeid numbers during 8 weeks after application. Van Den Brande & Heungens (1969), sampling about 10 months after application, found no effect of an annual disinfection with D-D, and Heungens (1969) reported higher enchytraeid densities 12 weeks after application of DBCP.

From the variety of observations under field conditions, it may be concluded, that not only the type and quantity of compound used, and the way of application, but also the time passed since the application of an insecticide or nematicide are important for establishing their effects, and that, moreover, such effects probably are intimately

related with properties of the ecosystem studied. The general impression appears, that both insecticides and nematicides may produce short-term negative effects on enchytraeid densities. In some cases, their application may eventually result in higher potworm densities. As Way & Scopes (1968) suggested, this may have to do with a decrease in competitors or predators, killed by the pesticides. Since little or no research has been conducted on the species level, however, it remains unclear wether application of such pesticides may result in a shift in species composition and/or functioning of the enchytraeid community.

2.2.4.2.2. Fertilizers

As enchytraeids, like most other soil organisms, depend on organic matter as a source of energy and nutrients, it is not surprising that generally higher abundances are reported from sites where organic fertilizers, like crop residues, compost, and manures, are applied (among others Franz, 1953; Alejnikova et al. (1975); Kitazawa & Kitazawa, 1980; Lagerlöf & Andrén (1985)). Possible changes in species composition, resulting from the application of organic fertilizers, have not been investigated.

Effects of the application of inorganic fertilizers on enchytraeid communities may occur directly through changes in the electrical conductivity of the soil solution (Heungens, 1980; 1984) and indirectly through their influence on primary production and the soil microclimate. In a number of studies an initial negative shock-effect was followed by an increase in enchytraeid numbers (Huhta et al., 1967, 1969; Marshall, 1977; Lohm et al., 1977; Hotanen, 1986; Nakamura, 1988). Abrahamsen & Thompson (1979) recorded a change in species composition following urea fertilization of a coniferous forest, indicating a species dependent sensitivity. Marshall (1974) reported significantly lower densities and a more downward distribution of enchytraeids in coniferous forest after a single application of urea, the effect being most marked between the 5th and 8th month after application. Again, in Polish meadows that were fertilized yearly with nitrogen, potassium and phosphorus, Makulec (1976) recorded less enchytraeids, with a more downward distribution, than in control plots. These differences were mainly attributed to differences in soil moisture regime as a result of the application of fertilizers, but there were also indications of a shift in species composition.

Utrobina (1976) investigated the influence of fertilization of potato-fields with ammonia-water, and found that enchytraeid densities sometimes were slightly less in the first months after application, while vertical migration to deeper layers occurred. Afterwards enchytraeid abundances in the treated plots increased above the control values. Standen (1984) showed that enchytraeid biomass in fertilized hay meadow plots was negatively correlated with phosphorus fertilization, but did not find a relation with or-

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ganic fertilization or nitrate. In an earlier study Standen (1982) found negative correlations between the number of enchytraeid species and the applied amount of nitrate and sodium.

As fertilizers are applied to enhance primary production, it might be expected that the soil community, including enchytraeids would benefit from their use. Yet, for several reasons reality seems to be more complex. In the first place, an initial negative effect, which may last for several months, may occur through direct toxic effects or changes in the soil microclimatological regime. Secondly, in most cases where fertilizers are applied, the majority of primary production is removed from the site of production, resulting in less dead organic material entering the soil system. Thirdly, fertilizer applications in most cases result in less diverse plant communities and hence less diverse dead organic material, reducing the number of niches for soil organisms. Thus, application of inorganic fertilizers may in some cases eventually result in higher densities of enchytraeids, and in almost all cases in a reduced species diversity.

2.2.4.2.3. Pollution

Little research has been directed to the impact of pollutants on the enchytraeid fauna. The littoral species *Lumbricillus lineatus* has been found to be quite resistant to oil pollution and even to be capable to excrete oil derivates or store them in its body tissue (Giere & Hauschildt, 1979). This species might be rather exceptional in this respect, as Coates & Ellis (1980) found it to be predominant in the outfall area of a pulp mill, whereas in less contaminated areas the species was replaced by associations of other enchytraeid species. Pirhonen & Huhta (1984) conducted a field experiment in which fuel oil and hydraulic oil was spread on forest soil plots. The enchytraeid population disappeared completely from the fuel oil plots, and started to build up again only after 18 months, but in the plots with hydraulic oil half of the population survived the treatment. Cianciara & Pilarska (1983) reported on a decrease in numbers, or even complete disappearance of enchytraeids in Polish meadows exposed to air pollution from activities of coal industry. Heungens (1970) showed that enchytraeid populations may be sensitive to treatment of the soil with copper sulphate. The influence of increased concentrations of copper, zinc and lead on enchytraeids was studied by Bengtsson & Rundgren (1982) and Bengtsson et al. (1988), who found a strong reduction, both in abundance, number of species and activity. In former refuse tips in Germany, Brockmann (1984) found rapid colonization by potworms, which indicates resistance to extreme conditions in at least some species.

Clearly, the effects of xenobiotic substances on enchytraeid communities are diverse. Due to their permeable epidermis they are sensitive to direct contact, and species of the genus *Enchytraeus*, that are relatively easy to culture, were therefore proposed by Römbke (1989a) and Römbke & Knacker (1989) as test organisms in toxicity tests. On the other hand, as truly soil dwelling organisms, they are less likely to come into direct contact with the substances as such, as long as these are applied on top of the soil. This would imply, that they mainly will be confronted with residues and with indirect effects via other members of the soil community and the living plants. The high incidence of pathogens and parasites in enchytraeid populations in polluted areas, reported by Purrini (1983, 1987), is an example of an indirect effect; apparently the vitality of the enchytraeids is impaired in these areas. As most enchytraeid species seem to be able to reproduce quickly, a single exposure to a harmful compound may be overcome rapidly. Repeated exposure, however, may result in less diverse communities. Important factors determining the impact of xenobiotic substances will therefore be:

- The frequency with which such substances enter the soil system.
- The persistence of the compound and its residues.
- The way of application. Spraying or dusting xenobiotics will influence enchytraeids less readily as does soil fumigation.
- The physiological effects of the xenobiotics, or the ability to deal with them. Earthworms are reported to be capable of biodegradation through hydrolysis of xenobiotic substances, notably organophosphorus compounds (Park et al., 1990). It may be worthwhile to investigate to what extent such mechanisms may be active in enchytraeids.
- The impact on other living organisms that are of importance for the enchytraeids, as food, competitors or predators.
- Soil characteristics (structure, texture, organic matter content, moisture content) will to a large extent determine the residence time and activity of chemical compounds in soil.

2.3. The role of Enchytraeidae in ecosystem functioning

2.3.1. Introduction

The importance of Enchytraeidae in ecosystem functioning will be determined by population sizes, species composition and type and level of activity. Species composition and population sizes are determined by various factors, as described in the previous paragraphs. Furthermore, the spatial and temporal variability of populations will cause the effects of enchytraeid activity to show a related variability. Important aspects of ecosystem functioning where influences of enchytraeid activities may be reflected are nutrient cycling and soil structure.

2.3.2. Soil structure

Among others, Zachariae (1964), Babel (1968), FitzPatrick (1984), Pawluk (1987), and Thompson et al. (1990) have pointed to the occasionally very large portion of enchytraeid excrements in mor and moder humus soils. According to Toutain et al. (1983), these excrements are very persistent, and may establish particulate layers on leaves or needles.

Jegen (1920) and Kubiena (1955) suggested that potworms may produce an extensive, be it spatially restricted, burrow system with a spongy appearance. Singer & Krantz (1967) mentioned a tendency of enchytraeids in laboratory cultures to tunnel through the substrate. Gelder (1984) described the tunneling behaviour of *Lumbricillus lineatus*; the substrate had to be sufficiently moist for the tunneling to occur, and the tunnels were stabilized with a lining of mucus. Górny (1984), on the other hand, stated that terrestrial Enchytraeidae are not able to burrow.

In view of the numerous authors mentioning mineral particles being transported by enchytraeids, whether after ingestion (among others O'Connor, 1967; Babel, 1968; Matschek, 1972; Toutain et al., 1983) or attached to the body surface (Ponge, 1984) it is reasonable to assume an influence of potworms on soil structure. In a field experiment with artificial soils Didden (1990) was able to show a significant effect of *Enchytraeus buchholzi* on air permeability, pore structure and aggregate stability, though the amount of mineral soil transported by this species through ingestion was very low (0.001 - 0.01% of the total soil volume).

2.3.3. Microdistribution of Enchytraeidae

Generally soil animals exhibit a contagious horizontal distribution, which may be correlated with factors like microclimate, the location of food, oviposition and hatching of egg batches, intra- or interspecific attraction or repellency, and competition (Usher, 1976; Rougharden, 1977; Verhoef & Van Selm, 1983; Bradley & Bradley, 1985). For the Enchytraeidae, several authors have examined this pattern in detail (Nielsen, 1954; Peachey, 1963; O'Connor, 1967; Matschek, 1972; Nakamura, 1979). Nakamura (1979) analyzed the distribution pattern of four Japanese species (two *Hemienchytraeus* species and two *Achaeta* species) using the index of patchiness and the ρ-index (Iwao, 1972). These analyses revealed a general trend in the species studied to coalesce in clusters of 200-400 cm², the clusters themselves having a random to slightly regular distribution. When the data of Peachey (1963), for *C. sphagnetorum*, and O'Connor (1967), for a population dominated by *Marionina cambrensis*, are analyzed in the same way, these results are corroborated. Analyses of Nielsen's (1954) data, from populations dominated by *Fridericia bisetosa*, show that the size of the clusters in this species varied from 100-1000 cm². The data of Matschek (1972) for *Achaeta affinis* suggest the occurrence of rather compact (100 cm²) randomly distributed clusters in this species.

In two other studies Nakamura (1982, 1985) established irregular temporal patterns in the aggregative behaviour of *Achaeta camerani* and *Hemienchytraeus bifurcatus*, respectively. Heck (1987) also demonstrated appreciable spatial and temporal differences in degree of clustering for several enchytraeid species. It would seem, therefore, that there may not only exist appreciable specific differences in size of enchytraeid clusters, but also spatial and temporal changes in the distribution pattern, probably related with heterogeneity and changes in biotic and abiotic parameters of the habitat. The importance of environmental factors in the formation of clusters was stressed by Chalupský & Lepš (1985), who demonstrated the occurrence of multi-species aggregation centres in enchytraeid populations.

In some studies (Head, 1967; Heungens, 1968; Way & Scopes, 1968; this thesis) a relation was established between occurrence of potworms and the rhizosphere, suggesting a connection with root exudates and decaying roots, either directly or via the microorganisms. This may be one of the habitat factors conducive to the formation of clusters.

The consequence of the specific and temporal differences in distribution patterns, is that there is no ideal size of sample units to be used in population studies. Abrahamsen (1969) and Abrahamsen & Strand (1970) arrived at the same conclusion, but argued that the size of a sample unit should be such, that the number of units without enchytraeids are low, thus enabling statistical analysis of the data. As a rule, the variation in the data obtained decreases with increasing size of the sample units (Abraham-

sen, 1969), but may increase again above a certain size (Lal et al., 1981). Generally, the size of the sample units is chosen as a compromise between accuracy of the resulting abundance estimates and the amount of work involved, and may range from 10 cm² (Springett et al., 1970) to 42 cm² (Nielsen, 1955a).

Vertical distribution of enchytraeids seems to be mainly related to organic material in the profile on the one hand, and to physical factors on the other. In most natural habitats the largest part of the population occurs in the upper layers, where the bulk of the organic material is located and most of the decomposition processes take place. In a German beech forest (Ellenberg et al., 1986), most enchytraeids occurred in the F–layer during all seasons; here comminution of litter was proceeded furthest. The importance of the location of suitable organic material is corroborated by observations in ploughed agricultural fields, where a large part of the populations can be found at the ploughing depth (Lagerlöf et al., 1989; this thesis).

Physical factors, notably soil moisture (Springett et al., 1970; Dash & Cragg, 1972a; Ellenberg et al., 1986) and temperature (Reynoldson, 1939a, b; Peachey, 1963; Dash & Cragg, 1972a; Erman, 1973; Ellenberg et al., 1986), may induce vertical migration in potworms. Hondru et al. (1971) reported that in Rumanian coniferous forests enchytraeid species groups could be characterized by the amplitude of their vertical migrations. Especially in extreme situations like drought or frost, it will, however, always be questionable what proportion of an actual vertical distribution may be explained by differential mortality (O'Connor, 1957) and what part by vertical migration.

Apart from the distribution of organic material and physical factors, the vertical distribution of potworms may also be species dependent. Gröngröft & Miehlich (1983), for instance, found that *Cognettia sphagnetorum* mainly lived in the litter layer in Scots pine stands, *Achaeta brevivasa* occupying the deeper layer and *Marionina clavata* taking an intermediate position. Healy (1987) recorded 13 enchytraeid species in an Irish quaking marsh, most of which were concentrated at the surface, but *Marionina riparia*, *Cognettia glandulosa* and three *Cernosvitoviella* species were more abundant in deeper layers.

2.3.4. Population dynamics

In two reviews on enchytraeid ecology, O'Connor (1967, 1971) points to soil moisture and temperature as dominating factors in the seasonal fluctuations in enchytraeid populations, either directly via their action on the animals or indirectly through a modification of their environment. In moist situations soil temperature would be decisive, in periods of drought moisture would be a limiting factor. This hypothesis was based mainly on research by Nielsen (1955b,c), O'Connor (1957) and Peachey (1963), all of which was conducted in temperate regions. Since then, more population dynamical

studies have been conducted, ranging from arctic habitats (Solhøy, 1975) to tropical soils (Thambi & Dash, 1973). In most cases the general trend in the seasonal variations in numbers and biomass corroborated the assumption of temperature and moisture being of primary importance for population dynamics.

Yet, there are a number of indications, some of which have been mentioned above, that these two factors do not suffice to explain seasonal dynamics. In a study of the enchytraeid populations in Norwegian coniferous forests, Abrahamsen (1972) found, apart from a correlation with soil moisture, a correlation between the type of vegetation and the time of occurrence of population maxima. In a number of studies deviations from expected population development were recorded, with enchytraeid populations growing in unfavourable moisture and temperature conditions, or declining in favourable conditions. Examples are Peachey's (1963) Nardus-site, a moist habitat, where a peak in population development occurred substantially later than in comparable sites in the same study, and a German spruce forest (Gröngröft, 1981; Gröngröft & Miehlich, 1983), where in continuously dry conditions, after an initial decline in abundance, a considerable population growth was recorded. Another indication is found in the experiments of Matschek (1972), who unsuccessfully tried to increase a field population of *Achaeta affinis* by manipulating soil moisture content and temperature. In population dynamical studies where enchytraeids are identified to species, often interspecific differences in dynamics are recorded (Möller, 1967; Dózsa-Farkas, 1973b; Klungland, 1981; Gröngröft & Miehlich, 1983). Observations like these suggest the existence of intraspecific adaptations to environmental stress, resulting in more complex mechanisms determining population development. Some of these adaptations may be:

- Entering an inactive state under adverse conditions. Cocoons are an example of such an inactive state, offering the embryos protection against adverse conditions. Willard (1972) found enchytraeids in diapause in dry periods and mentioned that in this state they apparently needed some time to become active again. Dózsa-Farkas (1973b,c) described a similar behaviour of *Stercutus niveus*, where during the summer months the animals live in small, dense, inactive clusters in the deeper soil layers, even under favourable temperature and moisture conditions. Ivleva (1969) described the formation of dense clusters (synaporia) of *Enchytraeus albidus* in flooded conditions, and mentioned this as a normal reaction in this species to environmental stress. Adaptations like this may result in smaller numbers of worms counted during certain parts of the year, through a lower extraction efficiency or a more contagious distribution.

When such inactive stages would belong to the phenology of a species, as in the case of *S. niveus*, this would result in recorded abundances developing against expectations that are based on values of physical factors. Indications for this are reported, among others, by O'Connor (1967) and Klungland (1981), who suggested that reproductive activity (cocoon production or, in the case of *Cognettia*

sphagnetorum, fragmentation) would mainly take place in autumn, the cocoons or fragments would hibernate and that population development in spring would result from mass hatching and regeneration of fragments. It is clear that more, experimentally obtained information on this subject would be desirable.
- Acceleration or retardation of the reproductive cycle as a response to environmental conditions. Giere & Hauschildt (1979) reported a large variability in the length of the various phases of embryogenesis in *Lumbricillus lineatus*. Thus, under unfavourable conditions development of the eggs may be retarded, leaving the embryos in the protection of the cocoon. In more favourable situations population growth may be explosive, as a result of the combined effect of acceleration of embryogenesis and simultaneous hatching of cocoons. It is quite conceivable that such a mechanism may operate in a number of enchytraeid species.

2.3.5. Production ecology

The direct contribution of potworms to energy and matter economics in terrestrial ecosystems is reflected in their consumption and assimilation of organic material. Indirect effects on the flows of energy and matter occur through feedback mechanisms to other trophic levels in the soil community and influences on chemical and physical habitat properties.

As the direct contribution of a taxon to the functioning of the decomposer subsystem can not be determined empirically under field conditions, it is quite common to make estimates based on standing stock figures and generalizations about population biology and physiological characteristics. A commonly used approach is based on the amount of energy utilized by a population, the assimilation (Petrusewicz & Macfadyen, 1970; Heal & MacLean, 1975). A somewhat different approach concentrates on the cycling of nutrients, and tries to quantify the amount of nutrients transformed by a population.

Petrusewicz & Macfadyen (1970) proposed the commonly used energy budget equations $C = A + F$ and $A = R + P$, where:

C=consumption, the amount of energy consumed

A=assimilation, the amount of energy used

R=respiration, the amount of energy used for maintenance

P=production, the amount of energy used for tissues, cocoons and excreta.

F=defecation, the amount of energy secreted or excreted

As for respiration, some experimentally obtained data exist for several enchytraeid species (Nielsen, 1961; O'Connor, 1963; Standen, 1973) . As these data were obtained under laboratory conditions, with the worms being rather inactive, actual respira-

tion in field conditions probably will be higher (Wightman, 1977); Hutchinson & King (1980) suggested that factual respiration of Enchytraeidae may be even 20% higher. Nevertheless, the experimentally obtained data have been used by several authors (Reichle, 1971; Persson & Lohm, 1977; Phillipson et al., 1979) to construct common respiration equations for Enchytraeidae, which are widely being applied.

Using an estimate of respiration, the other parameters in the energy budget may be obtained by applying estimates of the ecological efficiencies A/C and P/A (Heal & Maclean, 1975), or, alternatively, by using estimates of relative productivity (P/B, where B=biomass of the population) (Standen, 1980a; Makulec, 1983) and consumption (McBrayer & Reichle, 1971).

Table 2.2 lists mean biomass of Enchytraeidae, estimated respiration and the proportion of total soil respiration accounted for by enchytraeids, for a number of habitats across the world. Biomass figures originally presented as fresh weight were converted to dry weight using the fresh weight/dry weight ratios mentioned by the author (ranging from 5.0 [Standen, 1984] to 7.69 [Ryl, 1977, 1980]), or the value of 5.56 (Edwards, 1967) where no fresh weight/dry weight ratio was mentioned. The proportion of total soil respiration accounted for by potworms was either taken from the publication, or was expressed as a percentage of the energy content of the litter entering the soil (MacFadyen, 1963), if mentioned. Although considerable differences in standing crop and respiration were recorded, these data suggest that the direct contribution of enchytraeids to total soil respiration can be small but significant in all habitats. Highest values are reported for forests, but low values from this habitat fall well below the higher ones in the other habitats. Proportions range from 0.3% to 3.4% of the total soil respiration, but generally not more than 2% of the energy transformations can be attributed directly to potworms.

The construction of an energy budget allows propositions to be made on the proportion of the energy in the primary production utilized by enchytraeids. When the focus is on the cycling of nutrients, however, the contribution of potworms may even be more important, as a concentration of several nutrients, notably nitrogen and phosphorus, takes place from plant material via microbial to enchytraeid tissues, as is illustrated in Table 2.3. Enchytraeids may therefore, like soil fauna in general (Swift, 1977; Pokarzhevsky et al., 1989) play an important role in the turnover of nutrients. The amount of nutrients stored in enchytraeid tissue at any one time will be a significant parameter here. A noteworthy point in this respect is that production efficiency is inversely related to temperature, causing relatively less nutrients to be stored in enchytraeid tissue at higher temperatures. The composition of the food assimilated will also play a substantial part, but data on this subject are largely lacking.

Besides the direct effect of potworms on decomposition processes, there are indirect effects, that may result from enchytraeid influence on the microbial community

Table 2.2: Average biomass and production-ecological data of Enchytraeidae in various habitats.

Biotope	Country	Biomass (g d.w./m^2)	Respiration (kJ/m^2/yr)	Percentage of total soil respiration	Production (kJ/m^2/yr)	Author(s)
Grassland						
arctic meadow	Canada	0.59	10.7	0.3	13.0	Ryan, 1977; Whitfield, 1977
raised beach	Canada	0.18	6.8	1.5	8.1	
sedge meadows	Alaska	0.38	97.1	2.8	120.5	MacLean, 1980
tropical	India	0.02	-	<1.0	>1.2	Dash et al., 1974
grazed, 10 sheep/ha	Australia	0.12	143.0	1.1		Hutchinson & King, 1979
grazed, 10 sheep/ha	Australia	0.10	110.1	1.9		Hutchinson & King, 1980
grazed, 20 sheep/ha	Australia	0.05	62.4	1.0		
grazed, 30 sheep/ha	Australia	0.04	44.0	1.8		
grazed meadow	England	2.16	427.4	2.0		Macfadyen, 1963
hay meadows	England	1.76			77.4	Standen, 1984
meadow	Poland	0.26	132.3			Ryl, 1980
pasture, dry	Denmark	0.53	148.0			Nielsen, 1961
pasture, mesic	Denmark	0.55	193.8			
pasture, wet	Denmark	1.89	651.8			
ley	Sweden	0.34	56.3	0.5	37.5	Lagerlöf et al., 1989
lucerne ley	Sweden	0.54	108.4	0.9	72.3	
Moor						
spruce swamp	Finland	1.73	500.3			Hotanen, 1986
pine bog	Finland	0.09	24.7			
blanket bog	England	2.38	262.0	2.0	48.0	Standen, 1973
Forest						
deciduous, oak	The Netherlands	1.60	251.4	1.8		Van Der Drift, 1974
deciduous	England	3.96	700.0	2.7		Satchell, 1971
deciduous, beech	England	0.34	85.6	1.6		Phillipson et al., 1979
deciduous, beech	Germany (FRG)	1.64	334.9	2.6	502.4	Ellenberg et al., 1986
deciduous, beech	Germany (FRG)	1.31	369.2	3.4	95.0	Römbke, 1988
deciduous, beech	Germany (FRG)	0.42	116.8	1.4	43.8	Mellin, 1988
deciduous, beech	Germany (FRG)	0.60	177.0	1.3	70.0	Schaefer, 1990
deciduous	Japan	0.44	164.8	2.1		Kitazawa, 1971
Liriodendron forest	USA	0.50	156.6	0.6		Reichle et al., 1975; 1977
deciduous, ash-alder	Poland	0.32	71.0	0.9	47.3	Makulec, 1983
deciduous, oak-hornbeam	Poland	0.43	87.6	1.6	58.4	
mixed, pine-oak	Poland	0.45	104.2	1.9	69.5	
coniferous, pine	Poland	0.39	80.3	1.7	53.5	
coniferous	Wales	1.94	626.4			O'Connor, 1963
coniferous	S-Finland	0.23	30.8	0.6		Huhta & Koskenniemi, 1975
coniferous	N-Finland	0.17	8.1	0.3		
coniferous	Sweden	0.46	103.2	0.9		Lundkvist, 1982
coniferous, subalpine	Japan	1.17	383.4	1.6		Kitazawa, 1977
coniferous, subalpine	Japan	0.20	48.3	0.6		Kitazawa, 1971
subtropical rainforest	Japan	0.20	176.1	0.8		
Arable land						
barley	Sweden	0.59	109.3	1.5	73.0	Lagerlöf et al., 1989
lucerne	Poland	0.17	54.4			Ryl, 1980;
rye	Poland	0.11	61.1	0.9		Gołębiowska et al., 1974
sugar beet/wheat	Poland	0.51	77.9			
potato	Poland	0.32	134.8	0.4		
winter wheat	The Netherlands	0.20	58.8	0.8	39.2	this thesis
sugar beet	The Netherlands	0.55	241.2	3.2	160.8	

Table 2.3: Nutrient concentrations (percentage dry weight) in litter, microbial and enchytraeid
material. Legend to authors: 1: Zaboev et al., 1987; 2: Borkott, 1989; 3: Nielsen, 1961;
4: Olechowicz & Mochnacka-Lawacz, 1985; 5: Heal et al., 1978; 6: Swift, 1977;
7: Krivolutzky & Pokarzhevsky, 1977; 8: Flanagan & Van Cleve, 1977; 9: Tischler, 1965;
10: McKercher et al., 1979; 11: Pokarzhevsky et al., 1989; 12: Ausmus & Witkamp, 1973;
13: Cromack et al., 1975.

Nutrient	Plant material	Bacteria	Fungi	Enchytraeidae
Nitrogen	0.44-3.02 [5]	4-12 [9,11,12]	1.3-8 [6,8,9]	5.3-13 [1,2,3,11]
Phosphorus	0.013-0.16 [5]	0.9-3.0 [11,12]	0.09-1.0 [6,8,11]	0.32-1.6 [2,4,10,11]
Potassium	0.013-0.3 [5,7]	1.5-11.5 [11,12]	0.12-4.0 [11]	0.6-0.8 [2,4,11]
Calcium	0.08-0.85 [5,7]	0.95 [12]	0.07-3.3 [12,13]	0.22-0.51 [4,7]
Magnesium	0.031-0.53 [5,7]	0.15 [12]	0.07-0.19 [6,12,13]	0.11-0.4 [4,7]

and its activity; via comminution of organic material, mixing of organic material with the
soil, (selective) grazing on microorganisms and dispersal of spores, (among others:
Toutain et al., 1982; Ponge, 1984; Toutain, 1987; Wolters, 1988). Indirect effects may
also result from selective immobilization or excretion of nutrients like Ca^{++} (Anderson et
al., 1983). Such effects are very difficult to quantify, but are without doubt of major
importance in any ecosystem with an appreciable population of enchytraeids. An
indication for this was presented by Dózsa-Farkas (1978b), who calculated that up to
6.9% of the hornbeam litter produced in Hungarian hornbeam-oak forests passed
through the gut of the enchytraeid species *Fridericia ratzeli* and *F. galba*. Abrahamsen
(1990) established in a microcosm-experiment that the presence of *C. sphagnetorum*
enhanced N-mineralization by 18% on average. About 40% of this difference presuma-
bly originated from decomposing enchytraeid tissue. Wolters (1988) demonstrated that
the effects on decomposition processes of *Mesenchytraeus glandulosus* depend on
factors like population density of the enchytraeids, temperature, growth conditions of
the microflora, and the composition of the microbial community. Differences between
enchytraeid species as regards their feeding activity and food preference must be taken
into account, however, in assessing their function in decomposition processes (Dózsa-
Farkas, 1982).

2.4. Concluding remarks

The long held view of terrestrial enchytraeids as being a rather uniform group of species as regards their reaction to physical or biological factors seems to be obsolete. There are many indications for appreciable inter- and intraspecific variation within this oligochaete family. It may be concluded that the Enchytraeidae show as much ecological variety as any other faunal group. This brings the need for ecological research at the species level. Basic topics to be addressed in this respect are:

- The taxonomy of this group, which badly needs revision and elaboration, since the number of species and even genera is ever increasing, and confusion as regards the identity of species is a common problem, especially in the widespread genera *Enchytraeus*, *Fridericia* and *Marionina*.
- The culturing of enchytraeids, as until now only species from the genera *Enchytraeus* and *Lumbricillus* can be cultured in sufficient numbers to be used in ecological experiments.

The importance of Enchytraeidae in the functioning of terrestrial ecosystems is becoming increasingly clear. Yet, for a good understanding of their role, and a quantitative evaluation of the factors influencing population dynamics and activity, several points urgently need further study, notably:

- An analysis of the physiological and behavioral adaptations of enchytraeid species, which may be of much help in predicting the impact of changes in environmental conditions on enchytraeid populations.
- The interactions between environmental factors (soil factors, xenobiotics) in their effect on enchytraeid populations, as it is clear that the effect of any single factor will also be determined by others.
- Predation and parasitism undoubtedly influence enchytraeid population sizes. Quantitative evaluation of these effects may contribute to the understanding of their population dynamics.
- The feeding biology of enchytraeid species is a field where a lot of work has to be done, before the functioning of enchytraeids in soil systems may satisfactorily be described. There may exist several feeding strategies among potworm species, but as yet only very few species have been investigated in any detail, and insight in the impact of enchytraeid food relations is largely lacking.

Progress in these fields will be very useful for the understanding of ecosystem functioning, and for the development of ecologically sound management practices, both in natural and agricultural ecosystems.

3. Population dynamics and production ecology of Enchytraeidae in high and reduced input farming systems

Abstract

Population dynamics, production ecology and role in nutrient cycling of Enchytraeidae were studied in a 'conventionally' (with high input of energy and matter) managed arable field, along with three fields with various 'integrated' (with reduced input) management types. Mean enchytraeid abundance and biomass ranged from 11000 ind/m^2 to 43000 ind/m^2 and from 0.08 g C/m^2 to 0.42 g C/m^2 respectively. It was calculated that in the conventionally managed field 1.02 - 2.58% of the organic carbon input was respired by the enchytraeids, in fields with integrated management this was 0.52 – 3.73%. Nitrogen flux from the populations was calculated to range from 0.19 - 0.60 g N/m^2/yr.

In general no significant differences in seasonal dynamics, mean abundance and biomass occurred between the investigated fields. However, a pronounced difference between the field managed conventionally and the fields with integrated management was found as regards vertical distribution of the enchytraeids. There are strong indications that the vertical distribution was to a large extent influenced by soil tillage and the distribution of enchytraeids coincided with that of organic fertilizer and plant residues.

During the growing season, the enchytraeid distribution was also influenced by the position of the crop plants, indicating an association of the enchytraeids with root exudates.

3.1. Introduction

The present study is part of the Dutch Programme on Soil Ecology of Arable Farming Systems, which started in 1985. The programme focuses on the regulatory mechanisms of the pools and flows of carbon and nitrogen in the soil, and on the interactions between soil organisms and soil structure. Soil biology, soil physics and soil chemistry and meteorological parameters are measured in high and reduced input farming systems. Conventional agriculture in the Netherlands is considered a high input system. In reduced input (integrated) systems, nutrient inputs, soil tillage and use of biocides are cut down, and biological processes and interactions are expected to be more impor-

tant (Brussaard et al., 1988; Kooistra et al., 1989).

Within the framework of this programme Enchytraeidae are studied with respect to nutrient cycling and soil structure formation. Results on enchytraeid involvement in soil structure evolution have been published elsewhere (Didden, 1990). Here, the data are presented on population dynamics, respiration, production and nitrogen turnover of the enchytraeid populations in four of the fields under study.

Kasprzak (1982) reviewed the existing information on numbers and biomass of Enchytraeidae in agricultural systems, mainly from Poland, Sweden and Denmark. Since then, several more studies have appeared (Andrén & Lagerlöf, 1983; Lagerlöf, 1987; Parmelee, 1987; Lagerlöf et al., 1989). From the available data it appears that enchytraeids may constitute a significant mesofauna group in agricultural ecosystems of temperate regions, and that agricultural practice may considerably influence species composition, numbers and biomass.

As the importance of Enchytraeidae in nutrient cycling was supposed to be related with population development, species composition, and activity and depth distribution of the populations, a detailed population study was carried out over a three year period. To be able to relate management aspects to characteristics of enchytraeid populations, four arable fields, differing in management and/or history, were involved. The data of the population study were also used to calculate respiration, production and nitrogen flows for the enchytraeid populations, and the relative importance of enchytraeids in the four systems under study.

3.2. Methods and materials

3.2.1. The experimental site

The field work for this study was carried out on the experimental farm 'Dr. H.J. Lovinkhoeve' in the Dutch Noordoostpolder, reclaimed in 1942. The soil is a silt loam, with a silt fraction (particles < 16 μm) of about 30%, 10% calcium carbonate and a pH (KCl) of 7.5. At a depth of approximately 25 cm the texture changes into very fine loamy sand. The yearly rainfall is 650 - 800 mm. Crop rotation since 1985 consists of winter wheat - sugar beet - spring barley - potatoes. Types of farm management represented are: conventional (tillage depth 25 cm, high input of fertilizers and of pesticides), integrated (tillage depth 15 cm, 50 - 70% of conventional fertilizer use (depending on crop), green manure, low amounts of pesticides) and integrated with minimum tillage (tillage depth 5 cm).

The sampling comprised the period May 1985 to and including April 1988. Four fields were involved in the sampling programme: one conventional field, two integrated

fields (in this text referred to as 'integrated I' and 'integrated II') and one integrated field with minimum tillage (referred to as 'Minimum tillage'). Two of these fields were in-

Table 3.1:Characteristics of the four sampled fields (after Kooistra et al., 1989).

Field	Conventional	Minimum tillage	Integrated I	Integrated II
Management:				
previous* (since 1953)	Crop residues only	Crop residues plus green manures	Crop residues plus green manures, organic manures, and leys	Crop residues only
present	Conventional	Integrated with minimum tillage	Integrated	Integrated
since	1985	1986	1985	1985
Crops:				
1984	Potato	Potato	Potato	Winter wheat
1985	Sugar beet	Sugar beet	Sugar beet	Flax
1986	Winter wheat	Spring barley	Winter wheat	Winter wheat
1987	Sugar beet	Sugar beet	Sugar beet	Sugar beet
Organic matter (%):				
0 - 10 cm	2.09	2.35	2.67	2.26
10 - 25 cm	2.12	2.37	2.81	2.32
25 - 40 cm	1.90	2.32	2.07	1.87
sampled from:	May 1985	May 1987	May 1985	May 1987

*:contemporary Dutch tillage depth and pesticide use; organic additions as indicated.

cluded at a later stage of the sampling programme.

Table 3.1 lists the characteristics of the four fields. Organic matter input (organic fertilizer and crop residues) was estimated to be 140 g $C/m^2/yr$ in the conventional field and 210 g $C/m^2/yr$ in the other fields.

At the farm air temperature and precipitation were recorded daily. For soil temperature, use was made of data from 10, 20 and 50 cm depth at De Bilt (Royal Dutch Meteorological Institute, circa 80 km from the experimental site), as data on soil temperature at the Lovinkhoeve experimental site were not systematically collected.

3.2.2. Sampling procedure

Enchytraeids were sampled at monthly intervals, unless this was not possible by field conditions such as high rainfall, or when large enchytraeid numbers caused a prolonged elaboration time for the sample units. Per field per sample date 6 - 10 cores were taken. The procedure followed a random sampling design, except during the growing season, when the sample units were distributed within and between plant rows.

A 40 cm long steel split corer was used, containing 2.5 cm high plastic rings with

an inner diameter of 6 cm. Up to July 1986 sampling depth ranged between 25 and 32.5 cm, afterwards it was 40 cm. The cores were divided in 2.5 cm slices in the laboratory. Extraction was carried out according to O'Connor (1955), with application of increasing light and heat half an hour after the start of extraction and a total extraction time of 3 hours.

The collected animals were examined alive under a microscope, measured to the nearest mm, and identified following Nielsen & Christensen (1959, 1961, 1963) and the available more recent species descriptions. Presumably new species were assigned by characters. For all specimens the life stage was recorded as juvenile or adult.

From May 1985 to and including October 1985, hence before the start of the present management type, sampling was less detailed. Not all slices in a sample unit were extracted and the extracted potworms were not identified to species (Marinissen, unpublished). To be able to use the 1985 samples together with the subsequent samples, linear regression was used to estimate numbers and biomass of animals in slices that had not been extracted.

3.2.3. Analysis of the data

For the analysis of the data and presentation of the results, the soil profile was divided in 4 sub-layers: 0 - 5 cm, 5 - 10 cm, 10 - 25 cm, and 25 - 40 cm.

The sampling data were statistically analyzed using analysis of variance (after logarithmic transformation of the data) and using distribution-free methods.

Canonical correspondence analysis (program CANOCO, Ter Braak, 1987) was used to analyze the response of abundance and biomass of the various species and of the enchytraeid populations as a whole, to quantitative environmental variables (such as temperature and precipitation) and qualitative environmental variables (such as management type). The depth distribution of the enchytraeid populations was evaluated in these analyses by treating each species as four different species, one for each sub-layer discerned in the soil profile. As the time that elapsed from sampling till extraction of a sample unit could be of some influence in the analyses, it was included as a covariable.

3.2.4. Production ecological calculations

In May and June 1987 and January and February 1988 a number of enchytraeids from the field sampling were freeze-dried, and their individual weights determined on a Cahn electrobalance. Assuming a power function to give the best fit for the data (Abrahamsen, 1973), linear regression equations of length on weight were calculated (after logarithmic transformation of the data) for the species occurring at the Lovinkhoeve

experimental site. These equations were used to calculate the standing crop of enchytraeids.

To estimate the standing crop in 1985, it was assumed that the species composition in the various layers of the soil profile was the same as the average species composition in the next years.

Respiration was calculated from the standing crop estimates and the data on soil temperature, applying the approach of Persson et al. (1980), who used the formula $Q=33.6W^{0.67}$, where

$Q = mm^3\ O_2\ ind^{-1}\ hr^{-1}$

W = body weight (g fresh weight)

The same authors used a fresh weight/dry weight ratio of 6.67 and a Q_{10} of 2 above 5°C, assuming a linear decrease in oxygen consumption to zero level between 5°C and -5°C. For each enchytraeid species occurring in the field, a linear course in numbers in every length class between sampling dates was assumed. Soil temperatures were taken to vary linearly between the various depths of measurement (with air temperature prevailing at 10 cm above ground). In this way estimates of respiration for the enchytraeid populations were calculated on a daily basis for various depths.

Consumption and production were calculated from the respiration data. Use of the efficiency quotients proposed by Heal & MacLean (1975), assuming enchytraeids to be 20% saprovorous and 80% microbivorous (Whitfield, 1977; MacLean, 1980), resulted in the following efficiency quotients: P:C=0.112 and R:C=0.168 (P=production, C=consumption, R=respiration). Consumption and production were expressed as amounts of C or N. A C-content of 41% (dw) was assumed for organic matter input in the field and of 50% (dw) for enchytraeids (Lundkvist, 1982; Borkott, 1989). N-content (dw) of enchytraeids was taken to be 13% for Fridericia species and 11% for other species (Nielsen, 1961; Lundkvist, 1982; Borkott, 1989).

N-flux from enchytraeid tissue was calculated using the daily figures on standing crop and production. A net increase of nitrogen in enchytraeid tissue was taken to occur, when an increase in standing crop equalled or exceeded calculated production. In other cases it was assumed that a net decrease of the amount of nitrogen took place.

The data were compared on a year's basis. The data for Conventional and Integrated I in 1987 were used to estimate numbers and biomass for the period January to May in 1985 (for Conventional and Integrated I) and 1987 (for Integrated II and Minimum tillage), for which data were lacking.

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3.3. Results

3.3.1. Composition of the enchytraeid fauna

Table 3.2 lists the proportional composition of the enchytraeid fauna in numbers and biomass and the mean diversity and evenness in the upper 40 cm of the two, respectively four investigated fields for the two years of detailed sampling.

Table 3.2: Proportional abundance (A) and biomass (B) per year of the various enchytraeid species in the upper 40 cm of the investigated fields and mean diversity (Shannon's entropy) and evenness (Hurlbert, 1971) in the period May to and including April of the next year.

Species	Conventional		Minimum tillage		Integrated I		Integrated II	
1986	A	B			A	B		
Enchytraeus buchholzi	55.57	30.07			71.20	33.85		
Henlea perpusilla	10.63	9.42			5.99	6.01		
Henlea ventriculosa	-	-			0.87	2.28		
Buchholzia appendiculata	5.47	6.25			0.52	0.81		
Fridericia bulboides	-	-			0.74	1.26		
Fridericia sp. A	4.19	10.74			13.42	40.30		
Fridericia sp. B	13.55	35.93			3.58	11.46		
Fridericia sp. C	10.58	7.59			3.50	4.00		
Marionina sp.	-	-			0.17	0.04		
No. of species	6				9			
Diversity	1.06				0.92			
Evenness	0.64				0.47			
1987	A	B	A	B	A	B	A	B
Enchytraeus buchholzi	63.06	28.53	47.59	20.11	67.63	28.17	36.10	16.08
Henlea perpusilla	5.90	5.41	15.28	15.59	8.21	7.67	20.15	23.37
Henlea ventriculosa	5.08	11.37	0.95	3.16	4.83	26.53	0.19	1.81
Buchholzia appendiculata	1.66	2.37	11.62	10.64	3.20	4.58	16.67	15.59
Fridericia bulboides	0.49	0.54	1.86	2.09	1.03	1.90	15.72	16.60
Fridericia sp. A	1.48	4.07	3.52	9.78	9.17	21.84	9.24	23.73
Fridericia sp. B	15.54	42.33	15.08	35.38	3.48	6.86	1.44	2.61
Fridericia sp. C	6.78	5.37	4.09	3.24	2.35	2.46	0.45	0.20
Marionina sp.	-	-	-	-	0.11	0.01	0.04	0.00
No. of species	8		8		9		9	
Diversity	1.05		1.36		1.24		1.43	
Evenness	0.63		0.71		0.60		0.69	

In total 9 species of Enchytraeidae were recorded; the lowest number (6) of species occurred in the conventional field in 1986. In all fields *Enchytraeus buchholzi* was the most abundant species, with *Henlea perpusilla* and *Fridericia* species being second in abundance. As regards biomass, *E. buchholzi* was, due to its comparatively small size, not dominating; *Fridericia* species generally accounted for the larger part of the biomass.

Diversity was low in all fields, as was evenness, reflecting the low number of species and the numerical dominance of *E. buchholzi*. In 1987 diversity in Integrated I was significantly increased as opposed to 1986 (P < 0.05, Mann-Whitney test). For the conventional field this was not the case; in 1987 this field had lowest values for diversity and evenness of all four investigated fields, the differences in diversity with Minimum tillage and Integrated II being significant (P < 0.05 and P < 0.01 respectively, Mann-Whitney test).

3.3.2. Vertical distribution and relation to plant position

Figure 3.1: *Proportional vertical distribution, partitioned in occurrence in or between plant rows (sample units on intermediate positions discarded), in the upper 0.4 m of the profile during the growing season 1986 (crop: winter wheat). Values for the 0.1 - 0.25 m and 0.25 to 0.4 m divided by 3 for comparability with upper layers. Numbers denote mean number/m² on the sampling date.*

☐ *Between rows*   ■ *In plant rows*

Figs. 3.1 and 3.2 show the proportional vertical distribution of enchytraeid numbers in the sub-layers of the 0 - 40 cm layer, partitioned in occurrence in or between plant rows, for the growing seasons of 1986 and 1987, respectively. In the integrated and minimum tillage fields the enchytraeids were generally concentrated in the upper 10 cm
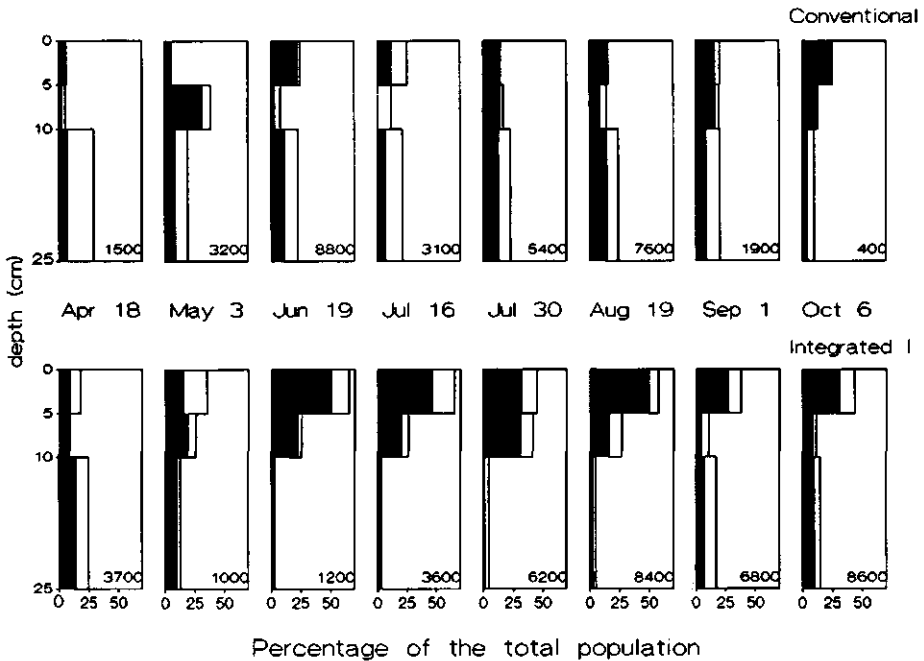
42
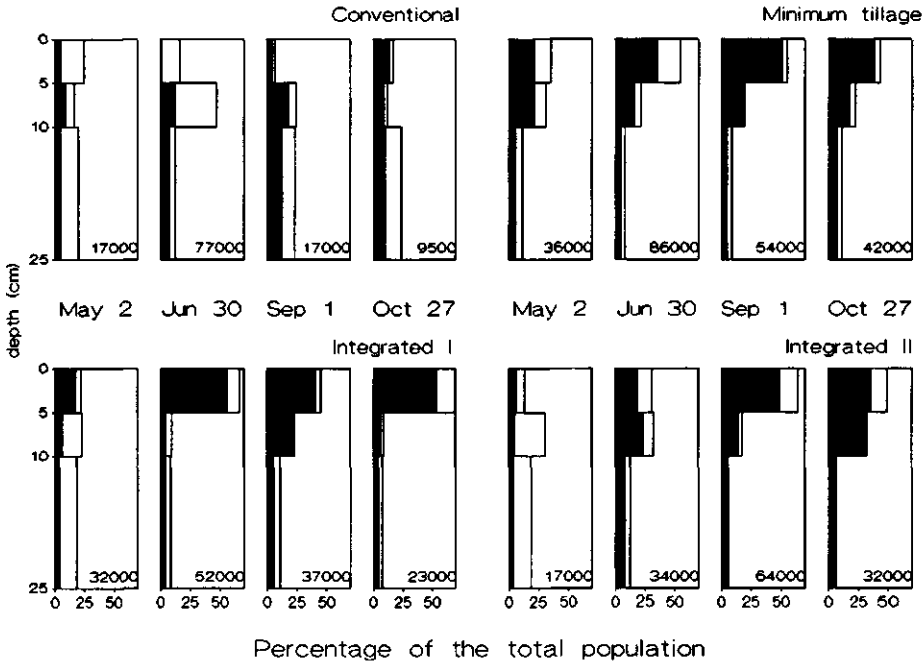
Figure 3.2: *Proportional vertical distribution, partitioned in occurrence in or between plant rows (sample units on intermediate positions discarded), in the upper 0.4 m of the profile during the growing season 1987 (crop: sugar beet). Values for the 0.1 - 0.25 m and 0.25 to 0.4 m divided by 3 for comparability with upper layers. Numbers denote mean number/m² on the sampling date.*

☐ *Between rows*   ■ *In plant rows*

of the soil profile (P < 0.01, Friedman test). In the conventional field significantly more animals occurred in the 10 - 40 cm layers during 1986 (P < 0.05, Friedman test); during 1987 no significant differences were found between the various layers of this field.

An effect of plant position is seen clearly in both years: in the upper 5 to 10 cm layers generally more animals were found in the plant row than between rows. Analy-· sis of variance, with plant position and time as factors, showed in most cases a significant (P < 0.05) effect of plant position in these layers. In Conventional the interaction of time and plant position was significant (P < 0.05) in the 0 - 5 cm layer in 1987. In Integrated II no significant effects of plant position could be established, due to large variability in the data.

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3.3.3. The canonical correspondence analyses
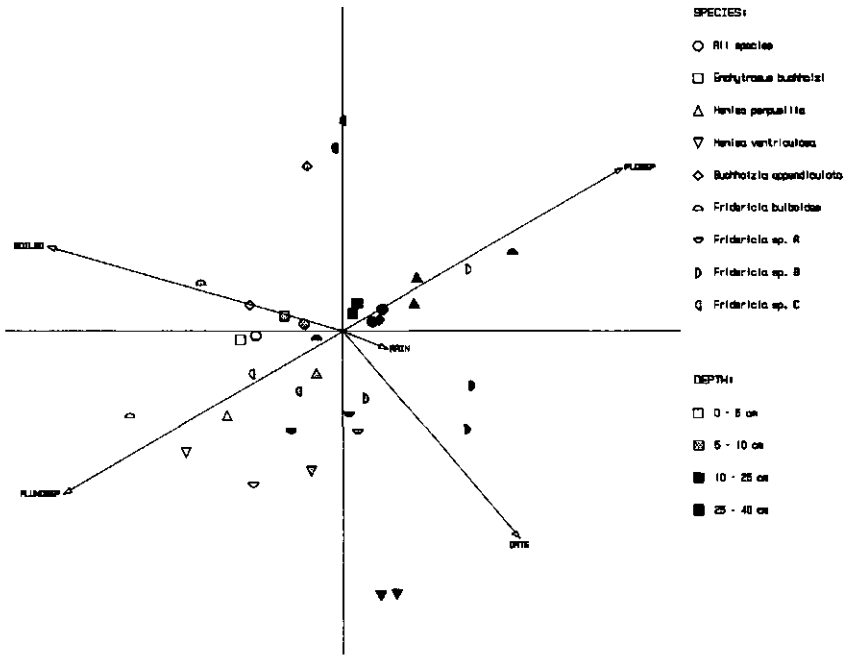
Figure 3.3: Ordination diagram based on canonical correspondence analysis of Conventional and
Integrated I. 78.9% of the variance accounted for. Scale of environmental variables -0.2 to 0.2;
scale of species -4 to 4. Eigenvalue of first axis 0.092, of second axis 0.043. Environmental
variables (arrows) are: DATE: number of days from the start of the sampling program; RAIN:
precipitation of the three weeks preceding a sampling date; SOIL20: mean soil temperature at
20 cm of the three weeks preceding a sampling date; PLDEEP: Conventional (conventional
ploughing depth); PLUNDEEP: integrated I (reduced ploughing depth).

Fig. 3.3 presents the ordination diagram for the first two axes in the analysis of the
abundance data of both years of detailed sampling for Conventional and Integrated I
(accounting for 78.9% of the variance) and fig. 3.4 the diagram from the first two axes in
the analysis of 1987, for all fields (accounting for 69.9% of the variance). In these
diagrams, projection of the head of an arrow on an axis indicates the relative impor-
tance of a factor for that axis, and projection of the species points on an arrow indicates
the response of the enchytraeids to that factor. For example: in Figure 3.3 the arrow for
"DATE" (i.e. no. of days past since the start of the sampling programme) runs south- ·
east. Thus, for a particular soil layer, a species occurs most frequently early in the
sampling programme if its symbol lies in the North-West part of the diagram, and later
in the sampling programme if it lies in the South-East part.

The main factors influencing enchytraeid abundance, species composition and
vertical distribution appear to have been the type of field, the soil temperature and the

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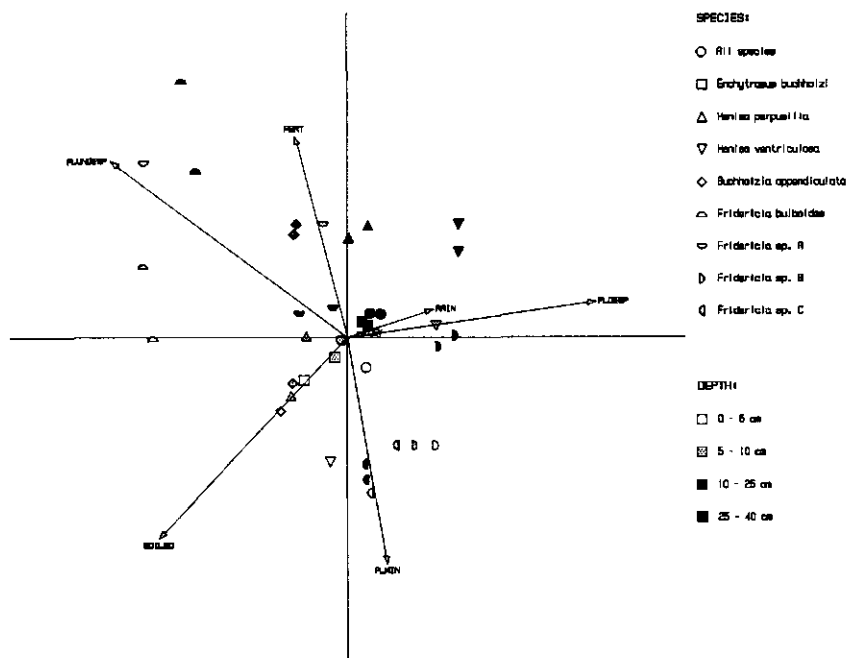
Figure 3.4: Ordination diagram based on canonical correspondence analysis of all sampled fields. 69.9% of the variance accounted for. Scale of environmental variables -0.2 to 0.2; scale of species -6 to 6. Eigenvalue of first axis 0.075, of second axis 0.052. Environmental variables (arrows) are: RAIN: precipitation of the three weeks preceding a sampling date; SOIL20: mean soil temperature at 20 cm of the three weeks preceding a sampling; PLDEEP: Conventional (conventional ploughing depth); PLUNDEEP: Integrated I and Integrated II (reduced ploughing depth); PLMIN: the integrated field with minimal tillage; LEY: the field which had leys in the former rotation (Integrated I); FERT: the fields with a conventional history (Conventional and Integrated II).

factor time (fig. 3.3, "DATE"), and much less the amount of precipitation of the preceding 3 weeks.

There also were considerable interspecific differences in the response to the factors included in the analyses. The conventional field (indicated by "PLDEEP") was characterized by populations occurring in the 10 - 40 cm layer, while in the other fields populations were concentrated in the 0 - 10 cm layer. At higher soil temperatures most species tended to occur near the surface, at lower temperatures in the deeper layers, except for *Fridericia sp. A* and *F. sp. C*, that were found more often in the 5 - 10 cm layer at low temperatures.

Figure 3.3 demonstrates a considerable change in time for the occurrence of some species. In the course of time *Fridericia sp. C* was found less, especially in the 10 – 40 cm layer, and *Henlea ventriculosa* occurred more often in the 10 - 40 cm layer. *Buchholzia appendiculata* occurred less in the 5 - 10 cm layer in the course of the

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sample programme.

Figure 3.4 shows that the fields with a conventional history (Conventional and Integrated II, indicated by "FERT") may be characterized by *F. bulboides* and *B. appendiculata* occurring more frequently in the 10 - 40 cm layer and *F. sp. A* in the 0 – 10 cm layer. The integrated fields, designated with "PLUNDEEP", were characterized by the more frequent occurrence of *F. bulboides* and also by *F. sp. A.* in the 0 – 10 cm layer. The integrated field with minimum tillage ("PLMIN") was distinguished by *H. ventriculosa* and *F. sp. B.* in the upper layer and by the more frequent occurrence of *F. sp. C.*

3.3.4. Relations between body weight and length

The data on length and weight of the freeze-dried potworms were used to calculate regression equations of length on dry weight for the species found in the investigated fields. Table 3.3 lists the resulting equations, and the number of specimens used in the calculations. For *Marionina sp.*, which very sporadically occurred, the equation for *Enchytraeus buchholzi* was used.

Table 3.3.: Regression equations for length on dry weight, correlations (R), and numbers of observations (N) for enchytraeid species found at the Lovinkhoeve experimental site. W = dry weight in µg; L = length in mm.

Species	Equation	R	N
Enchytraeus buchholzi	$W=0.924*L^{1.977}$	0.904	567
Henlea perpusilla	$W=0.810*L^{2.068}$	0.915	213
Henlea ventriculosa	$W=0.425*L^{2.620}$	0.956	36
Buchholzia appendiculata	$W=1.341*L^{1.776}$	0.907	38
Fridericia bulboides	$W=0.856*L^{1.912}$	0.956	38
Fridericia sp.A	$W=1.316*L^{1.677}$	0.937	129
Fridericia sp. B	$W=1.528*L^{1.703}$	0.907	196
Fridericia sp. C	$W=1.668*L^{1.569}$	0.933	19

3.3.5. Population dynamics

Figures 3.5, 3.6 and 3.7 show the dynamics of enchytraeid numbers and biomass in the upper 40 cm of the soil profile, and the depth distributions of the populations. For 1985 and 1987 the general picture is that maxima in abundance and biomass occurred in spring/early summer, and minima in late winter. In 1986, with a dry spell in June and July, low numbers also occurred in summer (Figures 3.5 and 3.6). As regards the

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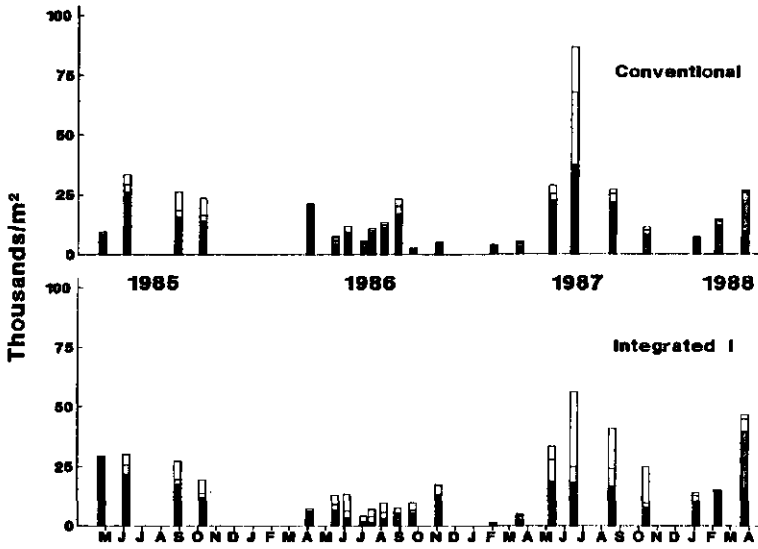
Figure 3.5: Mean abundance (numbers/m²), partitioned in various layers, from May 1985 to April 1988 in Conventional and Integrated I.

| | 0 - 5 cm | | 5 - 10 cm |
| | 10 - 25 cm | | 25 - 40 cm |
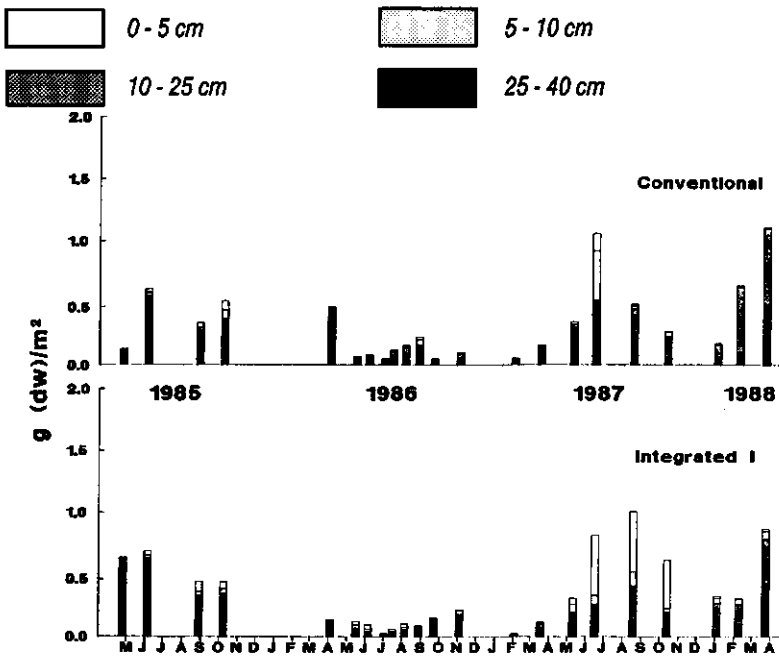
Figure 3.6: Mean biomass (g dw/m²), partitioned in various layers, from May 1985 to April 1988 in Conventional and Integrated I.

| | 0 - 5 cm | | 5 - 10 cm |
| | 10 - 25 cm | | 25 - 40 cm |
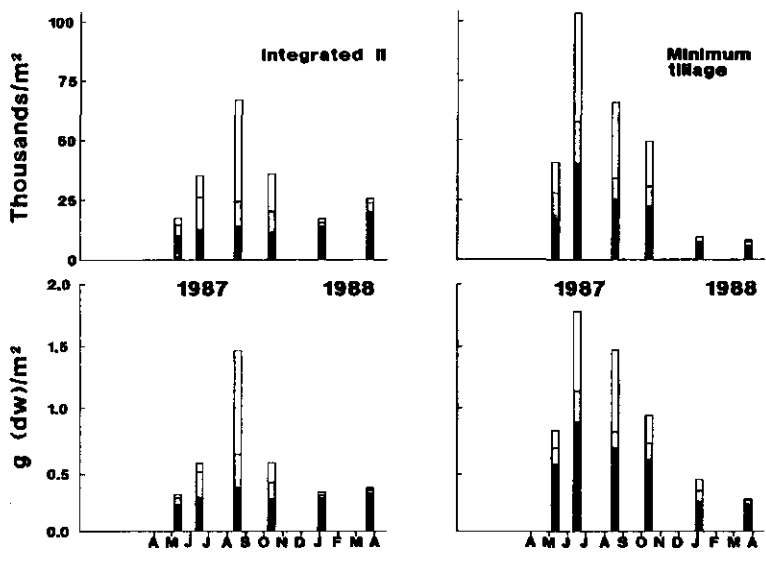
Figure 3.7: Mean abundance (numbers/m²) and biomass (g dw/m²), partitioned in various layers, from May 1987 to April 1988 in Integrated II and Minimum tillage.

☐ 0 - 5 cm	▨ 5 - 10 cm
▦ 10 - 25 cm	■ 25 - 40 cm

sampled profile as a whole, largest numbers and biomass were found in the minimum tillage field (P < 0.05, Kruskall-Wallis test), while the other three fields generally showed no significant differences in abundance or biomass. A clear exception to this occurred in the conventional field, where numbers and biomass were sharply declined in October 1986, three weeks after the soil in this field had been fumigated (1,3-dichloropropene, 150 l/ha).

Numbers and biomass in the conventional field were generally distributed deeper than in the other three fields, where populations were more concentrated in the upper layers. This was corroborated by analyses of variance of the data with time, soil temperature at 20 cm and precipitation of the preceding 3 weeks as covariables. These analyses showed a significant effect (P < 0.05) of the field for the upper 5 to 10 cm and for the 25 - 40 cm layers and highly significant (P < 0.001) effects of the interaction of field and depth. The minimum tillage field constituted an exception to this; on several occasions large populations not only occurred in the upper layers, but also in the 10 – 40 cm layers of this field.

3.3.6. Respiration and production

Table 3.4 lists mean abundance and biomass, and calculated respiration and consumption in g C/m^2 for 1985 to 1987 at various depths in the profile. In the conventional field numbers, and even more biomass, respiration and consumption, were concentrated in the 10 - 40 cm layer, indicating more and larger animals in these layers as compared with the 0 - 10 cm layers. This phenomenon was most extreme in the (relatively dry) year 1986. In integrated I the situation appears to have been more complex: in 1985 by far the larger part of the population was found in the 10 - 40 cm layers. In 1986 the proportion of the population in the 0 - 10 cm layer was increased relative to 1985 and in 1987 the greater part of the population occurred in these upper layers, showing a distribution that concurred with the other two integrated fields in this year.

Table 3.4: Mean abundance (A) in numbers/m^2 and biomass (B) in g C/m^2 and estimates of respiration (R) and consumption (C) as g C/m^2/yr in three consecutive years.

Field	Depth	1985 A	B	R	C	1986 A	B	R	C	1987 A	B	R	C
Conventional	0 - 5 cm	3465	0.013	0.285	1.699	1465	0.007	0.098	0.582	3538	0.013	0.348	2.073
	5 - 10 cm	1507	0.010	0.176	1.049	985	0.007	0.090	0.537	5489	0.035	0.765	4.551
	10 - 25 cm	7045	0.080	1.283	7.636	6552	0.064	0.687	4.089	9068	0.073	1.422	8.467
	25 - 40 cm	5810	0.170	0.961	5.718	4388	0.040	0.549	3.268	5750	0.061	1.080	6.428
	0 - 40 cm	17827	0.273	2.705	16.102	13390	0.118	1.424	8.476	23845	0.182	3.615	21.519
Integrated I	0 - 5 cm	3130	0.015	0.343	7.040	2382	0.008	0.170	1.013	10618	0.112	1.843	10.968
	5 - 10 cm	1804	0.011	0.213	1.270	1792	0.009	0.153	0.912	3922	0.024	0.493	2.936
	10 - 25 cm	9327	0.076	1.290	7.681	4112	0.038	0.452	2.689	8474	0.070	1.311	7.802
	25 - 40 cm	7810	0.180	1.305	7.769	2565	0.025	0.307	1.829	2558	0.034	0.524	3.117
	0 - 40 cm	22071	0.282	3.151	18.760	10851	0.080	1.082	6.443	25572	0.240	4.171	24.823
Integrated II	0 - 5 cm									12054	0.096	2.038	12.130
	5 - 10 cm									6392	0.056	1.157	6.888
	10 - 25 cm									6812	0.074	1.324	7.880
	25 - 40 cm									2016	0.030	0.433	2.580
	0 - 40 cm									27274	0.256	4.952	29.478
Minimum tillage	0 - 5 cm									16477	0.131	2.733	16.268
	5 - 10 cm									6890	0.050	1.049	6.247
	10 - 25 cm									11233	0.128	2.222	13.225
	25 - 40 cm									8407	0.113	1.819	10.829
	0 - 40 cm									43007	0.422	7.823	46.569

Compared with the years 1985 and 1987, 1986 seems to have been an extreme year, where the enchytraeid population was not much developed and consequently respiration and consumption were low. In this extreme year the population was better developed in the conventional field than in Integrated I, while in both other years the reverse was the case.

The estimates of respiration and consumption (Table 3.4) were lowest for integrated I in 1986 (1.08 and 6.44 g C/m^2) and highest in Minimum tillage in 1987 (7.82

and 46.57 g C/m^2). This corresponds with 0.52% to 3.73% of the organic carbon input (from organic fertilizer and crop residues) respired, and 3.07% to 22.18% of it consumed by the enchytraeids in the integrated fields. In the conventional field these ranges were 1.02% to 2.58% and 6.05% to 15.37% respectively.

3.3.7. Nitrogen turnover

In Figures 3.8 and 3.9 the calculated nitrogen turnover for bimonthly periods is shown for Conventional and Integrated I. These figures indicate that there was an appreciable nitrogen flux from the enchytraeid populations, with the exception of the February/March period in 1987 and 1988, when nitrogen was accumulated in the populations. As with numbers, biomass and respiration, most of the flux occurred in the superficial (0 - 10 cm) layers in integrated I from 1986 onwards, and in the deeper (10 – 40 cm) layers in the conventional field.
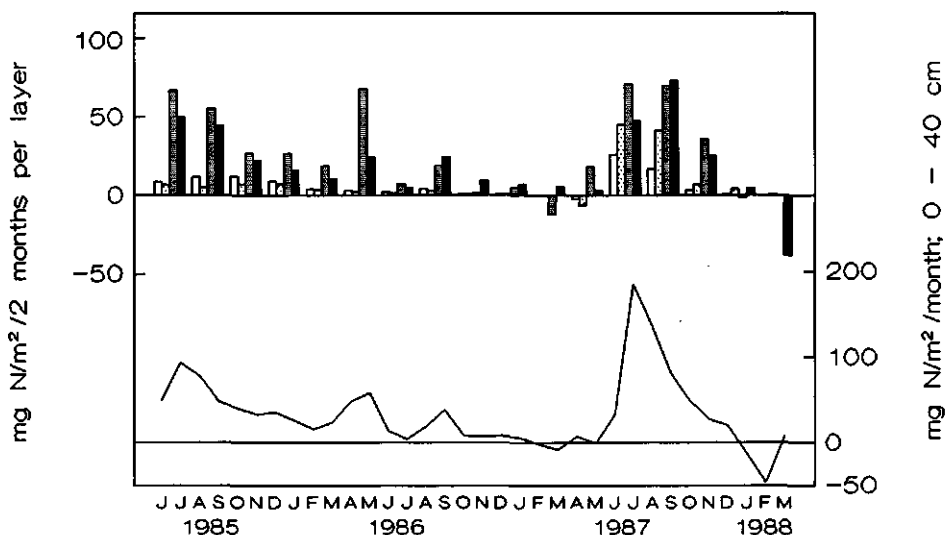
Figure 3.8: Estimated nitrogen turnover in enchytraeid tissue in Conventional. Bars denote bimonthly nitrogen turnover in various layers. The line denotes monthly nitrogen turnover in the complete sampled depth.

☐	*0 - 5 cm*	▨	*5 - 10 cm*
▨	*10 - 25 cm*	■	*25 - 40 cm*
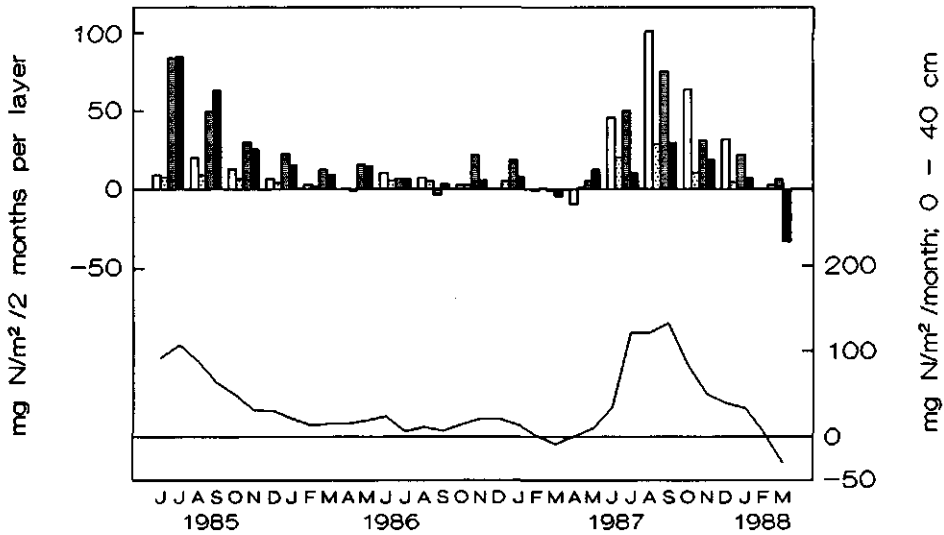
Figure 3.9: Estimated nitrogen turnover in enchytraeid tissue in Integrated I. Bars denote bimonthly nitrogen turnover in various layers. The line denotes monthly nitrogen turnover in the complete sampled depth.

	0 - 5 cm		5 - 10 cm
	10 - 25 cm		25 - 40 cm

Maximum nitrogen flux in the sampled profile occurred in 1987, in Integrated I in the period June-November with at least 0.13 mg N/m^2/month and in Conventional in June-September with 0.16 mg N/m^2/month. Total N-flux from the enchytraeid populations in 1987 amounted to 0.53 g/m^2 for the conventional field (fig. 3.8) and 0.60 g/m^2 for Integrated I (fig. 3.9).

In 1986 nitrogen flux was low as compared with 1985 and 1987, in Integrated I with a rather constant level of ca 0.02 g N/m^2/month and a total flux of 0.19 g/m^2, in Conventional more variable, with a maximum of 0.06 g N/m^2/month in May and a minimum of 0.004 g N/m^2/month in July, the total flux amounting to 0.27 g/m^2.

In Integrated II and Minimum tillage, the general picture in 1987 was the same as in Conventional and Integrated I, maxima occurring in Minimum tillage in the period July-September with 0.26 g N/m^2/month and in Integrated II in the period August-October with 0.17 g N/m^2/month.

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3.4. Discussion

The data on population dynamics and production obtained in the present study are in the same order of magnitude as those reported in a number of other studies on Enchytraeidae in arable fields (Ryl, 1977, 1980; Lagerlöf, 1987; Lagerlöf et al., 1989). Remarkable however, is the fact that, though mean abundances of enchytraeids are generally appreciably higher in the present study, biomass estimates are more close to the values obtained in these studies. Partly this may be due to methodological differences in the approach to estimate standing crop, partly with real population characteristics.

Abrahamsen (1973) presents regression equations of length on volume for a number of enchytraeid species groups. Assuming a specific density of 1.05 g/cm^3 and a fresh weight/dry weight ratio of 5.56 (Edwards, 1967) to 7.69 (Ryl, 1977) these equations can be compared with the ones obtained in the present study. For corresponding species (*Enchytraeus buchholzi*, *Buchholzia appendiculata*, *Fridericia bulboides* and *Henlea perpusilla*) there is good agreement, although for the Lovinkhoeve potworms the estimated weights tend to be higher for smaller size classes and lower for larger size classes as compared with the animals studied by Abrahamsen (1973). *H. ventriculosa* and *F. sp. B* would belong to Abrahamsen's group F, *F. sp. A* and *F. sp. C* to group E.

Ryl's (1977, 1980) data were obtained through weighing of enchytraeids preserved in alcohol. The range in average dry weights per individual found in this way was 12.48 - 36.92 µg (assuming the fresh weight/dry weight ratio to be 7.69). In the present study average dry weights per individual ranged from 12.71 µg (in Integrated I in 1986) to 23.53 µg (the conventional field in 1987). This may indicate a real difference in mean individual size or species composition with the animals found in the Polish study.

Lagerlöf et al. (1989) on the other hand, used estimates from Persson & Lohm (1977), assuming a dry weight of 5.94 µg for animals < 2 mm, 41.94 µg for animals of 2 - 6 mm and 144 µg for animals > 6 mm. Application of the regression equations for the Lovinkhoeve potworms results in the considerably lower dry weights of 1.1, 16.3 and 129.6 µg for the same classes, which is in good agreement with the findings of Abrahamsen (1973), although both weight determinations were obtained via different methods.

Most of the species-related differences that were found in the statistical and numerical analyses in the present study, can not satisfactorily be explained, because of the lack of specific ecological knowledge about the Enchytraeidae. The occurrence of these differences, however, may serve as an indication of appreciable ecological variation within this family, and stresses the need for research in this field.

The present management for the investigated fields at the Lovinkhoeve experimental site started only shortly before the start of the sampling programme; thus it is reasonable to expect that the soil communities were not yet adapted to the management. The history and successional stage of the fields may have played an important part. This is reflected in the significant increase in species diversity in Integrated I as opposed to the conventional field, where type of management was changed to a much lesser degree. Again, the large populations found in the deeper layers of the minimum tillage field may reflect the influence of the former management.

As the effects of the transition and of the previous management types will still have played an important role, the present treatments can not easily be evaluated at this stage. Moreover, as in the Lovinkhoeve Programme only nested replicates are present, it is not possible to establish a statistically significant effect of the different agricultural regimes. Yet, there are some indications of such effects. The sudden drop of enchytraeid numbers and biomass in the conventional field after fumigation with the nematicide 1,3-dichloropropene in september 1986, was not parallelled in Integrated I, where no such fumigation took place. This alleged effect of the fumigation probably lasted no longer than two months.

A longer lasting influence of the agricultural practice may originate from differences in tillage. Both in the analyses of variance and in the canonical correspondence analyses the conventional and integrated fields were characterized by differences in depth distribution of the enchytraeids. In the conventional field a large part of the population (on average 72% throughout the year) was found in the 10 - 40 cm layer. At this depth fresh organic material is buried with ploughing. In this respect, the course of the enchytraeid population in Integrated I, which had conventional tillage till autumn 1985, is illustrative. In 1985, on average 78% of the population was found in the 10 - 40 cm layer in this field. In 1986 and 1987, when ploughing was only to 15 cm, 62% and 43% respectively was found in this layer. Again, the integrated field with minimum tillage, which was conventionally managed till autumn 1986, still showed high numbers and biomass in the 10 - 40 cm layers in 1987. These findings correspond with data from Poland (Ryl, 1977, 1980), Germany (Zimmermann, 1987) and Sweden (Lagerlöf et al., 1989), where ploughing resulted in an even, vertical distribution, or even a concentration in deeper layers of the enchytraeid populations.

These data clearly suggest an association of enchytraeids with fresh organic material, whether directly as saprovores (Latter, 1977) or indirectly as microbivores (Toutain et al., 1982). The larger numbers of enchytraeids in the plant rows, also reported by Way & Scopes (1968), point to an association with decaying roots, with root exudates, or to more favourable abiotic conditions near the plant.

Seasonal dynamics of numbers and biomass did not differ much between the investigated fields. There was, however, a notable difference between years: 1986 on the one hand and 1985 and 1987 on the other. In 1986 a summer minimum occurred,

and mean abundance and biomass in this year were low as compared with 1985 and 1987. As this summer minimum coincided with the dry spell in summer 1986, a causal relation may be presumed, whether directly through adverse effects of drought on enchytraeids, or indirectly through a reduced activity of the soil microflora. In a number of other studies, e.g. Nielsen, 1955b; Möller, 1967; Gröngröft, 1981; Hotanen, 1986, moisture was identified as a key factor in the population dynamics of Enchytraeidae. Moreover, the conventional field showed higher numbers and respiration than Integrated I in 1986, and a greater part of the population in this field was always found in the 10 - 40 cm layers, that are less susceptible to drought. Yet, from the canonical correspondence analysis for Conventional and Integrated I in the period 1986 to 1988, it appears that precipitation was of minor importance as an explanatory factor for the population dynamics in our fields, and that the enchytraeid populations were much more influenced by the type of field and the course of soil temperature. Although the amount of precipitation does play a role on the third and fourth environmental axis in this analysis, that explain the remainder of the variance, these results indicate that soil moisture as such may not have been a key factor in the present study. Moisture conditions may largely influence enchytraeid populations through other factors, like temperature. Clearly, more research is needed to address this point satisfactorily.

Another factor that may have played a part in the differences between sample years, is the type of crop grown and the associated differences in management practices. Different types of crop may influence enchytraeid populations through qualitative and quantitative differences in organic material entering the soil system, and through microclimatological effects. Ryl (1977, 1980) suggested that root crops, like potatoes and sugar beet, are more suitable than cereals for the development of enchytraeid populations. From more natural habitats there also are indications that the type of vegetation may influence enchytraeid populations (among others: Abrahamsen, 1972; Standen, 1980b).

The response of the enchytraeids to low temperatures, as is seen in the canonical correspondence analyses, is another aspect of the seasonal dynamics. From these analyses it seems likely that the enchytraeids that survive the winter period as juveniles or adults, do this in the deeper layers. Exceptions are *Fridericia sp. A* and *F. sp. C*, that seem to survive mainly in the 5 - 10 cm layer. In view of the rapid increase in numbers in spring, a substantial part of the populations may hibernate as cocoons, or the reproductive potential of hibernated populations may be very high.

Agricultural measures however, notably ploughing and the use of pesticides, will have had an additional influence on the seasonal dynamics, which is reflected mainly in the conventional field, where numbers dropped to almost completely zero level after soil fumigation, and tend to be very high in the 10 - 25 cm layer after ploughing.

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The method used to calculate production biological parameters is more complicated than the ones proposed by Standen (1980a) and Moore & De Ruiter (in press), that are based on the use of average biomass. Yet, the former method was chosen because it allows for seasonal variability in intensity of population metabolism. Moreover, results of the latter methods strongly depend on estimates of population turnover, and too little is known about life histories, and their seasonal variability, of enchytraeids to apply this approach fruitfully. On the other hand, these methods may be used conversely, to obtain an estimate of enchytraeid population turnover and the ratio of production to average biomass (P/B ratio). Applying these methods to the present biomass data, and assuming the same ecological efficiencies, it was found that the population turnover and P/B ratio must have been approximately 10 on average in the investigated fields. Applied to the results of the Swedish study of Lagerlöf et al. (1989), an estimate of approximately 5 results, the lower value being a consequence of the higher individual biomass in that study. Standen (1980a), however, considered P/B ratios of 1-4 for terrestrial enchytraeid populations as plausible. These high estimates of P/B may on the one hand be explained by strong reproductive activity of enchytraeid populations in arable fields, that are notoriously unstable. On the other hand, the production efficiency of 0.4, as proposed by Heal & MacLean (1975), may be an overestimate, as in the present and, to a lesser extent, in the Swedish study, a large part of the populations consisted of small worms, which might mean relatively high respiratory costs and a lower production efficiency. For earthworms, Lee (1985) mentioned a P/B ratio of 2 to 7, which suggests that the present estimates may after all not be unrealistic.

The present estimates of production ecological parameters are, due to a greater sampling depth and larger numbers in combination with lower individual weights, generally higher than those found in other studies in arable fields (Kasprzak, 1982; Lagerlöf et al., 1989), but stay in the same order of magnitude. Paustian et al. (1990) reported from Swedish arable fields a proportion of 3.5 - 23% of total faunal respiration attributable to potworms. The available evidence thus makes it plausible that Enchytraeidae are an important faunal group, both in conventional and in integrated agriculture in temperate regions, and that the decomposition of organic matter in arable systems is considerably influenced by enchytraeid activity.

The estimates on nitrogen turnover support the idea that potworms constitute an important pool of nutrients. In this respect it must be taken into consideration that the estimates in this study only concern the amounts of nitrogen in enchytraeid tissue. Nitrogen in excrements, urines or mucus were neglected because of lack of knowledge about their nitrogen content and the amounts produced. Indirect effects of enchytraeid activity on nitrogen mobilization, via stimulation of microbial activity, were also ignored. When data for earthworms (Christensen, 1987) are taken as a cue, the estimates would at least be 15% higher. Abrahamsen (1990) estimated that the contribution of mineral nitrogen from dead tissue of *Cognettia sphagnetorum* was only 40% of the nitrogen

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mobilized through the activity of this enchytraeid species. Thus the actual contribution of enchytraeids to nitrogen mobilization may have been considerably higher than the estimates calculated in the present study. What part of the nitrogen flow from the enchytraeid populations consists of soluble nitrogen compounds (from decomposing tissue and excreta) and what part is immobilized in microbial or predatory tissue remains to be investigated.

In both systems maximum nitrogen flux occurred towards the end of the growing season, implicating an enhanced chance of loss of nutrients, as nutrient uptake of most crops is diminished then. The same was noted for earthworms by Christensen (1987), who suggested the use of fast growing cover crops to circumvent the problem of nitrogen loss in autumn. The same suggestion would be in place in the present case.

The main difference between the conventional and integrated agricultural management systems appears to lie in the depth at which the enchytraeid activity was concentrated, which coincided with the depth at which organic matter was added to the system. In the integrated fields enchytraeid populations were generally concentrated in the upper layers, which might render the enchytraeids susceptible to adverse temperature and moisture conditions. In the conventional field a greater part of the populations lived in deeper layers, more or less protected from adverse climatic conditions. Consequently, during the drought in 1986 more potworms were found in the conventional field than in the integrated field, whereas in the other years the opposite was the case. On the other hand, plant nutrients mineralized through enchytraeid activity may run a higher risk of being lost through leaching when this activity takes place in deeper layers, where crop roots are less abundant.

4. Life-history of *Enchytraeus buchholzi* Vejdovský, 1879 (Oligochaeta) and population development in artificial soil

Abstract

The research reported here concerned determination of life-history parameters of *Enchytraeus buchholzi*, and their applicability under field conditions. Laboratory experiments were carried out, in which development times, numbers of cocoons and eggs produced, and longevity were determined at various temperatures. By a simple simulation model, data on the population development under more natural conditions were compared with predictions based on the laboratory trials. The comparisons showed, that population development under field conditions may fall short to predictions as regards abundance, but on the other hand, that individual development could be appreciably faster than predicted. It seems probable, that the discrepancies found are related with the physiological condition of the experimental animals.

4.1. Introduction

Enchytraeus buchholzi was found to be the most abundant species at the Lovinkhoeve experimental farm in the Noordoostpolder, the Netherlands (this thesis), where the Dutch Programme on Soil Ecology of Arable Farming Systems is carried out. Knowledge of the life-history characteristics of this species was considered useful for gaining insight in the mechanisms governing population dynamics of enchytraeids, and also indispensable for population modelling. *Enchytraeus buchholzi* has been the subject of several life-history studies (Trappmann, 1952; Springett, 1970; Learner, 1972). However, considerable taxonomic difficulties are associated with the *buchholzi*-group (Bouguenec & Giani, 1987), which makes the identity of the species studied uncertain. Moreover, important life-history characteristics, such as longevity and length of the reproductive period, have not been determined yet. Thus, it was considered necessary to carry out a life-history study on the species found at the experimental farm. To avoid possible confusion with related species, all experiments were carried out with specimens that derived from a single individual.

Based on these experiments a model for population growth of E. buchholzi was developed. Predictions from this model were compared with data from microcosms resembling the field situation, thus enabling an evaluation of the life-history characteristics found in the laboratory.

4.2. Methods

4.2.1. Life-history characteristics

Experiments were conducted at 5 different temperatures: 4°C, 8°C, 10°C, 16°C and room temperature (18 - 20°C). The choice of these temperatures was a compromise between what was considered desirable and available equipment. The animals were kept in small, covered petri-dishes (4 cm diameter in the 4 and 8°C series, 6 cm diameter in the other series), on agar (1.3% solution in tap water) and using oat bran as food. The dishes were stored on trays in closed refrigerator boxes with a small quantity of water on the bottom, to avoid desiccation.

Each dish received a fresh cocoon of Enchytraeus buchholzi, from stock cultures that originated from one single specimen from the Lovinkhoeve experimental site. In this way, the genetical identity of the specimens was assured. Inspection took place at regular intervals, ranging from biweekly at 4°C to daily at 16 and 20°C. The dishes were supplied with quantities of oat bran large enough to be in excess for the worms, and small enough to keep thorough inspection of the dishes possible. At each inspection the number of worms and the number of deposited cocoons per dish were counted, and cocoons were removed. The number of eggs per cocoon was recorded by visual examination. The experiments continued till all the animals had died.

Another series of experiments was laid out to establish the growth rate of individuals. These experiments were conducted at 8 and 16°C, applying the same methods as above. However, 2 cocoons per dish were used, and at fixed intervals the animals from 4 dishes were removed and measured to the nearest mm. This occurred just after hatching, at the age of 1 week, 2 weeks, 4 weeks, 8 weeks etc. In these series the number of eggs per cocoon was also recorded.

4.2.2. Population development in artificial soil cores

Population development in more natural circumstances was followed in several experiments with artificial cores (41 mm diameter, 25 mm height) from Lovinkhoeve soil, prepared according to the technique described in chapter 5. To these cores 5 fresh cocoons of *E. buchholzi* were added. The cores were destructively sampled in the course of the experiments, and the extracted worms were counted, measured to the nearest mm and their phenological stage recorded.

One experiment was carried out in the laboratory, at 16°C, with various amounts of oat bran (0, 0.5, 1 and 2 g) added to the soil. A second laboratory experiment was conducted at 13°C and 15°C, with 0.3 g comminuted oat plant material added.

Data for a field situation were obtained from the experiment described in chapter 6 (this thesis), in which artificial cores, with 0 or 0.5 g oat bran added, were placed in soil.

4.2.3. The model for potential population development

To obtain an indication of the usefulness under more natural circumstances of the life-history characteristics found in the laboratory experiments on agar, predictions of population development based on these characteristics were compared with the results from the experiments with artificial cores. For this, a simple, temperature driven model for potential population development of *E. buchholzi* was constructed, based on the results of the life-history experiments (Table 4.1) and the growth experiments. The model ignored the variance in these data, as it was primarily meant indicative. To simulate the field situation, daily soil temperature data at 10 cm depth from the Dutch Meteorological Institute at De Bilt were used.

The model assumed a power relation between the various experimental temperatures for length of incubation time of cocoons, length of generation time, longevity, and individual growth. Equations used were:

$$I = 319.492 * T^{-1.146} \qquad (R=0.973)$$
$$M = 2399.504 * T^{-1.498} \qquad (R=0.976)$$
$$L = 14048.227 * T^{-1.706} \qquad (R=0.994)$$
$$DL = (120.101 * T^{0.356}) / (LE^{B}), \text{ where}$$

I = length of incubation time of cocoons (days) T = temperature (°C)
M = length of generation time (days) LE = length (mm)
L = longevity (days) $B = 6.938 * T^{-0.254}$
DL = length growth (mm/day)

Linear interpolations between data at the various experimental temperatures were used to obtain rates of cocoon production, percentages of viable cocoons and percentages of juveniles surviving till maturity at the various temperatures. It was assumed that the number of young hatching from a cocoon was 2.5 at all temperatures under consideration, and their length 2 mm.

Starting from a situation, in which number and stage of worms or cocoons were known, the model used daily temperature data to calculate the stage each group of animals or cocoons would have reached at the end of a day. Cocoons deposited on one day were treated as a new group. The number of worms in the artificial cores and the phenology of the populations were compared with the values predicted by the model.

4.3. Results

4.3.1. Life-history characteristics

Table 4.1 sums up the results of the life-history experiments, supplemented with data from the experiments on growth rate.

From this table it appears that under the conditions studied the optimum temperature for *E. buchholzi* is in the range between 10 and 20°C, as at these temperatures the percentages of viable cocoons and the number of cocoons produced per worm were highest. The response to temperature was most marked at lower temperatures, where incubation time and generation time decreased sharply with rising temperature.

At all temperatures, cocoon production continued till death, with irregular fluctuations in the course of time. However, the number of cocoons per worm was markedly less at lower temperatures.

In several instances only one worm hatched per cocoon. Such single worms produced new, and viable, cocoons at roughly the same rate as worms that were kept together, indicating the occurrence of parthenogenesis in *E. buchholzi*.

Table 4.1: Life-history characteristics of E. buchholzi in laboratory experiments. Time given in days.
n.d.: not determined.

Temperature (°C)	4	8	10	16	20
Initial no. of cocoons	50	69	20	37	15
% viable	78.00	88.41	100.00	100.00	93.33
Eggs/viable cocoon	3.44	4.00	2.30	3.41	2.36
Coeff. var.	42.73	33.25	28.70	42.82	39.41
N	39	61	20	37	14
% fertile	88.66	96.75	93.33	98.24	100.00
Incubation time	56.25	37.46	24.50	11.02	10.55
Coeff. var.	15.98	16.04	11.92	47.46	24.27
Worms/cocoon	3.03	3.87	2.10	3.35	2.36
Coeff. var.	47.52	35.14	21.43	45.07	39.41
No of worms	118	236	42	124	33
Generation time	239.10	145.11	84.57	31.69	25.94
Coeff. var.	35.35	23.11	45.57	27.64	15.15
N	118	280	42	300	33
% surviving till maturity	82.20	94.64	88.10	98.67	93.94
Longevity	640.52	415.14	n.d	112.01	91.70
Coeff. var.	54.18	36.46	n.d	32.37	35.14
Cocoons/worm	15.23	19.75	n.d	53.33	53.09
Coeff. var.	80.30	54.43	n.d	38.14	48.37
Eggs/cocoon	2.41	2.54	2.69	2.51	2.33
Coeff. var.	45.63	42.52	40.15	41.04	36.05
N	700	941	269	3002	88

4.3.2. Growth rates

The data from the growth rate experiments were used to calculate the following power regressions describing daily length growth:

at 8°C: $G=251.586*L^{-4.088}$
at 16°C: $G=321.910*L^{-3.428}$,

where G=proportional growth (percentage) and L=length (mm).

4.3.3. Comparison of model predictions with data from artificial cores

Tables 4.2 to 4.4 compare the population development and phenology, and the size of the worms in the artificial cores as calculated by the simulation model, with the values observed in the laboratory and field experiments. Highest numbers of worms were observed in the cores that had organic matter added. The observed numbers of worms in the field experiment (Table 4.4) were generally considerably lower than in corresponding cores in the laboratory experiment (Table 4.2).

From all 3 tables it appears that the number of worms hatching from the original cocoons were substantially lower than was predicted by the model, the numbers in the field experiment (Table 4.4) being lowest. In the laboratory experiments fewest juveniles hatched in the cores with comminuted oat plants (Table 4.3). Deviations from predicted values were in most cases substantial. The numbers predicted by the model were generally (much) higher than the observed numbers, which was to be expected from the fact that the model neglected factors like food availability, density of the population and non-natural mortality. The most extreme deviations were found in the artificial cores without added organic material. In cores with organic material, initial population growth was more or less concurrent with the predictions from the model, in some cases (Table 4.2) even considerably higher. In the course of time, these cores too fell behind the predicted values.

There were also strong deviations in the phenology of the population. In the laboratory experiments with oat bran added (Table 4.2), juveniles in the cores with 1 and 2 g oat bran added reached high densities earlier than predicted, indicating a shorter maturation time than expected or a shorter incubation time of cocoons. In the laboratory experiment with comminuted oat plant material added (Table 4.3), adults appeared earlier than expected in the 13°C treatment. This phenomenon was not found in the 15°C treatment. Again, in the field experiment (Table 4.4) in cores with oat bran added, adults appeared circa 100 days earlier than predicted. With no oat bran added, both in

Table 4.2: Comparison of population size and population phenology as predicted by the model with data from artificial cores at 16°C in the laboratory, with and without oat bran added.

| | Predicted | | Observed | | | | | | | |
| | | | oat bran: 0 g | | 0.5 g | | 1 g | | 2 g | |
Days	Number	Length	Number	Length	Number	Length	Number	Length	Number	Length
					Juveniles					
37	13	5.3	5.80 (±3.03)	2.48 (±0.69)	3.25 (±2.63)	2.38 (±1.12)	n.d	n.d	n.d	n.d
43	0	-	16.00 (±5.66)	2.69 (±0.97)	n.d	n.d	179.50 (±16.26)	2.56 (±0.58)	71	2.35 (±0.48)
86	533	4.2	33.00 (±38.18)	1.83 (±0.71)	n.d	n.d	303.00 (±22.63)	2.87 (±1.04)	236	3.64 (±1.22)
91	630	3.9	18.50 (±6.40)	2.43 (±0.66)	86.60 (±29.23)	3.50 (±0.94)	n.d	n.d	n.d	n.d
					Adults					
37	0	-	0	-	6.50 (±1.29)	6.92 (±0.39)	n.d	n.d	n.d	n.d
43	12	5.6	0.50 (±0.71)	5	n.d	n.d	17.50 (±3.54)	5.71 (±0.46)	6	5.17 (±0.41)
86	213	5.7	0	-	n.d	n.d	80 (±28.28)	4.38 (±0.49)	100	5.20 (±0.40)
91	315	5.8	0	-	0	-	n.d	n.d	n.d	n.d
					Totals					
37	13	5.3	5.80 (±3.03)	2.48 (±0.69)	9.75 (±2.50)	5.41 (±2.28)	n.d	n.d	n.d	n.d
43	12	5.6	16.50 (±4.95)	2.76 (±1.03)	n.d	n.d	197.00 (±19.80)	2.84 (±1.06)	77	2.57 (±0.89)
86	746	4.6	33 (±38.18)	1.83 (±0.71)	n.d	n.d	383 (±50.91)	3.18 (±1.13)	336	4.11 (±1.27)
91	945	4.5	18.50 (±6.40)	2.43 (±0.66)	86.60 (±29.23)	3.50 (±0.94)	n.d	n.d	n.d	n.d

the laboratory and in the field experiment, almost no mature worms were recorded. Yet, in the cores without organic matter added (Table 4.2), numbers of juveniles had substantially risen on the second sample date, pointing to an early maturation in these cores too. The observed percentages of juveniles were generally higher than predicted, except in the cases with early appearance of adults.

Due to the deviations from the predictions as regards the phenology of the populations in the experiments, size of the worms as observed may only be compared in the early stages of population development, before newly laid cocoons hatched. In cores without organic matter added, the size of the worms was usually less than the predictions of the model for these stages, while in cores with added organic material the worms grew according to the predictions.

Table 4.3: Comparison of population size and population phenology as predicted by the model with data from artificial cores at 13 and 15˚C in the laboratory, with 0.3 g comminuted oat plant material added.

| | Predicted | | | | Observed | | | |
| | 13˚C | | 15˚C | | 13˚C | | 15˚C | |
Days	Number	Length	Number	Length	Number	Length	Number	Length
				Juveniles				
14	0	-	13	2.6	1.00 (±1.73)	2.00 (±0.00)	1.00 (±1.00)	2.00 (±0.00)
42	12	4.9	0	-	0.40 (±0.55)	5.00 (±0.00)	2.75 (±2.50)	3.27 (±1.85)
84	205	3.6	505	4.2	21.40 (±28.94)	3.86 (±1.56)	91.33 (±81.47)	3.00 (±1.11)
111	425	4.3	2673	3.3	4.20 (±4.08)	4.33 (±1.93)	12.20 (±18.12)	2.90 (±1.40)
				Adults				
14	0	-	0	-	0	-	0	-
42	0	-	12	5.3	0.80 (±1.79)	4.75 (±0.50)	4.50 (±2.38)	4.89 (±0.96)
84	12	6.3	12	6.8	1.40 (±2.61)	7.57 (±0.53)	6.17 (±4.67)	5.24 (±0.72)
111	100	5.6	476	5.9	0.20 (±0.63)	7.50 (±2.12)	0.30 (±0.95)	6.33 (±2.52)
				Totals				
14	0	-	13	2.6	1.00 (±1.73)	2.00 (±0.00)	1.00 (±1.00)	2.00 (±0.00)
42	12	4.9	12	5.3	1.20 (±1.64)	4.83 (±0.41)	7.25 (±4.72)	4.28 (±1.56)
84	217	3.7	517	4.3	22.8 (±31.51)	4.09 (±1.76)	97.50 (±80.88)	3.14 (±1.21)
111	525	4.5	3149	3.7	4.40 (±4.58)	4.48 (±2.03)	12.50 (±18.95)	2.98 (±1.52)

Table 4.4: Comparison of population size and population phenology as predicted by the model with data from artificial cores placed in the field, with and without oat bran added.

| | Predicted | | Observed | | | |
| | | | oat bran: 0 g | | 0.5 g | |
Days	Number	Length	Number	Length	Number	Length
			Juveniles			
62	10	3.6	2.06 (±1.98)	2.00 (±0.00)	0.38 (±1.09)	3.17 (±2.14)
98	10	4.1	0.19 (±0.40)	1.67 (±0.58)	0.94 (±2.24)	2.53 (±1.36)
121	10	4.4	1.38 (±1.63)	1.68 (±0.48)	1.38 (±1.82)	1.91 (±1.02)
155	0	-	0.44 (±0.89)	2.00 (±0.82)	6.88 (±8.41)	2.37 (±1.10)
185	105	3.2	1.44 (±1.46)	1.74 (±1.10)	45.44 (±36.32)	2.44 (±1.04)
216	377	4.2	1.13 (±1.71)	2.83 (±1.38)	36.69 (±48.83)	2.56 (±1.01)
246	8690	3.8	0.38 (±0.83)	3.17 (±0.94)	3.81 (±7.38)	2.83 (±0.86)
			Adults			
62	0	-	0	-	0.19 (±0.54)	5.00 (±1.00)
98	0	-	0	-	0.50 (±0.73)	6.13 (±2.10)
121	0	-	0	-	0.38 (±0.62)	5.67 (±2.88)
155	10	5.2	0	-	2.63 (±3.63)	5.33 (±1.16)
185	10	6.1	0.19 (±0.75)	5.33 (±1.53)	6.50 (±7.20)	5.04 (±1.09)
216	138	5.7	0	-	1.13 (±1.89)	3.89 (±1.37)
246	662	6.1	0	-	0	-
			Totals			
62	10	3.6	2.06 (±1.98)	2.00 (±0.00)	0.56 (±1.36)	3.78 (±1.99)
98	10	4.1	0.19 (±0.40)	1.67 (±0.58)	1.44 (±2.73)	3.78 (±2.37)
121	10	4.4	1.38 (±1.63)	1.68 (±0.48)	1.75 (±2.08)	2.71 (±2.19)
155	10	5.2	0.44 (±0.89)	2.00 (±0.82)	9.50 (±11.25)	3.19 (±1.73)
185	115	3.4	1.63 (±1.93)	2.15 (±1.62)	51.94 (±41.17)	2.76 (±1.35)
216	515	4.6	1.13 (±1.71)	2.83 (±1.38)	37.81 (±48.90)	2.60 (±1.05)
246	9352	4.0	0.38 (±0.83)	3.17 (±0.94)	3.81 (±7.38)	2.83 (±0.86)

4.4. Discussion

4.4.1. Comparison of the present data with other life-history studies

In Table 4.5 literature data on the life-history of *Enchytraeus buchholzi* in laboratory experiments are compared with the data obtained in the present study. As regards the length of the incubation period, there seems to be good agreement. The other parameters reveal discrepancies between the various authors. The generation times recorded by Trappmann (1952) are shortest, followed by those from Learner (1972), the present study and Springett (1970) respectively. The reverse order is found in the number of eggs per cocoon, Springett (1970) reporting lowest numbers, Trappmann (1952) the highest. The number of observations on cocoon production is somewhat less, but point to appreciable differences, the values in the present study being highest at temperatures above 8°C.

One way of addressing these differences is to take into consideration the various culture methods that were used in the laboratory experiments. Trappmann (1952) used petri dishes lined with filter paper which was moistened with tap water. The worms were fed with oat bran and bread. Learner (1972) used the same setup, but here the worms received activated sludge as a food source. Springett (1970) cultured the animals in petri dishes with 1% soil extract agar sprinkled with soil and moistened the medium with distilled soil solution (Springett, 1964). As a food source leaves and peat particles were present. In the present study a 1.33% agar solution in tap water was used, and the worms were fed with oat bran.

It is conceivable that the differences found may at least partly be due to an effect of the culture medium (kind of substrate and the chemical composition of the water used) and quality and quantity of food. Filter paper would serve better as a medium than agar, and bread plus oat bran might be a better food source than oat bran alone or activated sludge. The low number of eggs per cocoon and the long generation time in Springett's (1970) cultures may have been caused by shortage of food, as was suggested before by Albert (1975), or by food deficiencies.

If the differences in generation time and productivity were caused by such external factors, this would mean that the development and phenology of populations of *E. buchholzi* in field conditions will vary widely, depending on the prevalent conditions. An indication for such externally induced response of this species was reported by Trappmann (1952), who found large differences in size of the adult worms in different feeding conditions; this response could be reversed or changed by changing the amount and type of food.

Table 4.5: Some literature data on the life-history of E. buchholzi, from laboratory experiments, and results from the present study. Upper lines: means, lower lines: ranges (if determined).

°C	Incubation period (days)	Hatched (%)	Generation time (days)	Cocoons/adult (per week)	Eggs/cocoon	Author
4.0	56.3	78.0	239.1	0.27	2.4	this thesis
	40-89		180-488	-	0-6	
8.0	39.0	76.0	93.0	1.45	3.0	Learner, 1972
	35-43		92-93	-	1-9	
8.0	37.5	88.4	145.1	0.51	2.5	this thesis
	26-61		89-404	0.06-1.36	0-6	
10.0	24.5	100.0	84.6	-	2.7	this thesis
	15-35		49-194	-	0-5	
10.0	35.0	100.0	>180.0	0.63	2.0	Springett, 1970
	-		-	-	2-2	
12.0	19.3	98.0	38.3	-	14.9	Trappmann, 1952
	14-25		-	-	1-44	
15.0	11.0	94.0	27.0	1.31	3.0	Learner, 1972
	-		-	-	1-9	
16.0	11.0	100.0	31.7	4.65	2.5	this thesis
	7-20		26-48	2.59-5.12	0-7	
18.0	9.4	94.4	18.4	2.80	14.9	Trappmann, 1952
	8-12		-	-	1-44	
20.0	10.6	93.3	25.9	5.65	2.3	this thesis
	6-15		23-36	2.94-6.47	-	
20.0	10.0	74.0	25.0	2.62	3.0	Learner, 1972
	-		-	-	1-9	
20.0	7.7	100.0	14.7	-	14.9	Trappmann, 1952
	6-11		-	-	1-44	

A second explanation for discrepancies between the various studies may be found in the taxonomic problems in the genus Enchytraeus, and especially E. buchholzi. This, and related species, present a hitherto unsolved systematic problem (Bouguenec & Giani, 1987). Thus, it is conceivable that in the various studies (mixtures of) different forms or even different species were used. In that case, the differences found may reflect species related differences.

4.4.2. Evaluation of the present life-history data

The model developed from the laboratory data in the present study describes population development and phenology under the assumption that the conditions for the enchytraeids remain the same, viz. a substrate of agar, excess oat bran as food, absence of predators, parasites and competitors, and no influence, positive or negative,

from population density. It seemed reasonable therefore, to expect that the model would predict higher population densities and a more rapid life cycle than recorded in field situations.

The comparison with population development in artificial soils which was carried out in this research only partly corroborated these expectations. Numbers of animals found in the artificial cores generally were lower than predicted by the model. Initial growth of the individual worms was roughly according to the prediction in the artificial soils that had extra food added, and was retarded in the cores without extra food. At the same time, appreciable deviations in phenological characteristics were recorded, the most important being:

- From the comparison of predicted and observed values it appears that survival of *E. buchholzi* in more natural conditions is appreciably lower than found in the laboratory. The numbers of worms that successfully hatched from the original 5 cocoons per core were in all treatments clearly lower than the values from the life-history experiments. This may indicate a lower viability of cocoons when put in soil, or a much more variable incubation time in soil, resulting in a postponement of hatching in the artificial cores.
- The presence or absence of oat bran in the artificial cores appeared to influence life-history characteristics considerably. Both in the laboratory and in field conditions the animals hardly matured in cores without oat bran, whereas in cores that had oat bran added, maturation time was shorter than predicted. In the laboratory experiment with artificial cores that had oat bran added, total numbers initially were much higher than predicted, indicating the presence of a new generation. It seems clear that in these cases both hatching time and generation time for the second, and possibly also later generations were shorter than expected. In cores with comminuted oat plant material added, this effect was hardly found, indicating the importance of food quality.
- The proportion of juveniles in the artificial soils was practically always higher than predicted. This may mean that either maturation was postponed for an appreciable proportion of the population, or mortality in the maturation period (or directly after maturation) was higher than the values found in the life-history experiments. As almost no mature worms were recorded in the artificial soil cores without oat bran added, it would seem that postponement of maturation is the most likely mechanism.

Even when the variability in life-history characteristics (Table 4.1), which were ignored in the model, is taken into account, the deviations in observed population phenology can not be explained. These findings, in combination with the data in Table 4.5, rather indicate that the amount and quality of food available has had a strong influence not only on the population development, which was to be expected, but also on the life-

history characteristics of *E. buchholzi*.

To explain the deviations from expected phenology, several hypotheses may be suggested:
- as oat bran was the sole food source for the enchytraeids in the life-history experiments, it is conceivable that a food deficiency did play a role, which caused the generation time to be prolonged. In other words, the worms needed more time to collect enough of certain nutritive substances to reach maturity. In the artificial cores, different food substances were present, allowing the worms to make up for the deficiencies in the supplied food.
- the physical environment may be very important for enchytraeids. Agar is not a very natural habitat for this species, and may impose different conditions on movement and locomotion than does soil. In the laboratory cultures the enchytraeids often were seen lying against the side of the culture dish. This may be because they need a solid substrate to function properly, which would imply a negative influence of the (rather soft) agar on the rate of development of the worms.
- the early occurrence of adults was most conspicuous in the field experiment in cores with oat bran. In these cases, a slightly accelerating effect of fluctuating temperatures on development (Reynoldson, 1943) may have invigorated the effect of the presence of oat bran as food.
- the low hatching success of the original cocoons in the artificial soils might imply that these cocoons were not well adapted to the conditions in soil. Any effect of the manipulation of the cocoons can be excluded, as the treatment of the cocoons was the same as in the life-history experiments on agar plates. Perhaps a protective layer around the cocoon was absent, which in the genus *Enchytraeus*, according to Christensen (1956), generally is deposited by the adult worm in soil. This could mean that some soil factors, possibly parasites or predators, adversely influenced cocoon development. The precise nature of these factors remains to be elucidated. In view of the very rapid population development which was recorded in the laboratory cores that had oat bran added, cocoons deposited later were better protected.

4.4.3. Synthesis

Based on the data presented, the following tentative conclusions on the development of an *E. buchholzi* population under field conditions may be formulated:
- The potential for rapid population development when sufficient food is available, in combination with the possibility of parthenogenetic reproduction, make *E. buchholzi* a typical r-species. Adverse conditions, like shortage of food are mainly survived through prolongation of the juvenile stage, or even a return to the juvenile stage, as was found with *Stercutus niveus* (Dózsa-Farkas, 1973c). The adult stage of this species, and, possibly, its cocoons are of minor importance in this respect. Under favourable conditions there will be an exponential population growth, initiated by accelerated maturation of juveniles and hatching of cocoons. Under unfavourable conditions the population will be reduced through retardation of hatching and maturation, and increased mortality.
- In the field experiment with artificial cores, temperature was variable, and moisture was probably not a limiting factor, as during the experiment no dry spells occurred. Thus, the results presented here indicate that the effect of temperature on the life-history was largely overruled by the effect of food availability. This could also be an explanation for the commonly found autumn peak in population density in enchytraeids. Probably, populations of this species react to the supply of fresh organic material and the effect of lower temperatures is of minor importance. The size of a natural population will therefore be mainly controlled by the quality and quantity of food. Predation and parasitism, moreover, may be of importance in determining the hatching success of cocoons.

For other enchytraeid species these mechanisms may not apply. As Springett (1970) has shown, there exist clear differences between various species of potworms as regards appearance of adults and the reproductive period. In view of the properties of *E. buchholzi* deduced here, it may not be excluded that this species lived under suboptimal conditions in the field studied by Springett (1970), which resulted in a prolonged life cycle. The same was found in the present study in the artificial cores without food added. It is hardly conceivable, however, that all species studied by Springett (1970) experienced such adverse conditions. It seems more likely that at least some of these species do have a longer life cycle and hence slower reaction than *E. buchholzi*.

The differences found between the observed and predicted population parameters, and the explanations that may be given for it, again stress that caution is needed in applying laboratory data to field situations. Development of field populations may fall short to predictions based on laboratory data, as is commonly observed, or may exceed those, as is shown in the present study.

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An acceleration of the life cycle under favourable conditions entails a higher activity level and faster population growth than predicted from laboratory observations. Under unfavourable conditions, the life cycle may be prolonged, and size and activity of a population lower than expected. For production ecological calculations this would mean that data on the physiological condition of a population, possibly reflected in its phenology, are indispensable for making adequate estimates of its activity.

It would be highly recommendable, therefore, to establish the main factors that determine the physiological condition of a species, and to carry out life-history experiments varying these factors from extremely unfavourable to extremely favourable. The influence of these factors on life-history characteristics should then be integrated in models for population growth.

5. A method to construct artificial soil cores from field soil with a reproducible structure

(with J.C.Y. Marinissen and B. Kroesbergen)

Abstract

A method is described that allows manipulation of soil structure as a variable in microcosm experiments while leaving other characteristics intact. The basic steps in the method are:
- homogenization of the soil by sieving
- partial sterilization, to eliminate larger biota
- compression of a predetermined amount of soil to a certain volume.

In this way, cores are produced with highly uniform soil physical characteristics. The structure may be adjusted to the needs of an experiment by varying the mesh size in sieving or the amount of soil to be compressed, by introducing artificial macropores, creating artificial barriers etc. The method has been used in experiments on the reactions of soil animals to various pore structures, studies on the changes in soil structure by structure forming animals and studies on root growth.

5.1. Introduction

Practical difficulties are often prohibitive for using soil structure as a variable in microcosm experiments. By definition, the structure of undisturbed soil cores is unknown at the onset of an experiment and large amounts of cores would be needed to account for the high spatial variability in the field. When clay minerals (like vermiculite (Van De Bund, 1972)) or inert material (like glass beads) are used to produce artificial structures, the deviation from natural conditions, for instance in the composition of the microflora and the presence or accessibility of organic material, may be undesirable. Here a method is presented to produce artificial soil cores with a highly reproducible structure using field soil. The method allows adjustment of porosity and, to a lesser extent, pore size distribution.

5.2. Description of the method

Parameters to be known about the soil are:

- specific mass of the solid phase
- the lower plastic limit (Attenberg limit (Burke et al., 1986)) of the soil, i.e. the gravimetric moisture content below which in normal agricultural practice occurring pressures can be exerted with negligible deformation of the aggregates. The cores are to be produced at a gravimetric moisture content below this value.

The desired porosity is to be chosen in advance. This can be total porosity or air-filled porosity. The amount of soil (A) needed can be calculated as follows:

$A=\rho_s V(1-\phi/100)(1+w/100)$ where ϕ is the total porosity aimed at, or

$A=\rho_s V(1-\phi_g/100)(100+w)/(100+\rho_s w)$ where ϕ_g is the air-filled porosity aimed at, and

ρ_s=specific mass of the soil (kg m^{-3})
V=volume of the cores (m^3)
w=gravimetric water content of the soil (% w/w)
ϕ=total porosity (% v/v)
ϕ_g=air-filled porosity (% v/v)

The steps in the production process are:

1. Freeze soil from the field so as to break clods along natural cleavage planes. This step may be skipped if no clods are present.
2. Sieve the soil to homogenize it and to remove coarse material such as stones, remaining large clods and plant debris. Mesh size of the sieve depends on the dimensions of the cores (large aggregates are not suitable for small cores) and the type of structure one wants to produce. Sieving must be done at a gravimetric moisture content well below the lower plastic limit to prevent deformation or disruption of aggregates.
3. Eliminate the larger faunal elements (meso- and macrofauna) by heating the soil to 50°C for at least 30 minutes in a stove. Excessive drying of the soil should be prevented by keeping it in a box or plastic bag.
4. Condition the soil (by spraying or evaporating) to the moisture content at which the artificial cores are to be produced and allow to reach an equilibrium. At this point the prepared soil may be stored in tightly closed plastic bags at low temperature

(to slow down decomposition of organic matter) until it is needed.
5. Weigh the calculated amount of soil needed, pour in a cylinder and compress to the desired volume, using a mechanical press and a stamp of slightly lesser diameter than the diameter of the core. When the press can be adjusted to stop at the right height, there will be no need to gauge pressure.

5.3. Practical considerations

- As a pressure gradient inevitably develops during compression, it is recommended to distinguish upper and lower ends of the cores when they are used in experiments.
- As the pressure gradient develops stronger as higher cores are produced, the ratio of height to diameter of compaction layers may not exceed 0.5.
- Depending on the properties of the soil used, the core will expand more or less after compression. It is recommendable to test to what volume compression should take place to produce the desired volume.
- To prevent unequal distribution of pressure, the soil and the stamp must be level when compressing.
- As heating to 50°C affects nitrifying bacteria, it may be advisable to add cultures of these after the heating process, if normal decomposition of organic matter is considered desirable.
- To obtain an undisturbed soil core after the experiment, a thin (stiff) plastic ring may be mounted to the inner surface of the cylinder (Figure 5.1). To push the core out of the cylinder, a stamp may be used with a diameter large enough to exert pressure to the strip instead of to the soil core.
- Control of animals leaving or entering the soil core can be realized by covering the open ends of the cylinder with nylon gauze, secured to the cylinder with a tight plastic ring (Figure 5.1).
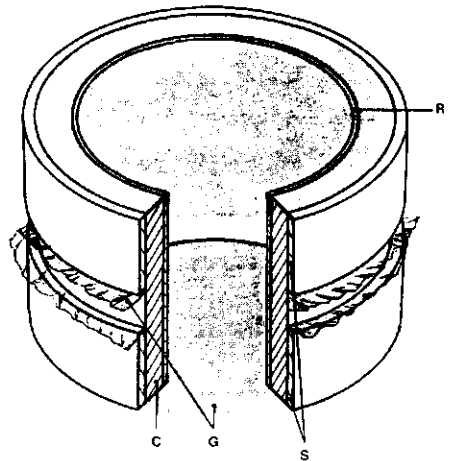

Figure 5.1: Schematic drawing of a cylinder (C) used for the production of artificial cores, with inner plastic ring (R) for obtaining undisturbed cores, nylon gauze (G) and securing rings (S). See text for further details.

5.4. Results

Table 5.1 shows the coefficients of variation in some physical characteristics of artificial cores produced from a marine loam soil compared with data for undisturbed soil cores in the same porosity range from the same field. Note the high uniformity of the artificial cores.

Figure 5.2 is a photograph of a thin section from the same kind of core, in which the occurring pressure gradient is visible, causing the largest pores to be found at the top of the core.

Table 5.1: Coefficients of variation of several physical parameters of field cores and artificial cores from a marine loam arable soil. Moisture content and air content measured at -0.01 MPa water potential. Field data from Anonymous (1984).

	Field cores	Artificial cores
Total porosity	6.26	0.41
Moisture content	4.94	0.78
Air-filled porosity	32.05	3.36
No. of observations	560	19
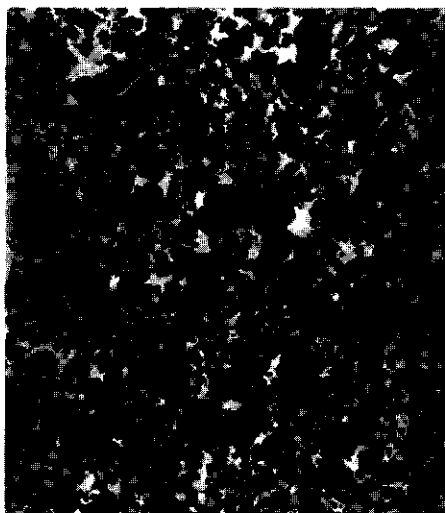
Figure 5.2: Thin section of an artificial core from a marine loam arable soil. Total porosity 46%. Natural width 43.5 mm. Soil sieved with a mesh size of 8 mm.

5.5. Discussion

Cores produced in this way are being used in structure related research on root systems, e.g. by Boone and Veen (1982), who also manipulated pore structure in these cores by making artificial macropores. Didden (1987) used the technique to investigate the reactions of an onychiurid collembolan to different degrees of soil compaction. Didden (1990) studied the influence of enchytraeid activity on soil structure using this technique. Marinissen & Miedema (in press) used multi-layered cores produced by this technique to study tunneling behaviour of earthworms.

The technique further offers possibilities for creating artificial barriers in soil, e.g. to investigate the effect of slaking on soil fauna. Also artificial macropores can be added to study the reaction of roots and/or soil fauna.

6. Involvement of Enchytraeidae (Oligochaeta) in soil structure evolution in agricultural fields

Abstract

The effects of enchytraeid activity on soil structure were recorded in a field study on population dynamics in agro-ecosystems, and in a field experiment, using artificially compounded soil cores. It was established that 21 - 35% of the enchytraeid population contained mineral grains. The estimated transport of mineral material in the upper 0.4 m amounted to 0.001 - 0.01% of the bulk soil per year. In experimental cores with enchytraeids present, the air permeability, the volume of pores in the size class corresponding to enchytraeid body width, and the proportion of aggregates corresponding to the size of their fecal pellets were higher than in cores without enchytraeids.

6.1. Introduction

The problem of soil structure deterioration is receiving increased attention in agriculture. It can be prevented or counteracted to some extent by the structure-forming activities of soil animals. The interactions between soil organisms and soil structure are being investigated as a part of the Dutch Programme on Soil Ecology of Arable Farming Systems (Brussaard et al., 1988), the objective being to accumulate basic knowledge for the development of ecologically sound alternatives to conventional agricultural practices.

When soil structure is defined as the size and arrangement of particles and pores in soil (Oades, 1984), the following aspects of faunal influence on soil structure can be distinguished:

1. Influence on pore structure, i.e. on size and arrangement of pores, through:
   - enlargement, by applying pressure or transporting soil material;
   - reduction, for instance by the filling of pores with material from elsewhere, or as an effect of external pressure;
   - formation of new pores by burrowing.

2. Influence on soil aggregates through:
   - a mechanical reduction in size;
   - joining particles or aggregates, e.g., as part of the formation of fecal pellets;
   - changing the stability of aggregates, for instance by physiological processes in digestion or secretion of mucilages.

For earthworms in particular, many studies have been devoted to the influence of soil fauna on soil structure. The importance of earthworms in the formation of pores, and thus their influence on aeration, drainage, and rootability, and in the production of stable aggregates, has been established beyond doubt (Edwards & Lofty, 1977; Lee, 1985). Other groups of the soil fauna, with the exception of ants and termites, have received much less attention. Yet, it can be expected that, by their way of life, many members of the soil fauna may influence soil structure, such as microarthropods contributing to humus formation (Zachariae, 1963) and dung beetles affecting pore structure (Brussaard & Hijdra, 1986). Enchytraeidae (potworms) are one of the least investigated groups, notwithstanding their abundance in many habitats. Jegen (1920) suggested that these organisms may produce an extensive, be it spatially restricted, burrow system with a spongy appearance. Zachariae (1964), Babel (1968), and Pawluk (1987) have reported occasionally very large portions of enchytraeid excrements in mor and moder humus, but the influence on pore structure has largely been ignored (O'Connor, 1967) or denied (Górny, 1984), and the enchytraeid influence via excrements has been disregarded.

In a field study of the population dynamics of Enchytraeidae in agro-ecosystems (this thesis), a considerable part of the population contained grains of mineral soil. To learn more about the significance of enchytraeid activity for various aspects of soil structure, a field experiment was carried out. This chapter reports the field data and the results of that experiment.

6.2. Methods and materials

6.2.1. The experimental field

Both the field sampling and the field experiment were carried out on the experimental farm 'Dr. H.J. Lovinkhoeve' in the Dutch Noordoostpolder, reclaimed in 1942. The cultivated layer is a silt loam, with a silt fraction (particles < 16 μm) of 30%, 10% calcium carbonate, and pH (KCl) 7.5. Below approximately 25 cm there is a layer of very fine loamy sand. The yearly rainfall is 650 - 800 mm. Since 1986 the crop rotation has comprised winter wheat - sugar beet - spring barley - potatoes.

6.2.2. The field sampling

From April 1986 up to and including April 1988, samples were taken to a depth of
40 cm, mostly at monthly intervals, in two fields at the Lovinkhoeve experimental site,
field 12B, conventionally managed, and field 16A, with an integrated management.
'Conventional' is used to denote ploughing to 25 cm and high inputs of fertilizer and
pesticides. 'Integrated' means a reduced ploughing depth (15 cm) and lower inputs of
fertilizer and pesticides. The organic matter content in the upper 20-25 cm of the two
fields was 2.3% and 2.9%, respectively. A detailed description of the sampling method
and the study area is given elsewhere (Kooistra et al., 1989; chapter 3 of this thesis).
At the Lovinkhoeve experimental site, daily recordings were made of precipitation and
air temperature.

The extracted potworms were individually examined under a microscope, meas-
ured to the nearest mm, and identified to species. From June 1986 onwards the pres-
ence of mineral material in the gut content was recorded during the examination in
three classes as no, few (occupying less than 1/4 of the body length), or many (more
than 1/4 of the body length occupied) mineral parts present. To estimate the quantity of
mineral soil present in the population at a sample date, it was assumed to comprise
quartz grains with a diameter of 60 μm (Babel, 1968) and a specific mass of
2650 kg m^{-3}, and that per mm body length, one such grain was present in animals with
few, and two in animals with much mineral material. To calculate an estimate of the
quantity of mineral soil transported per year by the enchytraeids, it was assumed that
the mean of the estimated amounts per sample date was present throughout the year.
Further, an estimate of the turnover time of the gut content was needed. Taking as an
indication the figures of Bolton & Phillipson (1976), who found a gut turnover time of
1 – 2.5 h for the lumbricid Allolobophora rosea, it was assumed that on average the
turnover time was 2 h.

6.2.3. The field experiment

Artificial soil cores were produced in polyvinylchloride cylinders, with an inner
diameter of 42 mm and a height of 25 mm. On the inner surface of the cylinders a stiff
plastic strip (Elastotherm, 0.5 mm) was mounted, reducing the inner diameter to
41 mm. This strip was used to push the core out of the cylinders without disturbing the
soil structure. The soil used was collected from the ploughed layer at the Lovinkhoeve
experimental site, after tillage. The soil was frozen (-40°C) to imitate the action of frost.
By sieving (wire gauze sieve, 8 mm mesh-size) the soil was homogenized and compo-
nents that could hinder the production of the cores (like stones, coarse organic material

and large soil aggregates) were removed. The soil was then heated to 50°C for at least 30 min, to eliminate macro- and mesofauna without killing all micro-organisms. The prepared soil was stored in tightly closed plastic bags at 4°C.

To produce the artificial soil cores, the moisture content of the soil was adjusted to 22.5% by weight, and 54.39 g soil was compressed in a cylinder. To half of the number of cores produced, 0.5 g sieved (0.3 mm) oat bran was added before compression, to raise the content of decomposable organic material in the soils. The soil cores produced in this way had air-filled pore volumes at a water potential of -0.01 MPa of 13.4 and 12.1%, respectively, with a standard deviation of 0.9% for both types. The physical characteristics of each type of soil core were highly uniform (Didden, 1987).

Three-quarters of the soil cores were supplied with five fresh cocoons of *Enchytraeus buchholzi* from laboratory cultures before the cores were brought into the field. The open ends of the cylinders were covered with nylon gauze of 40 μm mesh-size, which was secured to the cylinder with a tight plastic ring. This mesh size was considered sufficient to prevent even the smallest enchytraeids from leaving or entering the cylinders, while at the same time water movement through the soil cores was not impeded. The soil cores were then adjusted to a water potential of -0.01 MPa and their air permeabilities (according to Kmoch, 1961) determined.

In all, 512 soil cores were produced in this way, 384 of which were supplied with potworms. In the course of 3 weeks in November 1987 they were brought into the field at the Lovinkhoeve experimental site. Soil cores with a slightly larger diameter than the outer diameter of the cylinders were extracted with a steel corer. The artificial cores were placed in the hole, and the hole was closed with part of the previously removed soil core. The place of the cylinders in the field was marked with small sticks with colour bands that indicated the type of core underneath. During the experiment the soil was kept fallow. Half the soil cores were buried at a depth of 2.5 cm (from the top of the cylinder), the other half at 7.5 cm. In the course of the experiment no clear differences between these two groups emerged; they are treated as one group and analyzed as a 2x2 factorial experiment, the four treatments being:

1. Without potworms, without oat bran;
2. With potworms, without oat bran;
3. Without potworms, with oat bran;
4. With potworms, with oat bran.

From January 1988 onwards, 64 soil cores, 8 from each of groups 1 and 3 and 24 from each of groups 2 and 4, were selected every month at random and taken out of the field. In July 1988 the experiment was terminated with the removal of the remaining 128 cores.

The removed soil cores were adjusted to a water potential of -0.01 MPa and their air permeabilities determined. To keep track of the population development of the

enchytraeids, 16 (in July: 32) cores from groups 2 and 4 were extracted each month. To the remaining 8 (in July: 16) soil cores per group, treatments were applied as outlined in Table 6.1.

Table 6.1: Treatments applied to each experimental group of soil cores in the course of the experiment

Month	Impregnation	Determination of aggregate stability	Determination of water retention characteristics
January		4	
February	4		4
March	4	4	
April	4		4
May	4	4	
June	4		4
July	4	6	6

6.2.4. Treatments in field experiment

Extraction procedure followed O'Connor (1967), with slight modifications. The soil cores were left in cold water for 30 min, after which the light intensity, and thus the heat, were slowly increased to reach a maximum of approximately 60°C in 150 min. The total extraction time was thus 180 min.

Impregnation followed the method described by Miedema et al. (1974), after transferring the cores undisturbed from the polyvinylchloride cylinders to stainless steel cylinders of the same inner diameter. After the resin had hardened, the cores were sawn longitudinally and polished. They were studied under a binocular microscope at up to 40 x magnification.

For the determinations of aggregate stability, the wet sieving method (Burke et al., 1986) was used with slight modifications. The air-dried cores were carefully crumbled and the soil was sieved into the fractions 0.15 - 0.3, 0.3 - 0.6 and 0.6 – 1 mm. Each fraction was placed on top of a nest of sieves with decreasing mesh-size, slowly immersed in water, and carefully moved to and fro for 5 min in a standardized way. Afterwards, the amount of each fraction into which the aggregates fell apart was determined by drying and weighing the amount of soil in each sieve. The figures used in the calculations were the percentage left in the upper sieve and the mean weight diameter of the aggregates in the non-stable portion. Each determination was carried out in duplicate.

The water retention characteristics were determined after heating the soil cores, wrapped in plastic, for at least 30 min at 50°C, to terminate the activities of the pot-worms present. Measurements were made in the range -0.001 to -0.01 MPa water potential, representing equivalent pore diameters of 300 - 30 μm, on sand plates.

6.3. Results

6.3.1. The field sampling

Table 6.2 lists the percentages of the potworm population carrying mineral grains and the correlations with mean air temperature and total precipitation for various depths. At all depths, the percentage of potworms carrying mineral material in the gut was less in the integrated field, the difference being significant ($P<0.005$, t-test) for the 10 - 25 and 25 - 40 cm layers and for the sampled depth as a whole. In both fields there was a negative correlation with temperature [significant at the 5% level, except for the 10 - 25 cm layer in the integrated field (16A) and the 0 - 5 cm layer in the conventional field (12B)]. There was a slight positive correlation with the amount of precipitation (significant at the 5% level only for the 5 - 10 cm layer in the integrated field and the 10 - 25 cm layer in the conventional field).

Table 6.2: Percentages of the population carrying mineral grains, averaged for various depths over the sample period, and the correlations with mean air temperature (R_{Temp}) and total precipitation (R_{Prec}) of the 3 weeks preceding a sampling

	Field 16A (integrated)				Field 12B (conventional)			
Depth (cm)	0-5	5-10	10-25	25-40	0-5	5-10	10-25	25-40
% with grains	15.5	18.7	23.8	28.8	28.3	21.7	38.0	40.8
R_{Temp}	-0.25	-0.47	-0.15	-0.28	-0.08	-0.27	-0.37	-0.33
Probability	0.016	<.001	0.129	0.006	0.560	0.021	<.001	0.004
R_{Prec}	0.19	0.20	0.16	-0.02	0.03	0.15	0.20	0.21
Probability	0.072	0.049	0.097	0.882	0.800	0.220	0.038	0.071

Table 6.3 presents the relative abundance of the most abundant species and the percentages of their populations carrying mineral grains. This table shows appreciable differences between species in the carriage of mineral material. For *Enchytraeus buchholzi*, the dominant species in both fields, the percentage of animals carrying mineral grains was less than 20 in both fields, whereas the other species were relatively much more involved. In the conventional field, all species carried mineral material to a larger extent than in the integrated field, the difference being significant at the 5% level (t-test) for *Enchytraeus buchholzi* and *Fridericia sp. B* and highly significant (P<0.001, t-test) when all species were analyzed together.

Table 6.3:The most abundant species at the Lovinkhoeve experimental site, their relative abundance (as percentage of total population), and the percentage of their population carrying mineral grains, averaged over the sample period, layer 0 - 40 cm

Species	Field 16A (integrated)		Field 12B (conventional)	
	Relative abundance	Percentage with mineral grains	Relative abundance	Percentage with mineral grains
Enchytraeus buchholzi	65.3	12.2	57.3	18.5
Henlea perpusilla	8.3	32.6	7.2	39.5
Fridericia sp. A	9.9	33.7	3.1	35.0
Fridericia sp. B	10.3	54.3	27.0	70.2
All species		21.2		35.4

The estimated quantities of mineral soil transported by the enchytraeid population during the sampling period are given in Table 6.4. Here, the estimates for 1986 and 1987 are calculated separately because in the wet summer of 1987 the numbers of potworms, and thus the estimates of mineral material transported, were much larger. Generally, more mineral soil was transported in the conventional field (12B). In the upper 10 cm of the profile, however, more material was transported in the integrated field (16A). Expressed as a proportion of the bulk soil volume, the transport in both fields was in the order of merely 0.001 - 0.01%.

Table 6.4: The estimated quantities (g/m²/year) of mineral soil transported by the enchytraeid population at various depths

Depth (cm)	Field 16A (integrated)		Field 12B (conventional)	
	1986	1987	1986	1987
0 - 5	1.1	10.3	0.7	4.1
5 - 10	0.9	5.4	0.8	6.9
10 - 25	4.8	16.7	6.3	37.6
25 - 40	3.5	9.1	6.5	26.3
0 - 40	10.3	41.5	14.3	74.9

6.3.2. The field experiment

Figure 6.1 shows the population development of the enchytraeids in the experimental soil cores together with the percentage of their population involved in the transport of mineral material. There was a significant negative correlation between this percentage (P=0.003 for cores without oat bran, P<0.001 for cores with oat bran) and the mean air temperature for the 3 weeks preceding the sampling.
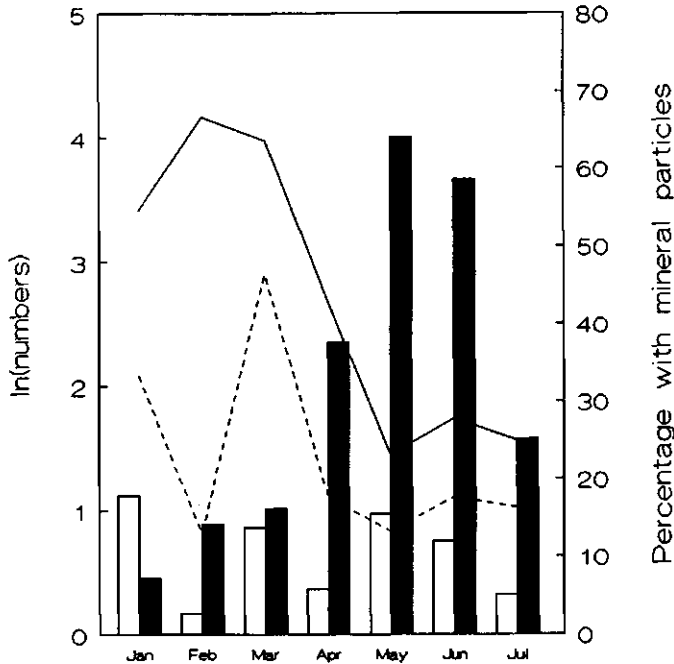

Figure 6.1: Population development of enchytraeids in experimental cores (bars) and the percentage of animals (lines) in the population containing mineral particles. Bars represent numbers (natural logarithms) per core

☐ Without oat bran   ■ With oat bran

In the cores without oat bran, population development started earlier, resulting in significantly more enchytraeids (P=0.05, Mann-Whitney test) on the first sampling occasion, in January 1988. Subsequently, the population development was most extensive in the cores with oat bran added (P<0.05, Mann-Whitney test, except in March and July). It is likely that the decline of the population after May 1988 coincided with depletion of the available food. Throughout the experimental period, the percentage of the population carrying mineral grains was largest in the soil cores without oat

bran. In both types, the highest percentages occurred in the period January through April. The actual numbers of animals carrying mineral grains remained fairly constant in the soil cores without oat bran, while in the cores with oat bran the highest numbers were found in the period from April through June. The total weight of transported mineral soil in the experimental period, using the same assumptions as above, was estimated as 0.5 mg for the cores without oat bran, and 3.5 mg for the cores with oat bran, where the population development was much more extensive. Expressed as percentages of the total cylinder volume on a yearly basis, this represented 0.001 and 0.004%, respectively.
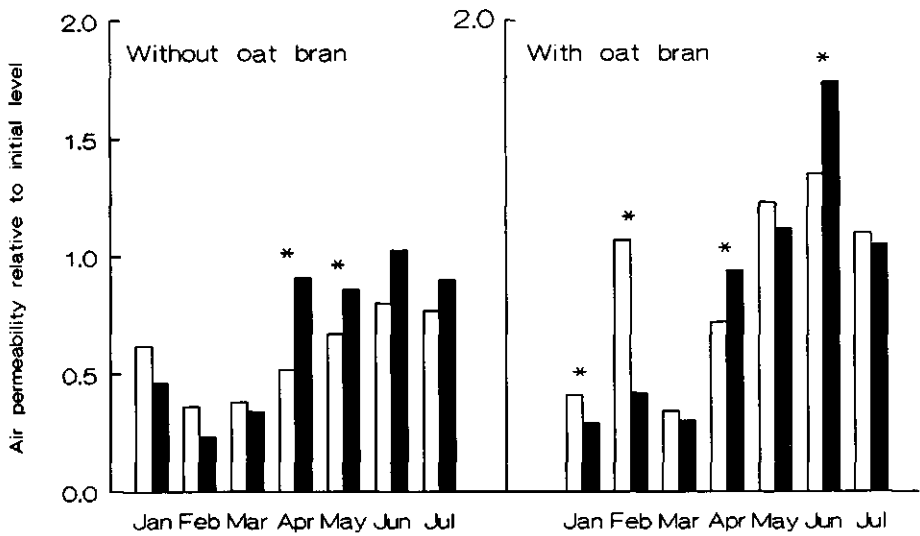
Figure 6.2: Air permeability in experimental cores, relative to values determined at start of experiment. *: P<0.01, significant difference in pairs, Mann-Whitney test

☐ Without potworms   ■ With potworms

The influence of the potworms on the pore structure of the soil cores was reflected in the measurements of air permeability and the water retention characteristics. Figure 6.2 shows the changes in air permeability, relative to the values determined at the start of the experiment. In the cores without oat bran air permeability initially declined, followed by a rise from April onwards to approximately the starting values. This trend was stronger in the cores with potworms present, the difference being significant in April and May (P<0.05, Mann-Whitney test). In the cores with oat bran this pattern was more complicated, with an additional rise in air permeability in February in the cores without potworms, and the difference between cores with and without potworms not as consistent from April onwards as in the cores without oat bran. Table 6.5 sums up the results of the analysis of variance, carried out separately on the cores with and without

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Table 6.5: Results of the analysis of variance (P values) of measured air permeability in cores with and without oat bran

Source of variation	Without oat bran	With oat bran
Time	<0.001	<0.001
Enchytraeids	0.004	0.692
Interaction	0.622	0.003
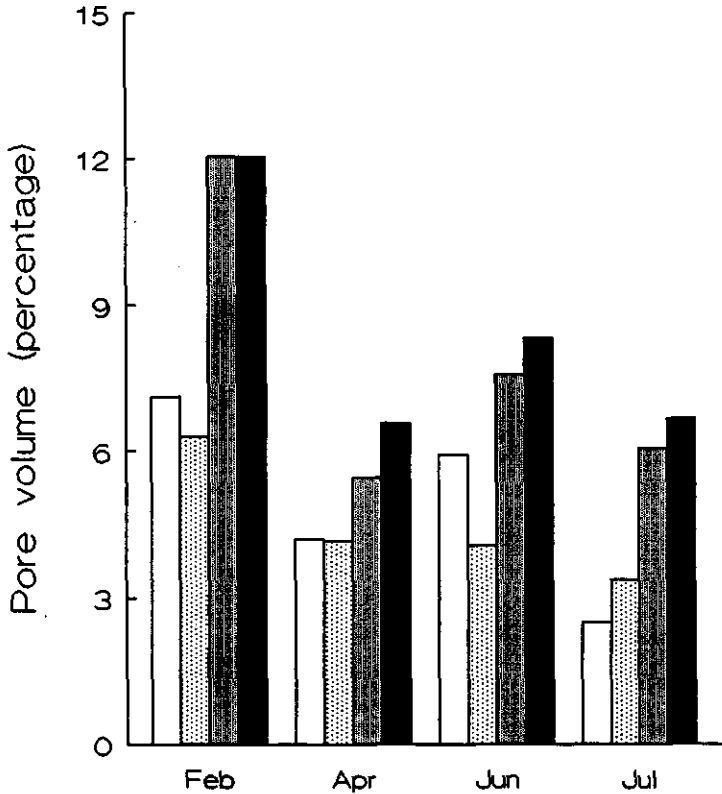
*Figure 6.3: Pore volumes (size class 50 - 200 µm), calculated from water retention characteristics, in the course of the experiment*

Without oat bran:	☐	Without potworms	▦	With potworms
With oat bran:	▨	Without potworms	■	With potworms

oat bran. In both types of cores the effect of time was highly significant; in the cores without oat bran there was also a significant effect of potworms and in cores with oat bran a significant interaction between time and potworms.

From the water retention characteristics the percentages (by volume) of several pore size classes were calculated. Figure 6.3 presents the results for the size class 50 - 200 μm. In cores with oat bran the pore volumes in this size class were on average 0.85% higher with potworms present (P=0.059; analysis of variance). In soils without oat bran and in other size classes no significant effects were detected.

A microscopic study of the resin-impregnated cores showed that the activity of the potworms was clearest at the periphery of the larger soil aggregates. At the start of the experiment these were, as a consequence of the production technique, more or less rounded. Probably as a result of the removal of material from the periphery of the aggregates by the enchytraeids, this shape changed to a more irregular form (Fig. 6.4).
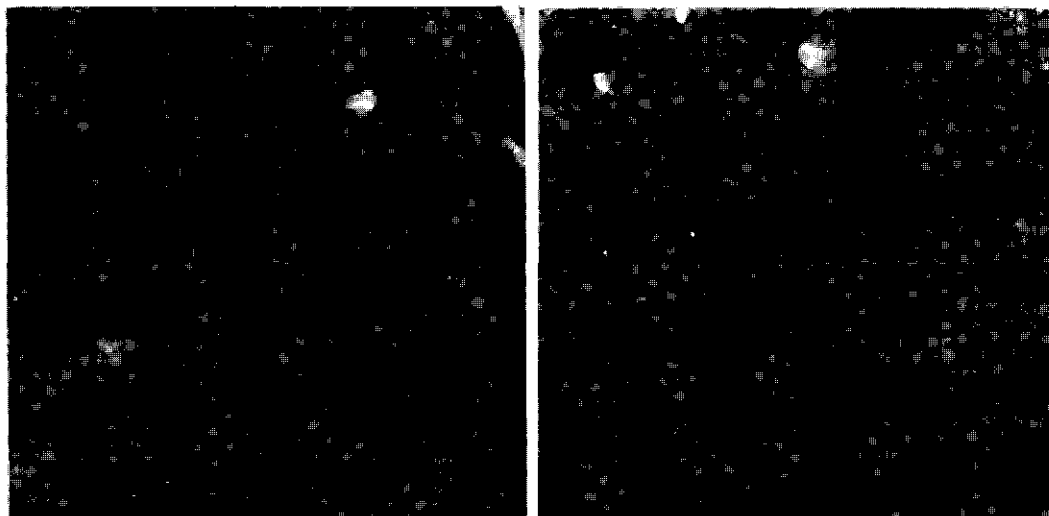
Figure 6.4: Indications of enchytraeid activity in experimental cores with oat bran added; photographs from polished blocks, with incident light; width of view 4 mm. Left, a core at the start of the experiment; Right, a core with enchytraeids after 6 months in the field

In all treatments aggregate stability declined in the course of the experiment. Figure 6.5 shows the aggregate stabilities and mean weight diameters of the non-stable portion for the size classes 0.6 - 1 mm and 0.3 - 0.6 mm. Table 6.6 lists the P values in the analysis of variance. In cores without oat bran, the aggregates in both size classes were generally less stable when potworms were present, but the decline in the course of time was also less. In the size class 0.6 - 1 mm the mean weight diameter of the non-stable portion became smaller in the course of the experiment, but less so with enchytraeids present. In the cores with oat bran no clear tendencies were detected.
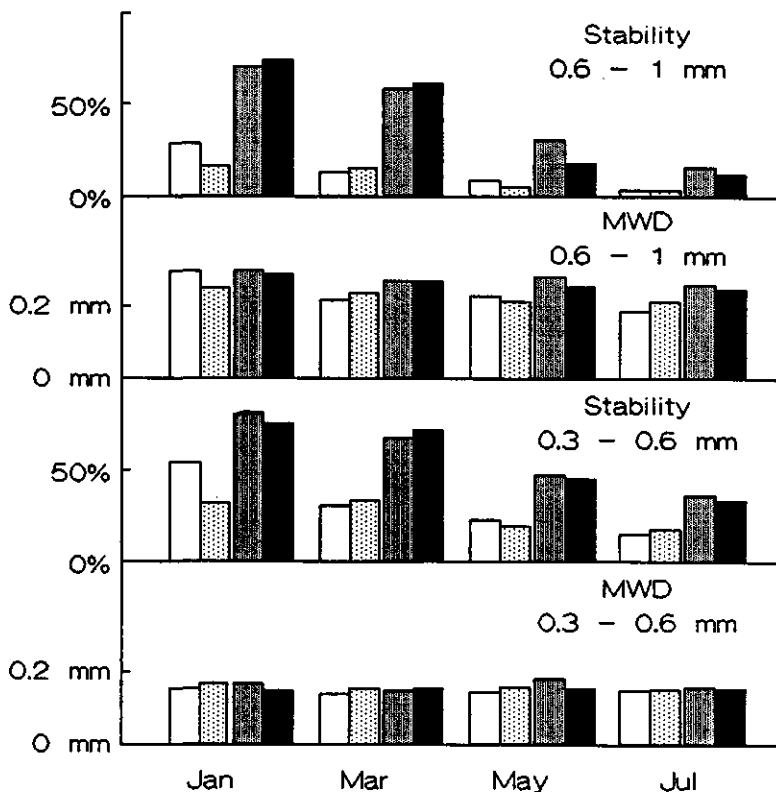
Figure 6.5: Course of aggregate stability and mean weight diameter (MWD) of the non-stable portion for the size classes 0.6 - 1 mm and 0.3 - 0.6 mm

Without oat bran: [ ] Without potworms   [░] With potworms

With oat bran: [▓] Without potworms   [■] With potworms

Table 6.6:Results of the analysis of variance (P values) for the stability of aggregates in the size classes 0.6-1 and 0.3-0.6 mm, and the mean weight diameters (MWD) of the non-stable portions

soil aggregates		0.6 - 1 mm		0.3 - 0.6 mm	
		Stability	MWD	Stability	MWD
Without oat bran:	Time	<.001	<.001	<.001	0.239
	Enchytraeids	0.006	0.219	0.034	0.464
	Interaction	0.001	0.010	0.036	0.368
With oat bran:	Time	<.001	0.002	<.001	0.008
	Enchytraeids	0.624	0.068	0.964	0.146
	Interaction	0.356	0.559	0.875	0.101

6.4. Discussion

There was an apparent difference between the two fields used in the field sampling in the estimated amounts of mineral material transported at various depths. In the conventional field most material was transported in the deeper (10 - 40 cm) layer, while in the integrated field the top layer was affected to a greater extent. Although the total amount transported was higher in the conventional field, this may imply that the influence of enchytraeid activity on conditions for germination of seeds and on soil aeration is stronger in the integrated field.

The negative correlation, found both in the field sampling and in the experiment, between the mean air temperature and the percentage of animals carrying mineral grains, remains a phenomenon that requires explanation. There may be a change in feeding behaviour in response to temperature changes. Assuming that enchytraeids feed mainly on microflora (Toutain et al., 1982) it is possible that at higher temperatures, when the microfloral growth on organic material is high, this material is preferentially selected. At lower temperatures it would be necessary for the animals to feed indiscriminately, ingesting mineral grains also, to be able to obtain enough food.

There was good agreement between the percentages of animals carrying mineral material in the field sampling and in the field experiment. This also held for the estimates of the amounts of mineral material transported, which in all cases was in the order of 0.01 to 0.001% of the soil volume. Both in the field sampling and in the field experiment the percentage of the population carrying mineral material was lower when the organic matter content was higher, indicating that enchytraeids feed more selectively on organic matter when this is available. In the experimental cores that had oat bran added, the amount of transported material was nevertheless higher, because of the much larger populations in these cores.

The decrease in aggregate stability with time, occurring in all treatments, may well agree with the findings of Guidi et al. (1988), who found a clear seasonal fluctuation in aggregate stability. In the soil cores without oat bran the activity of enchytraeids led to a generally lower aggregate stability in the size classes 0.6 - 1 and 0.3 - 0.6 mm. However, the stability of these aggregates and the mean weight diameter of the non-stable portion in the 0.6 - 1 mm size class decreased faster in the course of time when no enchytraeids were present. These results indicate that these aggregates might have been partly composed of fairly stable enchytraeid excrements, with a diameter of about 0.2 mm. No such effects were detected in the cores with oat bran added, in spite of the larger populations of potworms in these cores, where the stabilizing effect of the added organic matter might have masked their influence. Another possibility is that the properties of the excrements were influenced by the kind of food consumed, as found for earthworms (Shipitalo & Protz, 1988).

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The changes in air permeability that occurred in the field experiment, suggest that *Enchytraeus buchholzi* influenced the pore-size distribution or pore continuity. In the soil cores with oat bran added, there was an increase of about 0.85% in pore volume for pores in the size class 50 - 200 µm, indicating an influence on pore size distribution. The non-significant interaction between time and potworms in the soil cores without oat bran agrees with the fairly constant number of animals carrying mineral grains. As air permeability is very sensitive to changes in pore size and pore continuity, enchytraeids may affect either one or both aspects of soil structure. At the same time, the estimated amount of mineral soil transported per year by potworms was, both in the field sampling and in the field experiment, in the order of magnitude of only 0.001 - 0.01% of the bulk soil volume. In trying to reconcile this apparent contradiction, the following should be kept in mind.

1. Pore size distributions as determined from water retention curves are *equivalent* pore size distributions and pore necks play an important role in the calculated pore volumes (Bouma, 1977). Removal of pore necks may change the equivalent pore size distribution and give a better pore continuity, without much material being removed.
2. Enchytraeids do not only transport mineral grains. During feeding, organic material is also transported. In the soil cores with oat bran added, the rise in pore volume in the size class 50 - 200 µm may have been partly due to the clearing of pores from the oat bran. At the same time, excrements are produced and deposited in the soil, which may also influence the equivalent pore-size distribution and pore continuity.
3. Another way to produce changes in pore structure is by applying pressure to the pore walls, thereby enlarging some and diminishing others.

A preliminary microscopic study of polished blocks of enchytraeid-reworked soil has confirmed that removal of pore necks is a likely mechanism. Further analysis of the blocks will be undertaken.

It is concluded that enchytraeids may contribute significantly to the evolution of soil structure in agro-ecosystems. Although active burrowing is of minor importance in view of the low quantities of soil transported, enchytraeids increase pore continuity; raise the volume of pores of a size corresponding to their body size; and raise the proportion of aggregates corresponding to the size of their fecal pellets. For agricultural practice, this may mean better rootability of the soil, better aeration and a reduced sensitivity to slaking. These effects will be stronger when enchytraeid activity is concentrated in the upper layer of the soil, as is the case in fields with reduced tillage depth.

7. Synthesis

The central questions with which this study started out were:

1. What do Enchytraeidae contribute to soil structure evolution in differently managed agricultural fields?
2. What is the significance of enchytraeid populations in differently managed agricultural fields concerning decomposition of organic matter and nutrient dynamics?

An evaluation of the current knowledge on the ecology of terrestrial enchytraeids learned, that relatively little data on these questions are available, the paucity of information mainly originating from:

- The comparatively late start of ecological studies on enchytraeids, that, moreover, were largely conducted in natural habitats.
- The small number of ecological studies addressing this oligochaete family on the species level, and the resulting lack of data on species-related, ecological characteristics like food preference, ecological strategies, life-history, and energetical efficiency.

As a corollary of this lack of specific knowledge, an attempt to quantify the ecological significance of enchytraeid populations has to rely on the generalization of data on a few species or on general assumptions about this family. Therefore, the need for fundamental ecological research on the species level was stressed, and some basic research was conducted.

In this thesis, basic ecological data are given on length-weight relations of the enchytraeid species occurring at the Lovinkhoeve experimental site, and on the life-history of *Enchytraeus buchholzi*. In presenting the life-history data, the problematic character of the translation of laboratory results to field situations has been emphasized by comparing predictions from the laboratory study with observations from artificial soil cores. It appeared, that the population development of this species under field conditions could deviate strongly, both negatively and positively, from predicted development.

The results of population dynamical and production ecological research conducted at the Lovinkhoeve experimental site, made it clear that the enchytraeids constituted a noteworthy faunal group in the four farming systems studied. It was calculated, that the enchytraeid populations respired 0.5-3.7% of the organic carbon input to the systems,

and that the nitrogen-flux through enchytraeid biomass amounted to 0.19-0.60 g N/m²/yr.

Generally, there were no significant differences between the systems studied, as regards species composition, population densities, biomass and production ecological parameters. There were, however, significant differences concerning the vertical distribution of the enchytraeid populations. In fields with integrated management, the populations were generally concentrated in the upper layers of the soil profile, whereas in the conventionally managed field populations were more uniformly distributed, or even concentrated in deeper layers. These differences were associated with differences in tillage practices, which resulted in differences in the distribution of plant remains. These phenomena were also observed in data of various other groups of soil organisms on the same site (Brussaard et al, 1990).

Thus far, no quantitative research on the effects of enchytraeids on the evolution of soil structure had been conducted, notwithstanding the abundance of enchytraeids in many habitats, and only conjectures and qualitative indications existed. In this thesis, a method was presented to study interactions between enchytraeids and soil structure under controlled, near-natural conditions. For this, artificial soil cores were produced, that had a reproducible and largely predefined soil structure. The effects of enchytraeid activity on soil structure were recorded in a field experiment, using such artificially composed soil cores, and in a field study on population dynamics. It was established that in the experimental cores with enchytraeids present, the air permeability, the volume of pores in the size class corresponding to enchytraeid body width, and the proportion of aggregates corresponding to the size of their fecal pellets were higher than in cores without enchytraeids. From the field study it appeared that 21 - 35% of the enchytraeids in the Lovinkhoeve populations contained mineral particles, and hence were involved in translocation of this material. The estimated transport of mineral material in the upper 0.4 m, however, amounted to only 0.001 - 0.01% of the bulk soil volume per year.

There was an apparent difference between the conventional and the integrated farming systems in the calculated amounts of mineral material transported at various depths. In the conventional field most material was transported in the deeper (10 – 40 cm) layer, whereas in the integrated field the top layer was affected to a greater extent. Hence, this phenomenon was also associated with the distribution of plant remains.

Although until now only few studies have quantitatively addressed the effect of Enchytraeidae in arable systems, and the various studies can not be compared directly, some generalities are apparent:
- Enchytraeids play an appreciable role in the flows of energy and nutrients in agroecosystems. Direct contribution to total soil metabolism is in the order of

magnitude of only 1%, and is similar to that in more natural habitats (Gołębiowska & Ryszkowski, 1977; Parmelee, 1987; Lagerlöf et al., 1989; this thesis). Indirect effects (notably through their influence on microbial activity) probably will be much higher. Nitrogen flux through enchytraeid biomass may amount to 0.1 - 1 g $N/m^2/yr$ (Paustian et al., 1990; this thesis), and probably will be higher when the production of excreta are taken into account (Christensen, 1988). The total contribution (direct and indirect) of enchytraeids to nitrogen mineralization has not yet been established in agroecosystems, but results from microcosm experiments suggest that enchytraeid activity may enhance nitrogen mineralization by as much as 18% (Abrahamsen, 1990).

- Enchytraeids affect soil structure evolution through the production of excrements and mucilages (Babel, 1968; Pawluk, 1987; this thesis), that may have a stabilizing effect on soil structure (Toutain et al., 1983), and through their burrowing activity (Jegen, 1920; Kubiena, 1955; this thesis), thereby influencing aeration and rootability of the soil. In agricultural fields, these effects are possibly smaller than in more natural habitats (Thompson et al., 1990), but from the present study it appears, that they may be quantitatively important on a field scale.

- Enchytraeid populations are influenced by various agricultural management practices, notably through effects on amount and distribution of organic material in soil. It has repeatedly been shown that the quantity and quality of organic matter supplied to the soil affects enchytraeid numbers, biomass and activity (Sauerlandt & Marzusch-Trappmann, 1959; Kleyer & Babel, 1984; Lagerlöf & Andrén, 1985; Nakamura, 1988; this thesis).
Depth and type of tillage influences the vertical distribution of enchytraeid populations and hence their activity, through its influence on the distribution of fresh organic material (Ryl, 1977; Zimmermann, 1987; Lagerlöf et al., 1989; this thesis). The type of crop grown may also be of importance for the size and composition of enchytraeid populations in arable fields (Ryl, 1980; Lagerlöf et al., 1989), root crops being more favourable than cereals (Ryl, 1980).

Seasonal fluctuations in abundance and activity are an important aspect of enchytraeid effects on the functioning of arable systems. From the present study it appears, that maximum population sizes and maximum activity occur in spring and early summer, when crop demands for nutrients usually are highest. Beneficial effects of enchytraeid activity will at that time consist of their influence on soil structure and of their indirect promotion of nutrient mobilization. On the other hand, enchytraeid populations will constitute a, be it rather small, pool of immobilized nutrients, in the order of magnitude of 0.1 g N/m^2. These nutrients will be released in summer and early autumn, when populations, but also the need for nutrients of most crops, are diminishing. Assuming that enchytraeid tissue, like earthworm tissue, is rapidly decomposed and mineralized (Satchell, 1967; Christensen, 1988), this might imply a loss of nutrients

from the system. The use of fast growing cover crops, as was suggested by Christensen (1987) in connection with earthworm populations, might help to circumvent the problem of nutrient loss in this period.

A second important feature of the effects of enchytraeid activity in agroecosystems, is the vertical distribution of the populations. It may be supposed, that advantageous effects on nutrient mobilization and soil structure evolution will be largest, and chances of nutrient loss less, when enchytraeid activity is concentrated in the upper soil layers, where most of the roots are. This is the case in the integrated farming system studied. Conversely, enchytraeid activity concentrating in deeper layers, as in the conventional farming system studied, may be deemed less advantageous, because of the presence of less roots and, therefore, greater chance of leaching of nutrients.

Hence, enchytraeids do play an important part in the functioning of arable systems in temperate regions. It would seem however, that concentration of enchytraeid activity in the upper layers of the soil profile is more advantageous, and helps to diminish the risk of nutrient leaching and soil structure deterioration.

Integrated agriculture will benefit most from the activities of these animals, when management practices include shallow tillage, organic fertilization and the use of cover crops.

8. Summary

West-European contemporary ('conventional') agriculture is characterized by high inputs of energy and matter, and has led to serious environmental problems, such as pollution of water and atmosphere, side-effects of pesticides, and deterioration of soil structure. As a consequence of these problems, there is an increasing interest in ecologically sound agricultural systems, in which management practices are tuned to both economic and environmental demands. One of the approaches in this respect, is the development of 'integrated' agriculture, characterized by lower input, but more efficient use, of energy and matter, and by yield reduction, to be balanced by the reduction of costs. For more efficient use of energy and matter, an important part is to be played by biological processes in soil. To manage these processes properly, accurate knowledge of the contribution of organisms and groups of organisms to the functioning of agroecosystems is needed. This thesis deals with the question of the part played by enchytraeids (Enchytraeidae, Oligochaeta) in agroecosystems, both in the flows of energy and matter, and in soil structure evolution. The research reported here, was mainly conducted on various differently managed fields on the experimental farm 'Dr. H.J. Lovinkhoeve' in the Dutch Noordoostpolder.

Thus far, little is known about the part enchytraeids play in ecosystems, both natural and managed. A critical review of the ecological literature showed, that, although it is clear that enchytraeids must constitute an important faunal group in the soil of many terrestrial ecosystems, their part is difficult to quantify because of scanty knowledge of the factors influencing population dynamics and activity. This is because most studies have not been carried out at the species level, while it is clear that there exist appreciable interspecific differences as regards biology and response to environmental factors.

Population dynamics, production ecology and role in nutrient cycling of Enchytraeidae were studied during three years in four arable fields at the Lovinkhoeve experimental site. A 'conventionally' (with high input of energy and matter) managed field was studied, along with three fields with various 'integrated' (with reduced input) management types. Mean yearly enchytraeid abundance and biomass in these systems ranged from 11000 ind/m^2 to 43000 ind/m^2 and from 0.08 g C/m^2 to 0.42 g C/m^2 respectively. The direct contribution of enchytraeids to the flows of energy and matter was calculated, based on field data and parameters from the literature. In the conventionally managed field 1.02 - 2.58% of the yearly organic carbon input was respired by the enchytraeids, in fields with integrated management this was 0.52 - 3.73%. Yearly nitrogen flux from the populations (through storage in enchytraeid tissue) was calcu-

lated to range from 0.19 to 0.60 g/m². The indirect contribution to the flows of energy and matter, through the effects of enchytraeid activity on other organisms, notably microorganisms, could not be determined, but may well be higher.

In general no significant differences in seasonal dynamics, mean abundance and biomass between the investigated fields were found. However, a pronounced difference between the conventionally managed field and the fields with integrated management was found as regards vertical distribution of the enchytraeids: in the integrated fields the populations were more concentrated in the surface layers, and in the conventional field they were more evenly distributed in depth. There are strong indications that the vertical distribution was to a large extent influenced by soil tillage and the distribution of enchytraeids coincided with that of organic fertilizer and plant residues. As a consequence of this difference in vertical distribution, there may be a greater risk of leaching of nutrients from a conventionally managed field as opposed to fields with integrated management.

During the growing season, the enchytraeid distribution was also influenced by the position of the crop plants, indicating an association of the enchytraeids with root exudates, either directly or through microorganisms.

Part of the research reported in this thesis was of a fundamental nature, and concerned determination of life-history parameters of *Enchytraeus buchholzi*, the most abundant species at the Lovinkhoeve experimental site. Laboratory experiments were carried out, in which development times, numbers of cocoons and eggs produced, and longevity were determined at various temperatures. To determine the relevance of these parameters for processes occurring under field conditions, population development under more natural conditions was also studied. By a simple simulation model, these data were compared with predictions based on the laboratory trials. The comparisons/showed, that population development under field conditions may fall short to predictions as regards abundance, but on the other hand, that individual development could be appreciably faster than predicted. It seems probable, that the discrepancies found are related with the physiological condition of the experimental animals, and that the life-cycle may be prolonged under unfavourable conditions, but accelerated under favourable conditions.

The research addressing the influence of enchytraeid activity on soil structure evolution, made use of data from the population-dynamical study, and from a field experiment in which artificial soil cores were used, with highly reproducible soil physical characteristics. In this thesis, the method is described to produce such artificial soil cores in which soil structure may be manipulated as a variable. The basic steps in the method are:
- homogenization of the soil by sieving
- partial sterilization by heating, to eliminate metazoic animals

- compression of a predetermined amount of soil to a certain volume.

The structure may be adjusted to the needs of an experiment by varying the mesh size in sieving or the amount of soil to be compressed, by introducing artificial macropores, creating artificial barriers etc.

In the field study on population dynamics it was established that 21 - 35% of the animals in the enchytraeid populations carried mineral grains in the digestive tract. The calculated transport of mineral material in the upper 0.4 m amounted to 0.001 - 0.01% of the bulk soil per year. From this, it may be concluded that active burrowing by enchytraeids is quantitatively of minor importance.

From the field experiment, however, an appreciable effect of enchytraeid activity on soil structure appeared: in experimental cores from Lovinkhoeve soil, with enchytraeids present, the air permeability, the volume of pores in the size class corresponding to enchytraeid body width, and the proportion of aggregates corresponding to the size of their fecal pellets were higher than in cores without enchytraeids. This effect may be explained by the removal of pore necks during burrowing, and by the transport of organic besides mineral material. This hypothesis is currently being tested, using polished blocks from the artificial soil cores.

General conclusions can be summarized as follows:

- Direct contribution of enchytraeids (through their metabolism) to the flows of energy and nutrients in agroecosystems is in the order of magnitude of 1%, and is similar to that in more natural habitats. Indirect effects (notably through their influence on microbial activity) may be much higher.
- The evolution of soil structure is affected by enchytraeids in several ways: through the production of excrements and mucilages that may have a stabilizing effect on soil structure, and through their (selective) burrowing activity, thereby influencing aeration and rootability of the soil.
- Enchytraeid populations are influenced by various agricultural management practices, notably through effects on amount and distribution of organic material in soil. Thus, depth and type of tillage influences the vertical distribution of enchytraeid populations and hence of their activity. The type of crop grown may also be of importance for the size and composition of enchytraeid populations in arable fields.

Seasonal fluctuations in abundance and activity are an important aspect of enchytraeid effects on the functioning of arable systems. From the research presented in this thesis it appears, that maximum population sizes and maximum activity almost completely coincide with the period of maximum crop growth, when crop demands for nutrients usually are highest. Beneficial effects of enchytraeid activity will at that time

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consist in their influence on soil structure and in their indirect promotion of nutrient mobilization. Nutrients stored in enchytraeid tissue will mainly be released in summer and early autumn, when populations, but also the need for nutrients of most crops, are diminishing. The risk of loss of nutrients from the system, notably in conventionally managed fields, may be counteracted by the use of fast growing cover crops.

Ecologically sound agriculture will therefore benefit most from the activities of these animals, when management practices include shallow tillage, organic fertilization and the use of cover crops.

9. Samenvatting

De in West-Europa gangbare ('conventionele') landbouwmethodes worden geken-
merkt door een hoge input van energie en grondstoffen, en blijken aanleiding te geven
tot ernstige milieuproblemen, zoals vervuiling van water en atmosfeer, neveneffecten
van bestrijdingsmiddelen en verslechtering van de bodemstructuur. Tegen de achter-
grond van deze problemen bestaat er een toenemende belangstelling voor oecologisch
verantwoorde landbouw, waar in de beheersmaatregelen zowel met economische als
met milieu-eisen rekening wordt gehouden. Een van de benaderingen hierbij is het
streven naar 'geïntegreerde' landbouw, gekenmerkt door minder input, maar efficiënter
gebruik, van energie en grondstoffen, en door een lagere opbrengst, die wordt gecom-
penseerd door lagere kosten. Voor dit efficiënter gebruik van energie en grondstoffen
is een belangrijkere rol weggelegd voor biologische processen in de bodem. Om zo
goed mogelijk van deze processen gebruik te kunnen maken, is kennis vereist van de
bijdrage van organismen en groepen van organismen aan het functioneren van land-
bouwsystemen. In dit proefschrift staat de vraag centraal naar de rol van potwormen
(Enchytraeidae, Oligochaeta) in agro-oecosystemen, zowel wat betreft de energie- en
stofstromen die hier optreden, als wat betreft hun rol in de ontwikkeling van de bodem-
structuur. Het onderzoek waarvan hier verslag wordt uitgebracht concentreerde zich op
enkele verschillend beheerde akkers op de Dr. H.J. Lovinkhoeve in de Noordoost-
polder.

Wat betreft potwormen is nog maar weinig bekend over hun rol in oecosystemen,
zowel in natuurlijke als agro-oecosystemen. Een kritisch onderzoek van de oecologi-
sche literatuur op het gebied van potwormen leerde, dat enerzijds duidelijk is dat pot-
wormen in veel terrestrische oecosystemen een belangrijke groep van de bodemfauna
moeten vormen, anderzijds hun rol moeilijk te kwantificeren is, omdat in de meeste
gevallen geen duidelijkheid bestaat over de factoren die een rol spelen bij hun aantal-
sontwikkeling en activiteit. Dit komt voort uit het feit dat in de meeste gevallen geen
onderzoek op soortsniveau heeft plaatsgevonden, terwijl tegelijkertijd duidelijk is, dat er
aanzienlijke verschillen bestaan tussen soorten wat betreft hun biologie en hun reactie
op omgevingsfactoren.

Onderzoek aan de populatiedynamiek van potwormen, hun productie-oecologie en
hun rol in de stofkringlopen werd gedurende drie jaar uitgevoerd op vier akkers op de
Lovinkhoeve. Hier werd een 'conventioneel' (met hoge input van energie en grondstof-
fen) beheerde akker bestudeerd, naast op verschillende manieren 'geïntegreerd' (met
verminderde input) beheerde akkers. De gemiddelde jaarlijkse dichtheid en biomassa
van potwormen in deze systemen varieerden respectievelijk van 11000 ind/m^2 tot

43000 ind/m^2, en van 0.08 g C/m^2 tot 0.42 g C/m^2. De directe bijdrage van potwormen aan de energie- en stofstromen werd berekend op basis van de veldwaarnemingen en parameters uit de literatuur. In de 'conventioneel' beheerde akker werd 1.02 - 2.58% van de jaarlijkse input aan organische koolstof door de potwormpopulaties verademd; in de 'geïntegreerde' akkers was dit 0.52 - 3.73%. Tevens werd berekend dat de hoeveelheid stikstof die jaarlijks, via opslag in potwormweefsel, de populaties verliet, varieerde van 0.19 tot 0.60 g/m^2. Hun indirecte bijdrage aan de energie- en stof-stromen, via de invloed op het functioneren van andere organismen, met name bac-teriën en schimmels, kon niet worden bepaald, maar het lijkt waarschijnlijk dat deze hoger ligt.

Wat betreft seizoensdynamiek en gemiddelde aantallen en biomassa werden er over het algemeen geen duidelijke verschillen geconstateerd tussen de onderzochte akkers. Wel was er een onmiskenbaar verschil in de verticale verdeling van de pot-wormpopulaties tussen de conventioneel beheerde akker en de akkers met geïnte-greerd beheer: in de geïntegreerd beheerde akkers kwamen de populaties meer voor in de oppervlakkige lagen, in de conventioneel beheerde akkers meer gelijkmatig ver-spreid over het profiel. Dit verschil in verticale verdeling hing waarschijnlijk samen met verschillen in grondbewerking en de resulterende verdeling van gewasresten en organ-ische mest. Een mogelijk gevolg van dit verschil in verticale verdeling is, dat de kans op verlies van nutriënten door uitspoeling groter is in een conventioneel, dan in een geïntegreerd beheerde akker.

Gedurende het groeiseizoen werd tevens een positieve relatie geconstateerd tussen de horizontale verdeling van de potwormen en de positie van de gewasplanten. Dit wijst op een associatie van potwormen met wortelexudaten, hetzij rechtstreeks, hetzij via de hier voorkomende micro-organismen.

Een deel van het in dit proefschrift besproken onderzoek was van fundamenteel biologische aard, en betrof het vaststellen van life-history parameters van *Enchytraeus buchholzi*, de meest voorkomende soort op de Lovinkhoeve. Hiervoor werden in het laboratorium experimenten uitgevoerd, waarin ontwikkelingstijden, aantallen cocons en eieren per individu, en de levensduur bij verschillende temperaturen werden bepaald. Om de waarde van deze gegevens voor de onder veldomstandigheden optredende processen te bepalen, werd tevens de populatieontwikkeling onder meer natuurlijke omstandigheden bepaald. Met behulp van een eenvoudig simulatiemodel werden deze gegevens vergeleken met de voorspellingen op basis van de laboratoriumexperimen-ten. Hieruit kwam naar voren, dat enerzijds de populatieontwikkeling onder veldom-standigheden wat betreft aantallen kon achterblijven bij de voorspelde waarden, maar anderzijds de individuele ontwikkeling aanzienlijk sneller kon verlopen dan voorspeld. Het lijkt waarschijnlijk, dat de gevonden discrepantie samenhangt met de fysiologische conditie van de proefdieren, waarbij in ongunstige omstandigheden de levenscyclus kan worden verlengd en in gunstige juist verkort.

Voor het onderzoek naar de effecten van potwormactiviteit op de ontwikkeling van de bodemstructuur werd gebruik gemaakt van gegevens uit de populatiedynamische studie en uit een veldexperiment met kunstmatige bodems met in hoge mate reproduceerbare bodemfysische eigenschappen. In dit proefschrift wordt de methode beschreven om dergelijke kunstmatige bodems, waarin de bodemstructuur als variabele gemanipuleerd kan worden, te vervaardigen. De belangrijkste stappen in het proces zijn:
- homogeniseren van de grond door zeven
- gedeeltelijke sterilisatie van de grond door verwarming, waardoor de aanwezige meercellige dieren gedood worden.
- samenpersen van een vastgestelde hoeveelheid grond tot een bepaald volume.

Manipulatie van de structuur van dergelijke kunstmatige bodems kan gebeuren door variaties in de maaswijdte bij het zeven of in de relatieve hoeveelheid samen te persen grond, door het aanbrengen van kunstmatige macroporiën of hindernissen etc.

Tijdens het populatiedynamisch onderzoek werd bij 21 - 35% van de dieren in de potwormpopulaties minerale deeltjes in het spijsverteringskanaal aangetroffen. Op basis hiervan werd berekend dat het jaarlijkse transport van minerale deeltjes op deze manier 0.001 - 0.01% bedroeg van het bodemvolume in de bovenste 0.4 m van het profiel. Hieruit kan geconcludeerd worden, dat actief graven door potwormen kwantitatief van ondergeschikt belang is.

In het veldexperiment kwam echter een aantoonbare invloed van potwormactiviteit op de bodemstructuur naar voren: in kunstmatige bodems van grond van de Lovinkhoeve, waarin potwormen aanwezig waren, waren de luchtdoorlatendheid, het poriënvolume in de grootteklasse die correspondeert met de dikte van potwormen, en het aandeel van aggregaten in de grootteklasse van potwormexcrementen groter dan in bodems zonder potwormen. Dit effect kan verklaard worden, door aan te nemen dat de graafactiviteit van potwormen vooral optreedt bij vernauwingen in poriën, en dat behalve transport van mineraal materiaal, ook organisch materiaal wordt getransporteerd. Deze hypothese wordt nu getoetst aan de hand van polijstblokken die van de kunstmatige bodems zijn gemaakt.

De algemene conclusies kunnen als volgt worden samengevat:
- De directe bijdrage (via hun metabolisme) van potwormen aan de stromen van energie en nutriënten in agro-oecosystemen ligt in de orde van grootte van 1%, een waarde die vergelijkbaar is met die in meer natuurlijke systemen. Indirect, met name via hun invloed op microbiële activiteit, kan hun bijdrage echter veel groter zijn.
- De ontwikkeling van de bodemstructuur wordt door potwormen op verschillende manieren beïnvloed: door de productie van excrementen en slijm kan de struc-

tuurstabiliteit bevorderd worden, en door hun (selectieve) graafactiviteit hebben zij effect op de beluchting en bewortelbaarheid van de grond.

- Potwormpopulaties worden beïnvloed door het landbouwkundig beheer, met name waar dat effect heeft op de hoeveelheid organische stof in de bodem, en de verdeling daarvan. De verticale verdeling van potwormen over het profiel wordt zodoende beïnvloed door de vorm van grondbewerking die wordt toegepast. Ook het soort gewas wat wordt geteeld zou van belang kunnen zijn voor de ontwikkeling en activiteit van potwormpopulaties.

Een belangrijk aspect van de rol van potwormen in het functioneren van landbouwsystemen is de seizoensdynamiek in aantallen en activiteit. In het in dit proefschrift beschreven onderzoek vielen de maximum populatiegroottes en -activiteit vrijwel samen met de periode van de grootste gewasgroei, wanneer de behoefte van het gewas aan nutriënten het grootst is. Dit houdt in dat een gunstige invloed van potwormen in die tijd vooral zou bestaan in hun invloed op structuurvorming en hun indirecte effecten op de mobilisatie van nutriënten. De in de potwormpopulaties zelf opgeslagen nutriënten komen vooral vrij gedurende de zomer en het begin van de herfst, wanneer de populaties afnemen, evenals de behoefte aan nutriënten van de meeste gewassen. Het mogelijke verlies door uitspoeling wat hiervan, vooral in 'conventioneel' beheerde akkers, het gevolg kan zijn, kan worden tegengegaan door gebruik te maken van een snelgroeiend tussengewas.

In oecologisch verantwoorde landbouwsystemen kan dan ook het beste gebruik worden gemaakt van de activiteit van deze diergroep door het toepassen van ondiepe grondbewerking, organische bemesting, en tussenteelten.

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Wim Didden werd geboren op 4 december 1950 in Waalwijk. In 1970 behaalde hij het diploma Gymnasium-β aan het Dr. Mollercollege te Waalwijk. Daarna studeerde hij biologie en wijsbegeerte aan de Rijksuniversiteit Utrecht, en bewerkte in de doctoraalfase vakken in vegetatiekunde, biologie en samenleving, toegepaste zoölogische oecologie, en natuurbeheer en natuurbehoud. In juni 1977 studeerde hij af als algemeen bioloog.
Tot mei 1979 vervulde hij vervolgens zijn vervangende dienstplicht bij de afdeling Botanie van het Rijksinstituut voor Natuurbeheer in Leersum.
Van 1984 tot 1986 was hij achtereenvolgens werkzaam bij de vakgroepen Dieroecologie en Nematologie van de Landbouwuniversiteit, waar hij onder andere een studie verrichtte naar de invloed van de bodemstructuur op de verspreiding van springstaarten.
Vanaf januari 1986 is hij verbonden aan de vakgroep Bodemkunde en Geologie van de Landbouwuniversiteit; tot april 1989 als promotieassistent, daarna als universitair docent bodembiologie.